1. Ontogeny and development of dimorphism in some Silurian ostracodes

A study on the Mulde marl fauna of Gotland

By

Anders Martinsson

Contents

													Ρ	age
Introduction	. ,										•	÷		2
Material and methods			•			•	2		•	•	•			3
Notes on the composition of the population and	the	sar	npl	es	•	•	•	•	•		•	•	•	5
Ontogeny and growth							•		2				S.	7
Larval characters	• •	•	•			•		•	•		•			10
Dimorphism in preadult instars	• •	•	•			•	•		•		•		8	10
Sex and sex ratios						•	•			•	•	•		13
Taxonomy			•	• •		•	•		•		•	•		17
General notes								.						17
JONES'S originals from the Mulde marl														17
Terminology	• •											•		18
Family Beyrichiidae MATTHEW									•		•	•		18
Subfamily Beyrichiinae MATTHEW			2							2				18
Genus Beyrichia M'Coy		-	\mathbf{x} :			•			•					18
Beyrichia (Mitrobeyrichia) clavata Kol	MOL	DIN			×									18
B. (Beyrichia) dactyloscopica n. sp											•			20
B. (Beyrichia) subornata n. sp														22
Subfamily Treposellinae HENNINGSMOEN .														23
Genus Bolbiprimitia KAY											•	×.		23
Bolbi primitia inaequalis (JONES)														24
Family Primitiopsidae SWARTZ										÷				25
Subfamily Primitiopsinae SWARTZ										4				26
Genus Primitiopsis Jones														26
Primitiopsis planifrons Jones														26
Genus Clavofabella MARTINSSON														27
Clavofabella multidentata MARTINSSON										4				29
C. incurvata MARTINSSON														29
C. reticristata (JONES)														29
Subfamily Leiocyaminae n. subf														29
Genus Leiocyamus n.g.														30
Leiocyamus apicatus n. sp.														30
Genus Amygdalella n.g.														31
Amygdalella subclusa n. sp														31
														5

^{1 - 563272} Bull. of Geol. Vol. XXXVII.

																				Ρ	age
Family <i>Thlipsuridae</i> JONES							•			•	•			•				•			33
Genus Thlipsurella SWARTZ					•	•		•		•	·		•	\sim	•	•	•				33
Thlipsurella discreta (Jone	es)	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		33
Conclusions				4								x.							e		35
References			•	•				•				•	٠								37
Explanations of plates													, I			-					41

ABSTRACT.—The ontogeny of some ostracode species is reconstructed by measuring a large number of specimens in different instars. The existence of dimorphism in preadult instars is demonstrated, and sex ratios are calculated. Some new evidence is given for the determination of the sex of the dimorphs. The new genera *Leiocyamus* and *Amygdalella*, and the new species *Beyrichia* (*Beyrichia*) dactyloscopia, B. (Beyrichia) subornata, Leiocyamus apicatus, and Amygdalella subclusa are described. The subfamily *Leiocyaminae*, including the primitiopsid genera *Leoicyamus* and Amygdalella, is erected. Diagnosis is given for the genus Bolbiprimitia KAY.

INTRODUCTION

One of the fundamental requirements for the description of an animal or plant species is the knowledge of its natural variation. The palaeontologist working on taxonomy has mostly to resort to a very limited material which, in addition, may be badly or incompletely preserved.

The taxonomy of fossil ostracodes is further complicated by the fact that the organs or appendages providing the criteria for recent taxonomic units are not preserved in the fossils. With the experience from recent forms it may be expected that e.g. a smooth fossil ostracode species comprises several species as defined in neozoological taxonomy, owing to the fact that differences in carapace morphology are not discernible on subjective investigation of a limited number of specimens, if they are discernible at all.

Especially in the ostracode suborder *Palaeocopa*, hitherto known only as carapaces without any appendages, a very great part of the species exhibit carapace dimorphism, and are often found in a great number of moult instars.

This has resulted in the opposite taxonomic consequences, viz. that a true species has been described under two or more specific names. A telling example is provided by *Primitiopsis planifrons*, described by JONES in 1887, which has given the impetus to the author's studies on ostracode ontogeny. The name *P. planifrons* was given to the adult specimens with a dolonal pouch, while non-dolonate instars were named *Primitia valida* and *Primitia grandis*, including probably non-dolonate *Clavofabella* specimens. One dolonate specimen, deformed before fossilization, was named *P. planifrons* v. *ventrosa*. Finally the dolonate and non-dolonate forms were orientated in opposite ways, which still further concealed the relationships of the dolonate forms.

The dimorphs often differ more from each other than from related species, and this may also be true for moult instars during different parts of the ontogeny. It is therefore of great importance to get a completer picture of the ontogenetic development of morphological characters, to find out in what instar the dimorphic characters appear, and to establish whether they appear suddenly or gradually, with intermediate forms.

Ostracode ontogeny has been the object of comparatively few investigations, and very few authors treat an extensive material of fossil species, viz. SPJELD-NÆS 1951, KESLING 1952a, and MARTINSSON 1955. Historical surveys and references to earlier work on recent and fossil species are given in these papers and, especially, in a methodological paper by KESLING (1953).

This investigation forms a direct continuation of the author's paper mentioned above. It is intended to elucidate the ontogeny and ontogenetic development of dimorphic characters in the representative species of the Mulde marl fauna from which the material in the quoted investigations by SPJELDNÆS and MARTINSSON was derived. The taxonomy of the species investigated is treated, while the study of the population receives less attention. For more comprehensive references and for terms used in the discussion the reader is referred to the author's previous paper (op. cit).

MATERIAL AND METHODS

The Mulde marl has long been correlated with the Wenlockian by numerous authors (cf. HEDE 1942, p. 19). In the paper quoted HEDE tentatively refers the sediment to the uppermost Wenlockian of Gotland, suggesting a correlation with the *Cyrtograptus lundgreni* zone of the British graptolite sequence. Ever since the study of fossil ostracodes has been carried on in Sweden the Mulde marl has offered material for numerous studies (for references, see MARTINSSON 1955). In one of the most recent of these SPJELDNÆS (1951) proved the possibilities of the marl for the study of ostracode ontogeny, and the results of his investigation were used in KURTÉN's fundamental study on the dynamics of fossil populations (1953).

The classic locality for the Mulde marl ostracodes is the brickyard of Mulde in the parish of Fröjel, where the samples used in this study have been collected (mentioned or labelled as 1948: T, 1948: Q [coll. V. JAANUSSON], 1955: 1, 1955: 2, and 1955: 3 [coll. A. MARTINSSON]). Specimens in a sample from the same locality collected by C. WIMAN (1890: CW) have proved very easy to get perfectly clean, and have been used in the investigation and for some illustrations. The brickyard is now abandoned, and the sections in the marl-pits are old, so that the recovery of definitely undisturbed samples seems to require more extensive digging than was possible during the author's time in the field. Crustaceans of most groups, especially within the "Entomostraca", show great ecological variations. On account of the considerable lapse of time which may be required for the deposition of a sequence of strata variations in the ecological conditions can hardly be excluded, and a very wide and indefinite dispersion of the specimens of different instars might therefore be expected. A recent investigation by WINKLER (1955), also touching this subject, seems

3

to supply evidence in this direction. The results of the measurements, however, clearly prove that in the present samples these fears have little ground in fact. It is rather noteworthy that the two samples of *Primitiopsidae* analysed by the author (MARTINSSON 1955, Fig. 2A, and Fig. 8 in the present paper), brought home by different collectors and on different occasions, show closely similar dimensions and dispersion range; in order to appreciate the reliability of the measurements it may also be noted that these were made with different ocular micrometers and quite independent of each other.

The shell fragments were washed out from the marl in hot water, dried, and sieved into convenient size fractions to make it easier to pick out the ostracodes. This was done by the "wet method", i.e. the ostracodes were spread thinly over the bottom of a low tray ruled out into 1 cm² squares, then picked out with a fine paint brush moistened with concentrated alcohol and assembled by dipping the brush in cups filled with the same liquid. Alcohol has a convenient viscosity, and evaporates readily so that the brush may easily be freed from accidentally adhering fossil fragments; furthermore the ostracodes become cleaner and ready for measurements. This method may permit the same speed as the method worked out by TRIEBEL (1938), but requires much more movements of the hand; this is in any case inevitable if the ostracodes are to be separated into systematic groups.

All carapaces and valves of all species were picked out from the main sample 1955: 1). Where only a part of the individuals of a species were to be measured they were again spread out on the tray, and every second, third, or fourth specimen was picked out.

The carapaces of left valves were individually mounted, and orientated on a thin strip of plasticine on a microscopic slide, and measured with an ocular micrometer. As a binocular microscope was used, it was necessary to keep the micrometer scale vertical in the field of sight, and to rotate the object in order to avoid parallactic errors. As fixed points and distances as possible on the left valve were selected for the measurements, usually the total length or the length of the hingeline, and the height of the carapaces over the adductorial pit or sulcus.

The theoretical exactness obtained with the Reichert scale used with different objectives is for the following species:

Beyrichia clavata, instars 1-4	± 11.3 μ
B. clavata, instars $5-9$	\pm 5.6 μ
B. dactyloscopica	± 11.3 μ
Bolbiprimitia inaequalis	\pm 11.3 μ
Primitiopsis planifrons	\pm 8.4 μ
Clavofabella multidentata	\pm 6.5 μ
C. incurvata	\pm 6.5 μ
<i>C. reticristata</i>	\pm 6.5 μ
Thlipsurella discreta	± 6.5 μ

4

The scores obtained were plotted on "two-dimensional" scatter diagrams as dots or circlets. When the scores for two or more dots coincided they have been displaced systematically within the limits of exactness; when a part of the dispersion pattern of an instar was filled with dots it was left black, without further gradation of the intensity.

Only in two species have specimens from more than one sample been plotted on the same diagram.

The scales in microns have been transcribed graphically from the raw scores in scale divisions, and the size dispersion of the instars has been read from the diagrams.

NOTES ON THE COMPOSITION OF THE POPULATION AND THE SAMPLES

The samples used had a volume of about 1.3 dm³. After the sifting off of particles smaller than 0.125 mm there remains a residue of shell fragments, ostracodes, and small brachiopods, amounting to about 10% of the original volume of the sample (115 cm³ in the sample 1955: 1 on which these rough calculations are based). This residue contains about 12,000 ostracodes, counted as entire carapaces and left valves. Of these the big palaeocope species Beyrichia clavata dominates with about 4500 specimens, the small thlipsurid Thlipsurella discreta is estimated to be represented by about 3000, Primitiopsis planifrons by 1400, and the three Clavofabella species by 600 specimens together. These species have been subject to thorough investigation of the ontogeny. The residue of about 2500 specimens is dominated by some smooth species which may be easily distinguished from each other in the sample and afford material for studies on the ontogeny, but require much revision work even as to the major taxonomy. Of the palaeocopes in this residue Triemilomatella prisca, represented by 135 specimens, is treated and described in a paper to be published by JAANUSSON and MARTINSSON (1956); of the other minor palaeocope components Beyrichia dactyloscopica, B. subornata, and Bolbiprimitia inaequalis are treated here on account of important features in their dimorphism.

The two main samples, 1948: Q and 1955: 1, differ much in the proportions of the carapaces and the separated valves. In 1948: Q the carapaces dominate while they form a comparatively small part of the ostracodes in 1955: 1. This may be of some importance for the comparison of the two samples.

Ostracode marls of this type *in situ* would apparently provide an excellent material for the study of populations and population fluctuations. Here the numbers of specimens in the samples and their distribution on different instars are discussed only so far as they complete the author's previous studies on the *Primitiopsis* population in 1948: Q (1955, p. 4), and provide a part of the empiric material necessary for a further discussion on the subject.

The distribution of the instars of some species in Mulde marl populations

Table 1. Number and distribution in instars of some ostracode species from the Mulde marl fauna. The first sample is taken from SPJELDNÆS 1951, Table 1. The number of specimens and entire carapaces is given absolutely (n) and in

a :	9		8		7		6	,	5		4		3		2	;	1	[2
Species	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	
Beyrichia clavata 1951 : SPJ,																			
valves	17	2	309	32	210	21	146	15	92	9	75	8	70	7	42	4	19	2	980
B. clavata 1951 : SPJ, carapaces	5	6	53	64	10	12	6	7	4	5	I	I	0	0	I	I	2	2	83
B. clavata 1955: 1, specimens.	585	17	658	19	674	19	614	18	321	9	268	8	182	5	104	3	55	2	3461
B. clavata 1955:1, carapaces.	346	57	83	14	63	10	33	5	15	2	15	2	10	2	21	3	24	4	610
Primitiopsis planifrons 1948: Q,																			
specimens	_	_	-	_			19	4	50	II	110	24	119	26	103	22	59	13	460
P. planifrons 1948: Q, carapaces	-	_			_	_	18	4	50	12	104	24	106	25	97	22	57	13	432
P. planifrons 1955: 1, specimens	_	_	_				107	16	168	24	164	24	118	17	76	II	53	8	689
P. planifrons 1955: 1, carapaces	_	L_	_			_	78	20	89	23	83	21	59	15	49	13	33	8	391
Thlipsurella discreta 1955:1,																			
carapaces	—	-	—		—	_	—	_	-	-	33	7	134	28	146	31	159	34	472

per cents (%).

is given in Table 1. As it would lead to unwieldy consequences to number the instars beginning with the youngest—which might have escaped representation or be hidden in brood pouches—the instars are numbered in inverted order. When the material does not allow a definite grouping of the specimens in instars, the numbers of the supposed instars are placed within brackets. The number of specimens is computed from the number of carapaces and left valves. The distribution in per cent of the instars within the different species is transcribed graphically in Figs. 1 and 2.

The large proportion of entire carapaces and old instars—heavy specimens —in sample 1948: Q may be due to concentration by sorting during the deposition (MARTINSSON 1955, p. 4), but may also illustrate the original deposition of ostracodes. The new sample gives a picture more in accordance with SPJELD-NÆS's results in *Beyrichia clavata*, but the youngest instars are under-represented in all samples. This is very probably due to the brittle structure of the youngest specimens; in the youngest instar of *Beyrichia clavata* the proportion of the unparted carapaces is greater by far than in the older instars. Whether the other differences in the distribution of the specimens in instars, and in the proportions of carapaces *versus* separated valves are normal variations in the composition of fossil animal communities or not, cannot possibly be established from the existing published material, fossil or recent. A necessary requirement for further discussion is the knowledge whether the fossils represent dead bodies or exuviae (MARTINSSON 1955, p. 12–17). Provided that the samples are representative, a curve with the maximum in an intermediate instar must be

6



Fig. 1. Distribution in instars of two samples of *Beyrichia clavata*, from SPJELDNÆS 1951 (1951:SPJ) and the present investigation. In both investigations, instar 9 has been found both free and in brood-pouches.

Fig. 2. Distribution in instars of two samples of *Primitiopsis planifrons*, from MARTINSSON 1955 (1948:Q) and the present investigation. As pointed out in the text, sample 1948:Q was composed mainly of entire carapaces, while the separated valves dominate in sample 1955:1.

necrocoenotic, while a curve descending from a maximum in the youngest instar may be *pseudocoenotic* or necrocoenotic, or most likely, a combination of both. The author has earlier (l.c.) called attention to this and other obstacles to the study of the dynamics of fossil populations, or rather to the raising of this study beyond a merely descriptive stage.

Those of the studied species which occur in great numbers in the samples have very distinct instars, practically without overlap in the dispersion patterns. The minor components seem to be less stable in this respect and also somewhat more variable in ornamentation; the older instars dominate. This is true for *Beyrichia dactyloscopica* and *Bolbiprimitia inaequalis*, apart from the fact that the diagrams presented here are composed from two samples. *Triemilomatella prisca* JAANUSSON and MARTINSSON (1956), occurring with 135 specimens in the sample 1955: 1, has been found only as adult males and females, and there are in the material no specimens which could be younger instars. It is hardly possible to establish whether these minor components are immigrants or whether the absence of younger instars is caused by some other factor.

Thlipsurella discreta, finally, is measured only as carapaces which give a curve with minima in the youngest and oldest instars. The single valves are so often deformed or damaged that their inclusion is less desirable.

ONTOGENY AND GROWTH

Several investigations have proved that ostracodes double their volume in each instar (cp. KESLING 1952b). Provided that the growth is isometric, this would correspond to a linear growth factor of about 1.26, and it is this linear

factor which has been calculated in most investigations. The growth factors of some Mulde marl species are given in Table 2. The calculations are made in scale divisions, and the medians are constructed graphically.

The results obtained here confirm what has been stated in earlier investigations. The larval instars increase their size approximately in accordance with the factor 1.26. It is evident, however, that the increase of size immediately preceding the mature instar is smaller, as was stated already in SPJELDNÆS's investigation of *Beyrichia clavata* (op. cit.). In the males the length growth factor obtained between the two last instars is 1.18–1.21; the corresponding height growth factor is in one case as low as 1.12, in four cases 1.15. In the females of *Beyrichia clavata* the growth factor is lower still, for the length 1.18–1.19, for the height 1.03–1.04. This feebler linear growth does not correspond to an equally smaller volume growth, as the voluminous brood pouches are developed in this instar (cf. SPJELDNÆS 1951, p. 748). The dolonal pouches in *Primitiopsis planifrons* considerably increase the growth factor, but the development of the broad but thin dolon does not much increase the volume of the animal itself, the pouch being extradomiciliar in origin.

From the table and the diagrams it is evident that the number of free instars is 9 in *Beyrichia clavata* and 6 in *Primitiopsis planifrons*. The existence of still smaller free instars is not plausible. It was suggested, but not statistically ascertained, by MARTINSSON 1955 that the genus *Clavofabella* has 5 free instars. In the present *Clavofabella* material no specimens have been found which correspond to a smaller instar. The material of *Thlipsurella discreta* has shown only 4 instars. The diagram (Fig. 10) contains a couple of specimens which may fall within the variation limits of a smaller instar, but they are not numerous enough to suggest that such an instar has existed.

The development of surface ornamentation during the ontogeny takes place gradually. The type of ornamentation represented in the species investigated may roughly be divided into three groups: Beyrichia clavata and Triemilomatella prisca JAANUSSON and MARTINSSON (1956) are granulose, almost without other ornamental details on the lobes. The granulosity is generally somewhat more pronounced in the younger instars of Beyrichia clavata, and rather insignificant on the more protruding parts of the lobes in the older specimens (cf. SPJELDNÆS 1951, Pl. 103). In the second group, comprising Beyrichia dactyloscopica and B. subornata, a similar granulation exists, but these species have granules or warts also of a second degree, in B. dactyloscopica mostly extended into spines. These spines are more pronounced in the smaller instars (cf. Pl. I and II, Figs. 2-9). The third type of ornamentation, the reticulation, is present in the primitiopsids and in Bolbiprimitia inaequalis, and also in this case the development of ornamentation takes place so gradually that, e.g., the primitiopsid species may be recognized by ornamental characters through the larger part of their ontogeny.

The marginal structures, too, develop gradually, and this is true also of the

Table 2. Linear growth factors of the species measured in different investigations of the Mulde marl ostracodes. Values affected by the presence of the dolonal pouch are given in brackets. Males and females have not been separated in 1951: SPJ.

. 1	-					-	-		_					
· · ·		0+	в		61.1	1.04		(1.36)	1.17	(1.21)	1.15		_	21
- 6 -		5-]	M	Ļ	1.18	1.03		(1.36)	1.17	(22.1)	1.15	1	ц ц	i i
		۴Ö	B		1.21	1.15		1.19	I.20	1.18	1.15	2-	I	24 16
		5-	M	I.14	61.1	I.I2		1.19	1.19	1.18	1.15		N	ΗH
1		5	в	1	1.24	1.24		1.23	1.29	1.25	1.27		c	27
	ledian	3	Μ	1.27	1.26	I.24		I .24	1.32	1.24	1.25	4	5	11
	m = m	-3	B	1	1.24	1.24		1.26	I.24	1.25	1.25	3	I	29 26
	mean,	4	М	1.27	1.25	1.27		1.26	I.20	1.28	I.21		Z	ĨĨ
	s. M =	4-	В	I	1.27	1.31		1.26	1.25	1.27	1.27		c	26 31
	factors	2 [.]	Μ	1.28	1.24	1.26		1.24	1.24	1.25	1.33	-3	ц	i i
	rowth	-5	ш	1	1.23	1.24		1.30	1.29	1.26	1.30	4	I	27 34
	and g	9	Μ	1.30	72.1	1.29		1.30	1.26	1.26	1.29		N	ii
	Instars	-9	В	I	1.24	1.29		1	I		Ι			;;;
		7	Μ	1.27	1.23	1.27		1	I		Ι			::
		-7	В	I	1.20	1.25		Ι	I	I	1			
		×	Μ	1.29	1.21	I.28		Ι	I	I	Ι			
		8	В	I	I.22	I.22		I	Ι	I	Ι			::
		6	Μ	1.92	1.21	61.I		Ι	I	i	Ι			tr t
		Species		Beyrichia clavata 1951: SPJ Total length	Beyrichia clavata 1955 : 1 Hinge length	height	Primittopsis planifrons 1948: Q	Total length	height	Primitiopsis planifrons 1955:1 Total length	height			Thlipsurella discreta 1955:1, leng heig

ONTOGENY IN SOME SILURIAN OSTRACODES

9

velar structure of the males of the species studied. In contrast to this stands the sudden appearance of the female dimorphic characters in the last instar. There are some features, too, which are present in the younger instars, but disappear during the ontogeny. These phenomena will be treated in the two following chapters.

Dimensions and some details in the ontogeny of the respective species will be denoted in the taxonomic chapter.

Theoretically a large material of a fossil species with distinct ornamentation may fall into recognizable genetic groups, but this attractive supposition has no support in the investigation of the present material.

LARVAL CHARACTERS

Very few morphological features in the carapaces disappear during the ontogeny. In the *Beyrichiinae* the lobation is developed gradually from the youngest instar where only the adductorial sulcus is present. The *Primitio psinae* also develop from an instar with a sulcus-like impression in the adductorial region; this disappears in the subsequent instars, and in the adult specimens the only signs of lobation are the adductorial pit and the preadductorial node.

In the youngest instars of *Beyrichia clavata* the anterior and posterior corners of the right valve are drawn out into thin filiform rods, the *larval processes* (Fig. 3). They are never present in the left valves. In some instances they are straight and like bowsprits, in others they are curved or bent. In the youngest instar specimens have been observed in which the perforated marginal frill extends onto the anterior larval process and is fused with it.

The larval processes are always present in well preserved specimens of the youngest free instar (9). They are also present in the instars 8 and 7, but have with few exceptions disappeared in instar 6.

SPJELDNÆS (1951, p. 755) mentions a "rostrum" in the younger instars of *Beyrichia clavata*. As he gives the species the reverse orientation, this must be a posterior structure, possibly the posterior larval process.

The variations in the shape of the larval processes seem to be due to the fact that they were bent or curved before the carapace had hardened. They could possibly be associated with the preservation of the larvae in the brood pouches.

DIMORPHISM IN PREADULT INSTARS

Dimorphism in recent ostracodes is known only from the last instar. A very comprehensive survey of dimorphism in the palaeocopes is being published by JAANUSSON (1956) to which the reader is referred for historical references. SPJELDNÆS (1951) first pointed to the existence of specimens with brood pouches in *Beyrichia* cf. *jonesi* from the Upper Visby marl, corresponding in size to the penultimate instar. He considered it possible that they exhibit an

10



Fig. 3. Shape and ontogenetic disappearance of the larval processes of *Beyrichia clavata*. A and B: instar 9, right valves with marginal structure and larval processes. $60 \times .$ C-F: instar 9. G and H: instar 8. I: instar 7. In instar 6 the processes are usually traceable only in the more or less protruding corners. C-I: $30 \times .$

Originals: A and F: No. G 137. B: No. G 138. C: No. G 139. D: No. G 140. E: No. G 141. G: No. G 142. H: No. G 143. I: No. G 144.

early development of sexual dimorphism, but found it more probable that they were adults of another population living in a different and perhaps warmer environment. MARTINSSON (1955, p. 12) found that one of the three *Clavofabella* species in the Mulde marl, *C. multidentata*, develops dolonate specimens also in the penultimate instar. There is no reason to suppose an immigration from another population, and the specimens concerned have a very concentrated dispersion pattern. JAANUSSON (op. cit., Figs. 7–8) will establish similar conditions in two Ordovician species, *Euprimites suecicus* (THORSLUND) and *Oepikella tvaerensis* THORSLUND, which seem to exhibit dimorphism in two subadult instars.

JAANUSSON (op. cit.) refers to four different types of dimorphism in palaeocope ostracodes. Two of these types are represented here. The *cruminal dimorphism* occurring in the *Beyrichiidae* is characterized by pouch-like extensions of the domiciliar wall, the *cruminae*. The *velar dimorphism* exhibited here in the *Primitiopsidae* is characterized by differences in the development of the velum, typically with the extension of a part of it in one of the sexes as a broader *dolon*.

Preadult dimorphism, then, is reported from species with cruminal as well as velar dimorphism. The cruminate species in the Mulde marl — among them the numerous *Beyrichia clavata* — are dimorphic only in the last instar, with exeption of *Beyrichia dactyloscopica*. Two females of this species, corresponding in size to the penultimate instar, have been found. Unfortunately the material does not permit it to be established with certainty whether this is a case of preadult dimorphism or not (cf. p. 22).

The *Primitiopsidae* have been thoroughly examined in this respect. It has been confirmed that dimorphism is present only in the last instar in all primi-



Fig. 4. Ontogeny of *Beyrichia dactyloscopica*, compiled from two samples. Females are set down as circlets, ordinary tecnomorphs as dots, and very spinose tecnomorphs as spiked dots. Right valves are included in the diagram without special designation. Height over sulcus along the ordinate, hinge length along the abscissa. Owing to the indistinct dispersion of the specimens the instar numbers are placed within brackets.

tiopsid species except *Clavofabella multidentata*, where it occurs regularly in the two last instars. In the sample 1955: I the subadult dolonate specimens were incomparably more numerous (35 subadult against 27 adult) than in the sample 1948: T (5 against 22).

The size dispersion of the Primitiopsidae is illustrated in Fig. 5, and in Fig. 9 the dispersion pattern is given for the *Clavofabella* species in the two samples discussed. Owing to the fact that in 1948: Q the subadult dolonate specimens of *C. multidentata* were so few, and that their distribution area seemed to be overlapped by that of *C. incurvata*, the sample was re-examined, and another 2 specimens (incl. a right valve) of subadult *C. multidentata* were detected. There seems thus to be a real difference in the proportions of subadult and adult dolonate specimens between the two samples.

Here the question arises whether the subadult dolonate specimens had terminated the ontogeny of the respective species or were destined to moult once more in order to reach adult size. The number of subadult specimens compared with that of the adult ones does not suggest this to have taken place regularly, and the ratio non-dolonate : dolonate specimens in instar 2 (Table 3 and p. 16) strongly suggests that only the non-dolonate specimens have continued their development to adult size. In any case the mere existence of dimorphic characters in this subadult instar suggests that the subadult dolonate specimens were fertile. As in *Beyrichia dactyloscopica* they are essentially like the adult specimens.



Fig. 5. Size dispersion of females of different primitiopsid species. The diagram shows that all species except *Clavofabella multidentata* have adult females only. For the size dispersion in different samples, cf. Fig. 9. The diagram represents half of the specimens in sample 1955:1. Height over sulcus along the ordinate, total length along the abscissa.

SEX AND SEX RATIOS

It has generally been supposed that the dimorphism in palaeocope ostracodes is associated with reproduction. Another theory has also been proposed, viz. that an ecological dimorphism may exist, which might, nevertheless, be sexual (TRIEBEL 1941, p. 362), as the sexes of a species may have inhabited different biotopes (see also JAANUSSON 1956).

It has also been generally supposed that the dimorphs differing from the larval instars in shape, often by the development of cruminal or dolonal pouches, are the females. The pouches have generally been referred to as places for brood care. Here also TRIEBEL (op. cit., pp. 362 and 365) has drawn attention to two alternative theories, viz. that the dolonal pouches may have been associated with glands and served as secretion containers, and that the cruminal pouches may have served as sperm containers, as the spermatozoa are extremely large and morphologically complicated in the ostracodes. In this case the cruminate specimens were to be regarded as males.

It is necessary to treat the velar and the cruminal type of dimorphism separately (cf. HESSLAND 1949, pp. 123–126).

HESSLAND (op. cit.), while treating ostracode dimorphism and brood care, made the important observation that a thin section of a cruminate Beyrichia kloedeni contained two specimens of small instars, one of them in a brood pouch. SPJELDNAES (1951) examined sections of about 60 specimens of Beyrichia clavata, and found larvae in nearly half of them. He referred them to three different instars, the oldest of which is identical with instar 9 in the numbering used in this paper. The present author has examined 34 sections across the cruminae of this species. No specimen was found, however, which could with certainty be referred to the two youngest instars suggested in SPJELDNÆS's investigation, but the possibility cannot be excluded that one of the six larvae observed in the pouches may belong to a perhaps existing instar 10. All specimens were observed in cruminae filled by calcite crystals, not affected by accumulated marly particles. Larvae have been found also in other lobes (HESSLAND, op. cit., Pl. XIV, Fig. 9), which might give rise to the suspicion that they could penetrate into the carapaces from outside before any marl filling had accumulated. In this case they could also have been preserved in non-cruminate carapaces, but in 53 sections of such specimens they were entirely absent. Of foreign organisms only a chitinozoan was observed, during the grinding of one of the sections, in a marl-filled cruminate carapace.

The present investigation thus entirely confirms the earlier investigations quoted, and it may be regarded as definitely established that the cruminal specimens are the females. The earlier evidence that moulting has taken place in the cruminae has found little confirmation in the comparatively few specimens found in the cruminal space.

In one of the encountered species which exhibit velar dimorphism an extradomiciliar dolonal pouch is formed, viz. in *Primitiopsis planifrons*. Through pouches of this sort 58 sections have been prepared, but no larvae have been found. As the *Primitiopsis* carapace is very thick, they would obviously have been fossilized, if they were present in the dead animal.

We have thus no evidence that the *Primitiopsis* pouch has been used for brood care. Within the *Primitiopsidae* we find forms with open dolonal flanges, as in *Clavofabella*, and it is doubtful whether it is possible that the subdolonal space was adopted for brood care first after a pouch had been formed; this aspect seems to be too teleological. The author has earlier (1955, p. 11) pointed to the possibility of the brood being attached by adherence in secretion, or possibly by active clinging. This may be true for eggs or hatched larvae; JAANUSSON (1956), however, concludes that the dolon definitely has nothing to do with brood care, while, as far as we know, egg care cannot be excluded. The conclusions from the author's *Primitiopsis* investigation seem to corroborate this statement.

There exists, however, another strong indication for the dolonate specimens being females. Of the three *Clavofabella* species two exhibit normal dimorphism with dolonate and non-dolonate specimens. In the third species, *C. reticristata*,

14

only dolonate specimens are found in the last instar. There are, indeed, "nondolonate" specimens present in the material: three specimens in the samples 1948: T and 1951: I together. In all these specimens, however, the dolon can be traced as a faint ridge or bend on the hindmost part of the valve (Pl. IV, Fig. 33, cf. MARTINSSON 1955, Pl. II, Fig. 22 v), and they should most certainly be regarded as dolonate. As stated below the species seems to be parthenogenetic, as there are indications that ostracode males do not become mature in the penultimate instar. It is entirely improbable, however, that the males could have one instar more than the females. In any case, therefore, the dolonate specimens must be regarded as females.

Even if it is possible to determine the sex of the dimorphs, the terms "male" and "female" cannot immediately be used in practical work, where often only a limited material is available. The female can be recognized, raising only the question whether it is adult or subadult. But specimens not exhibiting major dimorphic characters may be either larvae or adult males. JAANUSSON (1956) therefore proposes that the specimens regarded as larvae and males with the above arguments be termed *tecnomorphs*, and the females, differing in appearance, *heteromorphs*.

Even the *histial* type of dimorphism is represented in the Mulde marl fauna, viz. in the hollinid *Triemilomatella prisca*. JAANUSSON and MARTINSSON are publishing their respective studies on this species in a special paper (1956). By analogy it could possibly be established that the heteromorphs are females also in this type. As in the case of velar dimorphism this is the conventional view.

Thlipsurella discreta (Fig. 10) does not exhibit special dimorphic characters. The specimens in the last instar may possibly be divided into two size groups, but the dispersion is not distinct enough to decide whether this is due to dimorphism or not. It will be further touched upon below.

In the author's study on the *Primitiopsidae* (1955, p. 11) the sex ratio of *Primitiopsis planifrons* was computed; the sample 1948: Q surprisingly proved to contain 43 presumptive males as against only 16 females. The sex ratios of the species treated by the author are given in Table 3.

The sex ratio for the examined species of *Beyrichia*, *Primitiopsis*, and *Triemilomatella* seems to be approximately 50:50. The ratios computed from the entire carapaces are more in accordance with this ideal ratio than those obtained from the total amount of specimens; in *Triemilomatella* the discrepancy between the two ways of calculation is considerable. As mentioned above the *Primitiopsis planifrons* sample 1948: Q is supposed to be unrepresentative, and the ratios obtained from it are placed within brackets.

In accordance with what has been established above the ratios in the genus Clavofabella are of special interest. Although the discussion is necessarily based solely on a single sample, this may give some information about the subadult dimorphism in C. multidentata and the absence of adult males in C. reticristata.

Service and served.	Nur	nber	Sex ratio in
Species and sample	55	ŶΫ	per cents
A. Computed from the total number of speci- mens (carapaces + left valves):			
Beyrichia clavata 1955:1	28	27	51:49
Primitiopsis planifrons 1948: Q	43	16	(73:27)
P. planifrons 1955:1	20	33	39:62
Clavofabella multidentata 1955:1	22	27	45:55
C. multidentata, instar 2, 1955:1	106	35	75:25
C. incurvata 1955: 1	32	73	30:70
C. reticristata 1948 : T	?0	27	0:100
C. reticristata 1955 : 1	?o	53	0:100
Triemilomatella prisca 1890:CW	37	55	40:60
T. prisca 1955: 1	32	103	24:76
B. Computed from the number of carapaces:			
Beyrichia clavata 1955:1	12	12	50:50
Primitiopsis planifrons 1948: Q	43	14	(75:25)
P. planifrons 1955:1	18	15	55:45
Clavofabella incurvata 1955:1	8	19	30:70
Triemilomatella prisca 1890 : CW	28	26	52:48
T. prisca 1955:1	4	4	50 : 50

Table 3. Sex ratios of some ostracodes from the Mulde marl fauna.

The sex ratio of adult *C. multidentata* in the present sample is 45:55, and the adult males and females of the species are thus represented in approximately the same proportions. The ratio non-dolonate: dolonate specimens in instar 2 (Table 3, italics) is 75:25. The non-dolonate specimens in this instar may contain three components, viz. (1) exuviae of the adult males, (2) exuviae of the adult females, and (3) subadult males, corresponding to the subadult females in the same instar. If in this case 35 specimens (cf. Table 3) are supposed to be preadult males, terminating their ontogeny in this instar, the remainder, 71 specimens, is numerous enough to contain the exuviae of the 49 adult specimens and, in addition, 22 dead specimens; with regard to the conditions in other species this seems to be a normal death rate for instar 2.

In *Clavofabella reticristata*, too, the penultimate instar has been measured —the *Clavofabella* species can be distinguished four instars backwards—and proved to contain 58 specimens as against the 53 adult ones. If the sample is representative the species must be regarded as parthenogenetic; an alternative supposition, viz. that even the males develop dolonal flanges, is quite improbable.

A statistical confirmation would make these suggestions conclusive; this requires, however, the separation, determination, and measuring of several samples of the same size as the sample treated in this investigation.

TAXONOMY

General notes

In this chapter three families will be treated. Two of them, *Beyrichiidae* and *Primitiopsidae*, belong to the suborder *Palaeocopa* (HENNINGSMOEN 1953). The third family, *Thlipsuridae*, was tentatively referred by HENNINGSMOEN (op. cit., pp. 260–261) to the suborder *Platycopa*, in accordance with TRIEBEL'S (1950, p. 116) attribution of the apparently related family *Healdiidae*. The palaeocope family *Hollinidae*, represented by two species in the Mulde marl, is treated separately by JAANUSSON and MARTINSSON (1956).

Very little is known about the stratigraphical and geographical distribution of the Mulde marl ostracodes. On the other hand we are extremely well acquainted with the variation of the different species within the Mulde marl itself. The only fauna where a number of these species seem to be identified with certainty, is the Scanian Colonus shale fauna described by HEDE (1919). Closely related, mostly well distinguished species are reported from the Wenlockian of England (cf. e.g. JONES 1865 and later) and from the Ludlovian of Norway (HENNINGSMOEN 1954). In the literature on the faunas of erratic boulders in northern Europe, references to ostracode species found also in the Mulde marl frequently occur, in many cases certainly due to insufficient determination.

As far as possible the type specimens designated in this chapter are chosen among the adult females. Characters given in the familiar, generic, and specific diagnoses are not repeated under the heading "Description" of the respective species.

JONES's originals from the Mulde marl

In his papers of 1887 and 1888, JONES described a number of ostracodes from the Mulde marl. In connection with the present author's study of the primitiopsids (1955), inquiry as to the originals was made at the British Museum (Nat. Hist.) and at the Swedish State Museum of Natural History, but both institutions reported that the specimens were not to be found in their collections, and neotypes were consequently designated for *Primitiopsis planifrons* and *Clavofabella reticristata*. On examining the ostracodes in the Swedish State Museum the present author later came across seven small slide-like containers of cedar wood, containing ostracodes collected by G. LINDSTRÖM in Gotland in 1887. From some annotations and the composition of the samples it can be definitely established that they contain JONES's originals of 1888, most of which can be identified with full certainty. The ostracodes were attached to the bottom of the containers with a water-soluble glue, and many of the valves were broken. As the author expects to treat the entire collection more thoroughly later, it should only be noted here, that the originals of *Primitiopsis planifrons* in JONES

2 - 563272 Bull. of Geol. Vol. XXXVII.

1888 are missing, while those of *P. planifrons* var. ventrosa and Clavofabella reticristata could be identified (Pl. V, Figs. 52 and 53), and consequently a lectotype of *C. reticristata* can be designated here, replacing the neotype in MARTINSSON 1955 which has not yet attained validity. The originals of *Bolbiprimita inaequalis* have also been identified (Pl. V, Figs. 50 and 51), and a lectotype of *Thlipsurella discreta* is chosen from the material of this species (Pl. V, Fig. 49).

Terminology

The terminology in this paper follows that of the papers by KESLING (1951) HENNINGSMOEN (1954, for *Beyrichia*), MARTINSSON (1955), and JAANUSSON (1956). The dimorphs are designated as males and females with the arguments mentioned above. The term *verrucose* is used for carapaces with wart-like tubercles (in *Beyrichia*).

Family Beyrichiidae MATTHEW 1886

Subfamily Beyrichiinae MATTHEW 1886

Genus Beyrichia M'Coy 1846

REMARKS.—This genus was split by HENNINGSMOEN (1954) into six subgenera. Two of them, *Beyrichia* and *Mitrobeyrichia*, are represented here. The specific diagnoses below are based on the subgeneric diagnoses given by HENNINGSMOEN (op. cit.).

Beyrichia (Mitrobeyrichia) clavata KOLMODIN 1869

Pl. I Fig. 1.

- 1869 Beyrichia clavata n. sp.—KOLMODIN, p. 18; Fig. 10.
- 1887 Beyrichia clavata KOLMODIN—JONES, p. 2.
- 1888 Beyrichia Jonesii var. clavata KOLMODIN-KIESOW, p. 15; Pl. II, Fig. 12.
- 1888 Beyrichia clavata Kolmodin—Lindström, p. 4.
- 1888 Beyrichia clavata KOLMODIN-JONES, p. 399; Pl. XXI, Figs. 6-9.
- 1901 Beyrichia Jonesii BOLL—CHAPMAN, pp. 151, 158.
- 1908 Beyrichia clavata KOLMODIN—ULRICH and BASSLER, p. 293; Fig. 5; Pl. XXXVII, Fig. 16.
- 1913 Beyrichia Jonesii Boll var. clavata Kolmodin-Bonnema, p. 73, Fig. 7.
- 1917 Beyrichia Jonesii BOLL-HEDE, pp. 24, 29.
- 1921 Beyrichia Jonesi BOLL-HEDE, p. 49.
- 1927 Beyrichia Jonesi BOLL-HEDE 1927a, pp. 38, 53.
- 1927 Beyrichia Jonesi BOLL-HEDE 1927b, pp. 21, 55.
- 1934 Beyrichia clavata KOLMODIN-BASSLER and KELLETT, pp. 67, 189.
- 1936 Beyrichia clavata Kolmodin-Swartz, Pl. 78, Fig. 8g, Pl. 84, Fig. 3d.
- 1951 Beyrichia jonesi BOLL—SPJELDNÆS, pp. 745-755, Pls. 103-104.
- 1955 Beyrichia (Mitrobeyrichia) jonesii BOLL—HENNINGSMOEN, Text-fig. 1.

partim 1919 Beyrichia Jonesi BOLL-HEDE, p. 132, ? A. 5, Fig. 8.

partim 1954 Beyrichia jonesii BOLL-HENNINGSMOEN, p. 46.

LECTOTYPE (designated here). — The male carapace pictured by KOLMODIN 1869, Fig. 10 (Pl. I, Fig. 1 in this paper), coll. N. P. ANGELIN (Mus. Pal. Inst. Uppsala, No. G 145).

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian.

TYPE LOCALITY.—Djupvik, parish of Eksta, Gotland.

DIAGNOSIS.—Original diagnosis given in Swedish by KOLMODIN 1869, p. 18. New diagnosis, based on the diagnosis of *Mitrobeyrichia* (HENNINGSMOEN 1954): Posterior lobe broadly triangular; the base of the isosceles triangle formed is limited by the sulcus; posterior horn pointed and protruding considerably over the hingeline. Zygal ridge faint, rounded. Crumina subglobular, constricted proximally. Surface finely granulose; granulosity in older specimens, and especially on the lobes, often effaced.

DESCRIPTION.—The carapace anatomy and the morphology of the different instars were thoroughly described and illustrated by SPJELDNÆS 1951; the species should, however, be given the reverse orientation, and the terms carina and velum should be replaced by *velum* and *marginal structure*, respectively (cf. HENNINGSMOEN 1953, p. 238). Some notes on the larval processes are given on p. 10 of this paper. The following table of size dispersion should be added (dimensions in microns),

Instar	Hinge length	Height over sulcus
цő	1800-2100	1290–1460
тÇ	1840–2060	1120–1360
2	1470-1730	1140–1340
3	1200-1460	860-1100
4	930-1160	670- 880
5	730- 930	510- 700
6	600- 730	410- 590
7	480- 600	310- 530
8	390- 500	240- 380
9	320- 410	200- 300

REMARKS.—KIESOW (1888, p. 15) included the species in B. jonesi described by BOLL (1856) in a letter to BEYRICH. BOLL depicts (op. cit., p. 322) two Beyrichia specimens, neither of them identical with B. clavata. This assertion is supported especially by the fact that KIESOW (op. cit., Pl. II) redrew BOLL's originals of B. jonesi side by side with specimens of B. clavata from the Mulde marl. The carapace structure of B. jonesi, distinctly and sparsely vertucose, is never found in B. clavata though a very faint tubercular structure may be observed under the posterior horn of specimens treated with ammonium chloride. In B. clavata the posterior horn always protrudes considerably over the hingeline; in one of the specimens of B. jonesi it does not even reach the level of the hingeline. In the other specimen, where the horn protrudes over the hingeline, the posterior lobe is provided with a ridge along the sulcus (BOLL, op. cit., Fig. 2). It is questionable whether the two specimens belong to the same species; neither of them belongs to *B. clavata* KOLMODIN.

KIESOW (l.c.) realized the sexual dimorphism of the species, while JONES (1887, 1888) speaks about "hypertrophied lobes" (= cruminae) in some specimens.

Beyrichia (Beyrichia) dactyloscopica n. sp.

Pl. I-II, Figs. 2-9.

DERIVATION OF NAME.—From Greek δάκτυλος, finger, and σκοπεῖν, search for (cf. dactyloscopy), alluding to the finger-print pattern on the inner side of the cruminae.

HOLOTYPE.—The adult female specimen in Pl. I Fig. 2 (Mus. Pal. Inst. Uppsala, No. G 146).

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian.

TYPE LOCALITY.—Brickyards of Mulde, parish of Fröjel, Gotland.

DIAGNOSIS.—Spinose; dimensions of the spines greatly varying. Anterior and both posterior horns protrude over the hingeline, the inner and outer horns of the posterior lobe strongly developed. A marked fissus present. Cruminae regularly verrucose, with the inner ventral part of the wall ornamented with a finger-print pattern.

DESCRIPTION.—Surface finely granulose. In both sexes exists a ventral, distal row of spines, subparallel to the velar structure. The anterior lobe has a single row of spines. Preadductorial node with some tubercles. The postadductorial part has a field of spines, some of them forming an indistinct row even on the outer posterior horn. Velum of the male with a distal row of tubercles or spines, mostly duplicated anteroventrally. Velum of the female interrupted by the brood pouches. The females occurring in instar 2 essentially like the adults. The larvae often strongly spinose. Right valve overlapping; the hingement consists of a simple groove in the right valve, corresponding to a ridge on the left valve. *Dimensions* of adult males: $2010-2490 \mu$, height $1450-1600 \mu$. Females in instar 2: length 1710μ , height $1080-1160 \mu$. Smallest specimen observed, probably belonging to instar 8: length 480μ , height 310μ . The ontogeny is illustrated in the diagram Fig. 4.

REMARKS.—This species is obviously recorded from the Mulde marl as *Beyrichia spinigera* in HEDE's faunal lists (1921, 1927a, 1927b); it has never been figured. It is not identical with *B. spinigera* described by BOLL 1862 (p. 133; Pl. 1, Fig. 7). In *B. spinigera*—as drawn by BOLL—the preadductorial node is entirely free from the anterior lobe, there are no posterior horns protruding over the hingeline, no fissus, and no arrangement in rows of the



tubercles and spines. *B. dactyloscopica* forms a very insignificant part of the present samples and shows great variations in spinosity. The strongly spinose specimens dominate the youngest instars; in the oldest they are absent. The material comprises about 70 specimens from different samples and collections from the Mulde marl which are estimated to represent at least 75,000 ostracode specimens (the smallest instars, however, are only picked out from the two samples in Fig. 4).

Owing to the fact that the species forms so insignificant a part of the population and that it shows such great variations in spinosity, there may still be some doubt as to its homogeneity. The encountered subadult females fall near the expected lower variation limit of instar 2. In the present material, however, it is impossible to distinguish a group of specimens as being the corresponding tecnomorphs (cf. Pl. II, Figs. 7, 6, and 8). The required number of adult specimens seems to be almost inobtainable.

Beyrichia (Beyrichia) subornata n. sp.

Pl. II, Figs. 10-12.

DERIVATION OF NAME.—Latin *subornatus*, "not fully ornamented", alluding to the faint ornamentation of the carapace sides.

HOLOTYPE.—The adult female specimen in Pl. II, Fig. 10 (Mus. Pal. Inst. Uppsala, No. G 154).

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian.

TYPE LOCALITY.—Brickyards of Mulde, parish of Fröjel, Gotland.

DIAGNOSIS.—Tumid species with high zygal region, very faintly verrucose, the velum provided with a number of small tubercles anteroventrally, usually 6–8. Anterior and inner posterior horn protrude over the hingeline, the outer posterior horn usually does not reach over the level of the hingeline. Fissus present. Cruminae with the inner ventral part of the wall ornamented with a finger-print pattern.

DESCRIPTION.—The faint verrucosity, almost unobservable without treatment with ammonium chloride, gives a very suggestive "goose-pimpled" appearance to the carapace sides. The pimples may be arranged in three indistinct and alternating rows on the lateroventral side of the valves and in an irregular field over the fissus. In the females they may be observed on the cruminae. As in *B. dactyloscopica* there is an ornamentation of minor degree, a granulation, but generally not as distinct as in the former species. Size of adult female (only one specimen completely preserved): length 1550 μ , height 950 μ . Adult males: length 1300–1550 μ , height 800–950 μ .

REMARKS.—This species occurs still more rarely in the population than *B. dactyloscopica*, and only 14 specimens have been found in the author's collections, including one complete female carapace and one damaged female valve. The specimens belong chiefly to the two last instars.



Fig. 7. Ontogeny of *Bolbiprimitia inaequalis*, compiled from three samples. Females are set down as circlets, tecnomorphs as dots. Right valves are included without special designation. Height over sulcus along the ordinate, total length along the abscissa.

The species differs from the closely related B. dactyloscopica by its very tumid appearance, its high zygal region, and by the absence of real spines. The adult specimens of B. subornata correspond in size roughly to instar 3 of B. dactyloscopica.

Subfamily Treposellinae HENNINGSMOEN 1954

Genus Bolbiprimitia KAY 1940

TYPE SPECIES.—B. fissurella (ULRICH and BASSLER), by original designation (KAY 1940, p. 234).

DIAGNOSIS.—One narrow, distinct sulcus, in the lower part slightly curved forwards, cutting nearly two thirds of the carapace height. Known species reticulated; the sides without further ornamentation. Velum developed round the whole of the non-dorsal part of the lateral outline. Cruminae medioventral, coherent with the postadductorial part of the carapace.

SPECIES:—Bolbiprimitia inaequalis (JONES) and B. fissurella (ULRICH and BASSLER 1923).

REMARKS.—B. fissurella was referred by ULRICH and BASSLER (op. c., p. 514) to the genus Halliella. The type species of Halliella is the Devonian species H. retifera, described by ULRICH (1891, p. 185) and designated as genotype by MILLER 1892 (cf. WARTHIN 1948, p. 646). Also specimens of B. inaequalis have

been referred to *Halliella* (see below). *H. retifera* has an adductorial pit and a slight sulcal impression, and differs considerably from *Bolbiprimita* in lateral outline. HENNINGSMOEN (1953, p. 248) suggested that *H. retifera* might belong to the *Kirkbyidae*, this suggestion being based on the fact that KESLING (1951 a, p. 157) had drawn attention to its close resemblance to a species named *Amphissites lacrimosus* SWARTZ and ORIEL. This species, however, *Hibbardia lacrimosa* (SWARTZ and ORIEL), was later subjected to a thorough investigation by KESLING (1953) who figured the dimorphism; it is of the same kind as in the present *Bolbiprimitia* (cp. KAY 1940, pp. 234, 240, 252). *Hibbardia* and *Bolbiprimitia* were referred by HENNINGSMOEN (1954) to the *Treposellinae*. KAY founded the genus *Bolbiprimitia* in current text (1940, pp. 234, 240, 252), with the designation of the genotype under the heading *Euprimitia* (p. 252).

Both species are Silurian; *B. fissurella* from the Tonoloway limestone, Keyser, West Virginia. The Devonian *Halliella* aff. *fissurella* (POLENOVA 1955, p. 208; Pl. VI, Fig. 1) and *H. pulchra* (BASSLER 1941, p. 22, Fig. 2) may possibly also belong to this genus.

Bolbiprimitia inaequalis (JONES 1888)

Pl. II-III, Figs. 13-19; Pl. V, Figs. 50-51.

- 1887 Primitia inaequalis n. sp.—Jones, p. 5; nomen nudum.
- 1887 Primitia seminulum Jones, var.—Jones, p. 5; nomen nudum.
- 1888 Entomis inaequalis JONES—JONES, p. 408; Pl. XXII, Figs. 17a-b.
- 1888 Primitia seminulum JONES—JONES, p. 406; Pl. XXII, Figs. 20a-c.
- 1888 Entomis inaequalis JONES—LINDSTRÖM, p. 5.
- 1888 Primitia seminulum Jones—LINDSTRÖM, p. 5.
- 1889 Entomis inaequalis Jones-KRAUSE 1889a, p. 14.
- 1889 Entomis inaequalis Jones—Krause 1889b, p. 12.
- 1921 Primitia seminulum (JONES)—HEDE, pp. 49, 98.
- 1927 Primitia seminulum (JONES)—HEDE 1927b, pp. 21, 55.
- 1934 Entomis inaequalis (JONES)—BASSLER and KELLETT, pp. 67, 302.
- 1934 Halliella seminulum (JONES)—BASSLER and KELLETT, pp. 67, 323.

LECTOTYPE (designated here). — The female specimen in JONES 1888, Pl. XXII, Figs. 17a-b (Sw. State Mus. Nat. Hist. No. Ar 25697: I; Pl. V, Fig. 51).

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian of Gotland. TYPE LOCALITY.—Mulde brickyard, parish of Fröjel, Gotland.

DIAGNOSIS.—Crumina coherent with the ventricose postadductorial part of the carapace, reaching the middle of the ventral part of the anterior lobe. Ornamentation of anterior part and ventral side of the crumina effaced. Distinctly reticulated.

DESCRIPTION.—In proportion considerably longer than *B. fissurella*. In the female the posterior lobe is extremely inflated laterally, the ventral outline of the cruminal part being nearly circular. The velum runs as a low ridge over the

proximal part of the crumina. In the male the velum is somewhat broader, running along the whole of the non-dorsal part of the lateral outline. In both sexes the velum is smooth. A marginal structure is present. Both the preadductorial lobe and the postadductorial part form low but sharp dorsal ridges. The sulcus cuts nearly two thirds of the height of the valve, and is slightly bent forward round the site of the preadductorial node which is totally fused with the anterior lobe, but may be traced especially in the younger instars. The younger instars are essentially like the adult male. Size dispersion of the specimens recorded in Fig. 7 (dimensions in microns):

Instar	Total length	Height over sulcus
I ♂	1670–1740	900- 970
I ♀	1720–1840	1060-1090
(2)	1200–1480	690- 820
(3)	1000–1130	540- 700
(4)	760– 840	530- 510
(5)	(640– 660)	390

REMARKS.—It can be ascertained from JONES'S original figure of *Beyrichia* seminulum (1855, Pl. 6, Fig. 24) that this species is not identical with the present species from Mulde. The diagnosis (op. cit., p. 173) says that the lateral outline is "almost symmetrically semicircular" and the valves "coarsely punctate". The velum is of the same type as in *Bolbiprimitia*, but the sulcus is proportionally shorter than in this genus. For further references, see BASSLER and KELLETT 1934.

Family Primitiopsidae SWARTZ 1936

The Silurian species of this family were revised by MARTINSSON 1955 and were distributed into two genera, *Primitiopsis* and *Clavofabella*. Here two new genera are added, *Leiocyamus* and *Amygdalella*. They closely resemble each other, and fit in well with the diagnosis of the family. They are, however, very distinctly separated from the reticulated *Primitiopsidae* in general outline and development of the velar structures, and it is evident that they must be referred to two different families or subfamilies. With the present concept of taxonomy the latter division is preferred. The only satisfactorily described Devonian genus, *Sulcicuneus* KESLING (1951b), cannot be referred to any of these two subfamilies. As we know little about the phylogeny of the *Primitiopsidae* it is, for the present, left out of consideration. The Ordovician "*Primitiopsis*" species *P. bassleri* HARRIS, and *P.* (?) *circumreticulatum* HESSLAND, cannot be proved to be primitiopsids (cf. HESSLAND 1949, p. 241; MARTINSSON 1955, p. 19).

27-563272

The possibility is great that a posterior dolon has been developed convergently in more than one group; this may also apply to the two Silurian subfamilies, though they seem to be closely related.

Subfamily Primitiopsinae SWARTZ 1936

Type Genus.—Primitiopsis Jones 1887.

DIAGNOSIS.—Velar structure—bend or ridge—along the non-dorsal part of the lateral outline of both sexes. Distinct adductorial pit, rudiments of a preadductorial node present.

GENERA.—Primitio psis JONES 1887 and Clavofabella MARTINSSON 1955.

REMARKS.—The preadductorial node is usually traced only as an internal preadductorial impression. All species except C. cristata (JONES 1885) have a very typical reticulation.

Genus Primitiopsis Jones 1887

Primitiopsis planifrons JONES 1887

REMARKS.—The ontogeny is illustrated in Fig. 8. The present investigation confirms that the species has six free instars. The dimensions of the different instars are given in the following table (expressed in microns):

T	Total	length	Height over adductorial pit					
Instar	Instar 1948 : Q		1948 : Q	1955 : 1				
1 ♂ 1 ♀ 2 3 4 5 6	1090-1250 1280-1440 880-1050 710- 860 590- 700 460- 570 380- 420	1160-1310 1290-1430 960-1090 750- 910 600- 710 460- 560 380- 440	800-900 780-900 680-790 510-640 400-530 330-410 260-310	800-900 810-900 680-800 530-640 410-530 310-420 230-320				

The two valves are almost equal. Dimorphism is known only in the last instar. Even the smallest instars are easily distinguished from the *Clavofabella* species. The smaller instars differ from the adult in the development of the sulcal region which is distinctly depressed in instar 6, the depression gradually disappearing in instars 5 and 4, very faint in older instars. The instars are illustrated in MARTINSSON 1955, Pl. I.



Fig. 8. Ontogeny of *Primitiopsis planifrons*. Females are set down as circlets, tecnomorphs as dots. Height over sulcus along the ordinate, total length along the abscissa. The diagram is based on half of the carapaces and left valves in sample 1955:1, representing 689 specimens. Cf. the diagram based on sample 1948:Q in MARTINSSON 1955, Fig. 2.

Genus Clavofabella MARTINSSON 1955

REMARKS.—The *Clavofabella* species are, as mentioned, easily distinguished from *Primitiopsis*. The present investigation seems to confirm that the genus has only 5 free instars. These may be distinguished without difficulty in all instars except the youngest; the four other instars are depicted here. The ornamental characters referred to in the author's previous study (1955) have proved to be extraordinarily constant. In the following discussion the ontogeny will be briefly described, the measurements based on the sample 1955: I are published, and some notes on dimorphism and sex ratios are given under each species.

The genus is of great theoretical interest as it contains in the same population three closely related species with very distinct specific characters; these species, moreover, exhibit interesting differences in dimorphism and, obviously, in sex ratio. Only the older instars have been measured (see the chapters on dimorphism and sex ratios); the youngest are too alike for the different species to be distinguished, and in instar 4 well preserved specimens are still needed for the specific determination. In Fig. 5 the size dispersion of the *Clavofabella* females is illustrated graphically. In Fig. 9 the size dispersion patterns in the samples 1948: T and 1955: I are compared.

3 - 563272 Bull. of Geol. Vol. XXXVII.



Fig. 9. Compilation of the size dispersion pattern of the females of the *Clavofabella* species, from two different samples. Cf. Fig. 5.

This and other primitiopsid genera exhibit considerable differences in size between the two valves (Pls. II–III, Figs. 26, 27, 38, 39). The author has chosen the left valve or side of the carapaces for measurements and illustrations, because the overlap is illustrated and the marginal denticles or tubercles easily visible—on the right valve they are denser and much smaller.

Clavofabella multidentata MARTINSSON 1955

Pl. III, Figs. 20–27.

REMARKS.—The species is dimorphic in the two last instars. The sex ratio in the last instar suggests that males and females are about equally represented; the significance of the difference in sex ratio of the two last instars is discussed above. Sizes of the left valve of the females in instar 1: length 800–1020 μ , height 640–730 μ . Females in instar 2: length (730–)760–830(–870) μ , height 530–590(–640) μ .

Clavofabella incurvata MARTINSSON 1955

Pl. IV, Figs. 28-32.

REMARKS.—The species is dimorphic in the last instar only. The sex ratio exhibits a considerable majority of females, 70 for 30 males. Size of the females: length $800-950 \mu$, height $560-680 \mu$.

Clavofabella reticristata (JONES 1888)

Pl. IV, Figs. 33-37; Pl. V, Fig. 53.

LECTOTYPE.—The adult dolonate specimen in JONES 1888, Pl. XXII, Fig. 15 (Swed. State Mus. Nat. Hist. No. Ar. 24697: 5; Pl. V, Fig. 53 in this paper). This lectotype replaces the invalid neotype of 1955 (cf. p. 18).

REMARKS.—Dimorphic characters developed in the last instar only which obviously contains only dolonate specimens; a few specimens have rudimentary dolonal flanges. The present samples suggest that males are entirely absent, and that the species was parthenogenetic.

To the author's earlier description should be added that a marginal frill is observed in several specimens also of this species. Arising from the discussion above it should be stressed that the pictured non-dolonate specimen (MARTINS-SON 1955, Pl. II, Fig. 22) should be regarded as dolonate (cf. Pl. IV, Fig. 30c in this paper).

Subfamily Leiocyaminae n. subf.

TYPE GENUS.—Leiocyamus n. g.

DIAGNOSIS.—Velar structure absent in the tecnomorphs; the velar structure in the females consists exclusively of the dolon. Smooth or finely pitted species, without adductorial pit and external preadductorial node. GENERA.—Leiocyamus n. g. and Amygdalella n. g.

REMARKS.—The two included genera differ from each other in about the same respect as *Clavofabella* from *Primitiopsis*: In *Leiocyamus* the dolonal edges are free, while they form a nearly closed chamber in *Amygdalella*. In *Leiocyamus*, but not in *Amygdalella*, the dolon extends forwards along the ventral side. *Primitiopsis dorsoplicata* HENNINGSMOEN may be a member of this subfamily. It has a posterior dolon continued along the ventral part of the valve. The homogeneity of the species and the nature of its dimorphism require further investigation.

An undescribed species from the Upper Silurian of Gotland has the finely pitted ornamentation mentioned in the present diagnosis.

Genus Leiocyamus n. g.

DERIVATION OF NAME .- From Greek λεΐος, smooth, and χύαμος, bean.

TYPE SPECIES.—Leiocyamus apicatus n. sp.

DIAGNOSIS.—Dolon continued forwards along the ventral side of the valve, not forming a chamber.

SPECIES.—Leiocyamus apicatus n. sp.

Leiocyamus apicatus n. sp.

Pls. IV-V, Figs. 38-42.

DERIVATION OF NAME.—Latin *apicatus*, pointed, alluding to the shape of the dorsal ridge.

HOLOTYPE.—The female carapace in Pl. IV, Fig. 40. (Mus. Pal. Inst. Uppsala No. G 178.)

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian.

TYPE LOCALITY.-Mulde brickyard, parish of Fröjel, Gotland.

DIAGNOSIS.—Dorsal ridge in adult specimens protruding in a point above the centre of the hingeline.

DESCRIPTION.—Dorsal outline narrow, slowly tapering from the central, widest part towards the ends. Valves differing much in shape, the right being considerably broader and overlapping the left (Pl. IV, Figs. 38 and 39). The pointed dorsal ridge somewhat longer on the left valve. Velar structure developed only in the female and consisting in a broad posterior dolon, continued forwards as a narrower ventral flange on each valve. Marginal tuberculation dense, about 35 tubercles/mm on the ventral part of the left valve. Hingement consisting of a simple groove in the left valve, somewhat broader towards the ends, corresponding to a ridge on the left valve. Surface quite smooth. Adductor muscle insertion and preadductorial node not observed on the inner side of the valves. The male closely resembles the female, except in the total absence of velar structures; marginal structures not observed. Only one larval specimen observed, with a very faint dorsal ridge. Size in microns:

		Left v	alves	Right	valves
Sample	Specimen	Total length	Height	Total length	Height
1955:1	Ŷ		-	1290	970
1955:4	Ŷ	1250	810	_	_
1948 : T	Ŷ	1270	890	1320	1000
1955:1	ę		_	1190	890
1955:1	Ŷ	1190	800	_	-
1955 : 1	Ŷ	1080	780	1150	86o
1955:1	9	_		1140	900
1955:2	õ	1360	860	1410	970
1955 : 1	larva	1000	720	_	

Genus Amygalella n. g.

DERIVATION OF NAME.—Diminutive of Latin amygdala, almond.

TYPE SPECIES.—Amygdalella subclusa n. sp.

DIAGNOSIS.—Dolon posterior, not extended along the ventral side of the carapace, forming a nearly closed pouch.

SPECIES.—Amygdalella subclusa n. sp.

REMARKS.—Yet another species, named *Aparchites obsoletus* (JONES & HOLL) by KRAUSE 1891, should be referred to this genus. Its relations to the *Primitiopsidae* were proved by KUMMEROW 1924. As is mostly the case with species described from glacial drift boulders, the possibilities of taxonomic identification are either very small or absent.

Amygdalella subclusa n. sp.

- 1891 Aparchites oblongus (Jones & Holl)—KRAUSE, p. 493; Pl. XXX, Fig. 2a, b, c.
- 1894 Schmidtella oblonga (JONES & HOLL)—ULRICH, p. 640.
- 1896 Aparchites oblongus (JONES & HOLL)-KOKEN, p. 431.
- 1916 Aparchites oblonga (JONES & HOLL)—BOTKE, p. 26.
- 1924 Primitiopsis oblonga (JONES & HOLL)—KUMMEROW, p. 22; Pl. 20 (numbered 21), Figs. 23, 24. (Jahrbuch 1923).
- 1932 Primitiopsis oblonga Jones & Hall-Bonnema, p. 293.
- 1933 Primitiopsis oblonga (JONES & HOLL)-KUMMEROW, p. 46; Fig. 4.
- 1933 Primitiopsis sp.—BONNEMA 1933a, Figs. 30, 31.
- 1933 Primitiopsis oblonga (JONES & HOLL)—BONNEMA 1933 b, p. 151 (sep. edition p. 2).
- 1934 Primitiopsis oblonga (Jones & Holl)—Bonnema, p. 87.
- 1934 Primitiopsis oblongus (JONES & HOLL)—BASSLER and KELLETT, pp. 71, 465.
- 1936 Primitiopsis oblonga (JONES & HOLL)-SWARTZ, p. 555; Pl. 83, Figs. B 3a-f.
- 1937 Primitiopsis oblonga (JONES & HOLL)-KUMMEROW, pp. 465-467.
- 1938 Primitiopsis oblonga (Jones & Holl)—Bonnema, pp. 104, 105; Figs. 1-19.
- 1941 Primitiopsis oblonga (JONES & HOLL)-TRIEBEL, pp. 357, 358.
- 1949 Primitiopsis oblonga (JONES & HOLL)—HESSLAND, p. 240.

DERIVATION OF NAME.—Latin *subclusus*, alluding to the almost closed dolonal pouch.

HOLOTYPE. — The female valve figured by BONNEMA 1938, Fig. 19. (Mus. Geol. Inst. Tartu [Dorpat] No. Os 2805). Unfortunately the best preserved specimens in BONNEMA's figures (also in SWARTZ 1936, Pl. 83) cannot be identified with certainty, as more than a hundred specimens of this species from Vollenhove are in the collections of the museum.

OCCURRENCE.—Glacial drift boulders in northern Germany and Holland (the holotype from *Beyrichia* limestone from Vollenhove, Holland).

DIAGNOSIS.—The high and arched dorsal ridge merges without interruption into the other parts of the subelliptical lateral outline. Dorsum broad. The overlapping part of the right valve very thick.

DESCRIPTION.—In the female the dolon as well as the arched dorsal ridge form part of the almost perfectly subelliptical outline. The valves are very unequal in size, the left valve falling entirely within the lateral outline of the right. The dolonal flanges form a posterior pouch, but a slit is left open in the hindmost part. The male has no velar structures. The valves are very thick, especially the ventral part of the overlapping right valve. The overlapped part of the left valve has a transversally striated marginal structure.

REMARKS.—As pointed out earlier by the author (1955, p. 19) this species is not identical with *Primitia oblonga* JONES & HOLL 1865. It was introduced into literature by KRAUSE 1891 who depicted it as *Aparchites ? oblongus*. This determination has been accepted in later papers. KUMMEROW (1924) first referred it to the *Primitiopsidae* by placing it in the genus *Primitiopsis*. It formed one of the recurrent motives in the polemics between BONNEMA and KUMMEROW (Il. cc. 1924–1938 in the synonymy list). BONNEMA (1938, p. 104) believed the species to be related to *Leperditia*, and not to *Primitiopsis planifrons*, basing himself upon the development of the margin of the left valve (op. c., Figs. 8, 17). The other authors retained it as a primitiopsid. SWARTZ, supported by HESSLAND (Il. cc.), pointed to the necessity of placing it in a genus of its own.

Amygdalella subclusa is one of the most discussed and best illustrated ostracodes in literature (BONNEMA 1938). This seems to be a sufficient motive for a taxonomic treatment; in this respect a great number of the species described from glacial boulders in the "Geschiebe" literature will most certainly be abandoned in the future. The author has not made use of the possibility of giving the name oblonga also to this species, as might have been considered fitting. The specific name oblonga is hardly significant, and has already been given to at least 17 ostracode species (RICHTER 1948, p. 110).

KRAUSE 1877 and ROEMER 1885, both recording *Primitia oblonga* without illustrations should probably be added to the list of synonyms. *Primitia oblonga* in ALTH 1874 is not a synonym. *P. oblonga* is mentioned also in a paper by SIEMIRADSKI 1906 which has not been accessible to the present author.

Family Thlipsuridae ULRICH 1894

Genus Thlipsurella SWARTZ 1932

REMARKS ON THE ORIENTATION.—In his thorough revision of the *Thlipsuridae* (1932), SWARTZ gives these ostracodes a reversed orientation. The hingement of *Thlipsurella* is situated near the end with the sharply rising terminal facets. When the carapace of *T. discreta* is opened there is thus very little space between the valves, while these gape widely at the other end. It seems to be difficult to explain how the animal was able to swim if the facetted end was the anterior, as there is little space for stretching out the antennae and antennulae. The adductor muscle insertion is almost central, and the sides of the carapace are almost parallel, and do not exhibit criteria for the orientation. If the facetted end is regarded as the posterior, there is a close agreement with, e.g., the conditions among the *Healdiidae* which HENNINGSMOEN (1953) claims to be related to the *Thlipsuridae*; the hingement is then posterior and the left valve overlapping. LEVINSON (1950), however, on studying the hingement of *Thlipsurella fossata* (ROTH), concluded that the orientation of ROTH (1929) and SWARTZ (op. cit.) is the correct one.

With the above arguments the present author accepts the orientation with the blunter end as the posterior. In *Thlipsurella discreta*, seen in lateral view, the two adjacent furrows are then posterior and the single one anterior.

Thlipsurella discreta (JONES 1888)

Pl. V, Figs. 43-49.

- 1887 Thlipsura v-scripta var. discreta, nov.-Jones, p. 6, nomen nudum.
- 1888 Thlipsura v-scripta var. discreta JONES-JONES, p. 404; Pl. XXII, Figs. 9, 10.
- 1888 Thlipsura V-scripta var. discreta Jones-LINDSTRÖM, p. 5.
- 1901 Thlipsura v-scripta var. discreta Jones—Chapman, p. 153.
- 1921 Thlipsura V-scripta discreta Jones—Hede, p. 98.
- 1927 Thlipsura V-scripta discreta JONES-HEDE 1927 a, pp. 38, 54.
- 1927 Thlipsura V-scripta discreta JONES-HEDE 1927b, pp. 21, 56.
- 1929 Thlipsura v-scripta var. discreta JONES-ROTH, p. 356.
- 1932 Thlipsurella v-scripta var. discreta (JONES)-SWARTZ, p. 47.
- 1934 Thlipsurella v-scripta var. discreta (JONES)—BASSLER and KELLET, p. 68; p. 487, partim.
- 1954 Thlipsurella v-scripta discreta (JONES)—POKORNÝ, Fig. 622.
- cf. 1919 Thlipsura V-scripta var. discreta Jones—Hede, pp. 139, 147; Pl. 6, Fig. 1.

LECTOTYPE (designated here). — A right valve in the collection used by JONES 1888 (Swed. State Mus. Nat. Hist. No. Ar. 25726: 10; Pl. V, Fig. 49 in this paper). The specimens figured by JONES cannot be identified.

DIAGNOSIS.—In the posterior end two straight furrows which are never fused with each other, cutting each other at an angle of about 45°; the ventral one is almost horizontal. In the anterior end one slightly curved transversal furrow.



Fig. 10. Ontogeny of *Thlipsurella discreta*. Only carapaces measured; the 472 carapaces in the present diagram represent one third of the specimens in sample 1955: I. A two-dimensional or three-dimensional diagram, based on a selection of well preserved specimens, would probably give a more distinct distribution pattern than the present. The single valves are to a very great extent too badly preserved for measurement.

DESCRIPTION.—Carapace in lateral view slightly subreniform, somewhat tapering towards the posterior end. In dorsal view the lateral surfaces of the valves are subparallel, curved in anteriorly so that the anterior end is gently rounded. The posterior facets cut each other at an obtuse angle, and are separated from the lateral sides of the valves by a distinct ridge. Left valve over-lapping; on the central part of the ventral side the overlap is somewhat broader, and the contact line of the valves is very slightly curved with the convexity to the right (Pl. V, Fig. 43v). Hingement consisting of a sharp ridge in the left valve corresponding to a groove in the right valve. The adductor muscle insertion is situated almost centrally, in the triangle formed by the furrows.

Four instars established. The smallest (4) is subelliptic, and the angle between the posterior facets is acute. The subreniform outline is sometimes established already in instar 3. During the ontogeny the angle between the posterior facets becomes gradually more obtuse, passing 90° in instar 2. Similarly the anterior end gradually becomes blunter. It is not established whether the species is parthenogenetic or syngamic; there are no signs of dimorphic differences except possibly in size (see Fig. 10). Size in microns:

34

Instar	Length	Height
I	860–1040	440-615
2	690– 835	390-515
3	525– 660	325-430
4	390– 515	240-320

REMARKS.—JONES (1887) identified the species with *Primitia minuta* KRAUSE, but the species in KRAUSE's illustration (1877, Pl. I, Fig. 19) could not possibly be identical with the present one. KRAUSE (1892, Pl. XXII, Fig. 17) figured another *Thlipsurella* specimen as *Thlipsura v-scripta* var. *discreta* JONES, and this figure has been reproduced in several papers. It differs, as *Th. v-scripta* JONES & HOLL, from *Th. discreta* by the fused posterior furrows forming the letter "v" from which fact the name of the former species was derived. In the papers by JONES 1887 and 1888 a differential diagnosis and good illustrations are given.

CONCLUSIONS

THE MATERIAL.—The ostracode populations from the Mulde marl provide an excellent material for the study of ostracode ontogeny. The size dispersion pattern obtained from the species dominating the population numerically are very distinct, with well distinguished instars; the species constituting minor components of the population exhibit less distinct dispersion of the specimens. There are great variations between the samples studied as to the proportions of carapaces and separated valves.

THE POPULATIONS.—There are wide differences in the distribution of the specimens of different instars in the samples studied. In a sample with essentially separated valves the distribution curve descends from a maximum in one of the youngest instars. In a sample with a majority of carapaces the curve has its maximum in an intermediate instar. Except in the adult instar it is not possible to ascertain to what extent the fossils represent dead animals or exuviae.

The population is in all samples dominated by three species: *Beyrichia* (*Mitrobeyrichia*) clavata, *Thlipsurella discreta*, and *Primitiopsis planifrons*. Most of the other species are closely related to these, occurring mostly in much smaller numbers. There are some species represented by only 1–2 specimens per 10,000.

THE ONTOGENY.—All the species examined have instars which are essentially like the preceding or following ones; if instars from quite different parts of the ontogeny are compared, however, they may be very different in shape, as in the *Beyrichiidae*.

The growth ratios obtained are in close accordance with BROOKS's law, with a linear growth factor of about 1.26. All species have shown a smaller growth factor for the last moulting.

For practical reasons the instars are numbered in reversed order, with the adult as no. 1.

The number of free instars has proved to be maximally 9, in *Beyrichia*. *Primitio psis planifrons* has 6 instars, while in the primitiopsid genus *Clavofabella* 5 instars have been demonstrated. *Thlipsurella discreta* has only 4 instars.

LARVAL CHARACTERS.—Most features in lobation and carapace ornamentation develop gradually during ontogeny. In *Beyrichia clavata* the anterior and posterior corners of the right valves are extended into *larval processes* present in the youngest instars and disappearing during ontogeny.

ONTOGENETIC DEVELOPMENT OF DIMORPHISM.—The dimorphic characters usually appear only in the last instar. Preadult *velar* dimorphism is shown by *Clavofabella multidentata*. The preadult *cruminal* dimorphism earlier suggested in *Beyrichia* may be present in *Beyrichia* (*Beyrichia*) *dactyloscopica*; the homogeneity of the species, however, is questionable

THE SEX OF THE DIMORPHS.—The old view that the *heteromorphs* are female and the adult *tecnomorphs* male is strongly supported as regards the cruminal and velar dimorphism. As in earlier investigations discussed the cruminae of *Beyrichia* have proved to contain larvae; it is evident that the specimens in the pouches have not come in from outside. *Clavofabella reticristata* has only dolonate specimens in the last instar; as it is improbable that both sexes are dolonate, and also that the males could have finished the ontogeny in a preceding instar, this confirms that also the dolonate forms are females. This seems to be a background for regarding even the heteromorphs of other types of dimorphism as females, by analogy.

SEX RATIOS.—Most of the examined palaeocopes have sex ratios of about 50:50. *Clavofabella reticristata* is evidently parthenogenetic. *C. incurvata* in the examined sample has proved to have a sex ratio of 30 males to 70 females. Thus each of the three closely related *Clavofabella* species has a characteristic development of dimorphism. *Thlipsurella* has no special external dimorphic characters; the treatment of this species, however, has not been pursued as far as possible.

TAXONOMY.—It is indicated by the present species and by material from other strata consulted by the author for comparison that these ostracode groups contain series of closely related but well distinguished species, and that the specific variation must be considered to be more limited than hitherto. It must be insisted upon that the description of a species be based on a sufficient material from well defined localities and strata. Unfortunately many of the older descriptions and original illustrations of ostracode species are too incomplete for the revision of the species on these lines. Especially when working with ostracodes described in the literature on glacial drift boulders in northern Europe, the originals of which are frequently reported to be lost during the war, the reviser is compelled to base the differentiation of the species on promi-

36

nent features in the illustrations with no guarantee that these represent the conditions in the original specimens.

The author's studies on the Mulde marl fauna have aimed at the establishment of the variational phenomena within the species, the knowledge of which is necessary for taxonomic work, and it is the author's intention to continue with a treatment of the Silurian ostracodes of Gotland on broader taxonomic lines. As there is a great variety of *Beyrichiidae* and *Primitiopsidae* — of both subfamilies — from different strata in the sequence of Gotland, the present concentrated taxonomic treatment of the Mulde fauna may be expected to be systematized and elaborated considerably when the morphological and diagnostic characters of the entire material are accessible.

Acknowledgements

The author is greatly indebted to the following persons for the promotion of this investigation from field work to a finished publication: to Professor P. THORSLUND for advice and institutional resources; to Dr. V. JAANUSSON for valuable discussions and for access to an unpublished manuscript; to Miss CHRISTINA BACKMAN, F. M., and Professor O. ZDANSKY for linguistic advice and corrections; and to the technical staff of the Palaeontological Institution: Mrs. EVA EKLIND (typing, etc.), Mr. N. HJORTH (photographs), Mrs. MEIT LINDELL (preparations), Mr. E. STÅHL (thin sections, retouch), and Mrs. INGA THOMASSON (drawings).

Mr. R. BAKER, British Museum (Nat. Hist.) and Dr. L. SARV, Tartu (Dorpat), have kindly placed information about JONES's and BONNEMA's originals at the author's disposal.

References

- VON ALTH, A., 1874: Über die palaeozoischen Gebilde Podoliens und deren Versteinerungen. Kaiserl. königl. geol. Reichsanstalt, Abh. Bd. VII, H. 1. Wien.
- BASSLER, R. S., 1941: Ostracoda from the Devonian (Onondaga) chert of west Tennessee. *Journ. Wash. Acad. Sci.* Vol. 31 No. 1. Menasha.
- BASSLER, R. S., and KELLETT, B., 1934: Bibliographic index of Paleozoic Ostracoda. *Geol. Soc. America, Spec. Papers.* No. 1. Washington, D.C.
- BOLL, E., 1856: Herr BOLL and Herrn BEYRICH (Briefliche Mitteilung). Zeitschr. Deutsch. Geol. Ges. Bd. 8. Berlin.
- 1862: Die Beyrichien der norddeutschen silurischen Gerölle. Arch. Ver. Freunde der Naturgesch. in Mecklenburg. 16. Jahr. Neubrandenburg.
- BONNEMA, J. H., 1913: The orientation of the shells of Beyrichia tuberculata KLÖDEN sp. Koninkl. Akad. Wetensch. Amsterdam, Proceedings, Vol. 16. Amsterdam.
- 1932: Orientation of the carapaces of Paleozoic ostracoda. *Journ. Pal.* Vol. 6. Tulsa (Menasha).
- 1933 a: Die Orientierung der Schalen der paläozoischen Ostracoden. Zeitschr. Geschiebef. Bd. IX. Leipzig (Grimmen).
- 1933 b: Über paläozoische Ostracoden. Ibidem.
- 1934: Über die Aufstellung der Schalen der paläozoischen Ostracoden. Ibidem. Bd. X.
- 1938: Zum allerletzten Male: Die Aufstellung der Schalen der Paläozoischen Ostracoden und die Brutkammer von Primitiopsis oblonga J. & H. Natuurhistorisch Maandblad. Jaarg. 27, No. 10.

- BOTKE, J., 1916: Het geslacht Aechmina, JONES et HOLL. Verh. Geol. Mijnbouwk. Genootsch. voor Nederland en Koloniën. Geol. Ser., Deel III. 's-Gravenhage.
- CHAPMAN, F., 1901: On some fossils of Wenlock Age from Mulde, near Klinteberg, Gotland. Ann. Mag. Nat. Hist. Ser. 7. Vol. 7. London.
- HEDE, J. E., 1917: Faunan i kalksandstenens märgliga bottenläger söder om Klintehamn på Gotland. Sv. Geol. Unders. Ser. C. No. 281. Stockholm.
- 1919: Om en förekomst af colonusskiffer vid Skarhult i Skåne. *Geol. Fören. Förh.* Bd. 41. Stockholm.
- 1921: Gottlands silurstratigrafi. Sv. Geol. Unders. Ser. C. No. 305. Stockholm.
- 1927a: Berggrunden (Silursystemet). In MUNTHE, HEDE och LUNDQVIST: Beskrivning till kartbladet Klintehamn. Ibidem. Ser. Aa, No. 160.
- 1927b: Berggrunden (Silursystemet). In MUNTHE, HEDE och von Post: Beskrivning till kartbladet Hemse. *Ibidem*. Ser. Aa, No. 164.
- 1942: On the correlation of the Silurian of Gotland. Medd. Lunds Geol.-Min. Inst. No. 101 (in Lunds geologiska fältklubb 1892–1942). Lund.
- HENNINGSMOEN, G., 1953: Classification of Paleozoic straight-hinged ostracods. Norsk geologisk tidsskrift. Bd. 31. Bergen.
- 1954: Silurian ostracods from the Oslo region. *Ibidem.* Bd 34.
- HESSLAND, I., 1949: Lower Ordovician Ostracods of the Siljan District, Sweden. Bull. Geol. Inst. Upsala. Vol. XXXIII. Uppsala.
- JAANUSSON, V., 1956: Middle Ordovician ostracodes of central and southern Sweden. Manuscript announced for publication in the Bull. Geol. Inst. Uppsala (Publ. Pal. Inst. Uppsala).
- JAANUSSON, V. and MARTINSSON, A., 1956: Two hollinid ostracodes from the Mulde marl of Gotland. *Manuscript* announced for publication in *Bull. Geol. Inst. Uppsala* (*Publ. Pal. Inst. Uppsala*).
- JONES, T. R., 1855: Notes on Palaeozoic bivalved Entomostraca. No. II. Some British and foreign species of Beyrichia. Ann. Mag. Nat. Hist. Ser. 2. Vol. 16. London.
- — 1865: Notes on the Palaeozoic bivalved Entomostraca. No. VI. Some Silurian species
 (*Primitia*). *Ibidem.* Ser. 3, Vol. 16.
- 1887: Notes on some Silurian ostracoda from Gothland. Stockholm.
- 1888: Notes on the Palaeozoic bivalved Entomostraca. No. XXV. On some Silurian Ostracoda from Gothland. Ann. Mag. Nat. Hist. Ser. 6, Vol. 1. London.
- KAY, G. M., 1940: Ordovician Mohawkian Ostracoda: Lower Trenton Decorah Fauna. *Journ. Pal.* Vol. 14. Tulsa (Menasha).
- KESLING, R. V., 1951 a: Terminology of ostracod carapaces. Contr. Mus. Pal. Univ. Michigan. Vol. IX. Ann Arbor.
- 1951b: A new genus of primitiopsid ostracod from the Devonian Traverse group of Michigan. *Ibidem.* Vol. VIII.
- 1952a: A study of Ctenoloculina cicatricosa (WARTHIN). Ibidem. Vol. X.
- 1952 b: Doubling in size of ostracods in each molt stage. Journ. Pal. Vol. 26. Tulsa (Menasha).
- 1953: A slide rule for the determination of instars in ostracod species. Contr. Mus. Pal. Univ. Michigan. Vol. XI. Ann Arbor.
- KIESOW, J., 1888: Über Gotländische Beyrichien. Zeitschr. Deutsch. Geol. Ges. Bd 40. Berlin.

KOKEN, E., 1896: Die Leitfossilien. Leipzig.

KOLMODIN, L., 1869: Bidrag till kännedomen om Sverges siluriska ostracoder. Upsala.

KRAUSE, A., 1877: Die Fauna der sogen. Beyrichien- oder Choneten-Kalke des norddeutschen Diluviums. Zeitschr. Deutsch. Geol. Ges. Bd 29. Berlin.

- KRAUSE, A., 1889a: Beyrichien und verwandte Schalenkrebse in märkischen Silurgeschieben. Sitzungsber. Ges. Naturf. Freunde Berlin. Jahrg. 1889. Berlin.
- 1891: Beitrag zur Kenntnis der Ostracoden-Fauna in silurischen Diluvialgeschieben. Zeitschr. Deutsch. Geol. Ges. Bd XLIII. Berlin.
- 1892: Neue Ostrakoden aus märkischen Silurgeschieben. Ibidem. Bd XLIV.
- KUMMEROW, E., 1924: Beiträge zur Kenntnis der Ostracoden und Phyllocariden aus nordischen Diluvialgeschieben. Jahrb. Preuss. Geol. Landesanstalt. Vol. 44. Berlin.
- 1933: Zur Paläobiologie der Ostracoden und Trilobiten. Zentralbl. f. Min. Geol. Pal. Jahrg. 1933, Abt. B. No. 1. Stuttgart.
- 1937: Die Bruteinrichtungen paläozoischer Ostracoden, sowie über Receptaculites und einige ordovizische Kalkalgen der Gattung Apidium. Jahrb. Preuss. Geol. Landesanstalt. Vol. 57 (1936).
- KURTÉN, B., 1953: On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76. Helsingforsiae.
- LEVINSON, S., 1950: The hingement of Paleozoic Ostracoda and its bearing on orientation. *Journ. Pal.* Vol. 24. Tulsa (Menasha).
- LINDSTRÖM, G., 1888: List of the fossil faunas of Sweden. II. Upper Silurian. Stockholm.
- M'Coy, F., 1846: A synopsis of the Silurian fossils of Ireland. Dublin.
- MARTINSSON, A., 1955: Studies on the ostracode family Primitiopsidae. Publ. Pal. Inst. Uppsala. No. 4 (in Bull. Geol. Inst. Uppsala. Vol. XXXVI). Uppsala.
- MATTHEW, G. F., 1886: Illustrations of the fauna of the St. John Group, continued, No. III. Descriptions of new genera and species. *Proc. and Trans.* (1885) *Royal Soc. Can.* Ser. 1. Vol. 3. Ottawa.
- Рокоrny, V., 1954: Základy zoologické mikropaleontologie. Praha.
- Роlеноva, Е. N. (Поленова, Е. Н.) 1955: Остракоды Девона Волго-Уральской Области. Труды Всесоюзного Нефтяного Научно-Исследовательского Геологоразведочного Института (ВНИГРИ). Ленинград.
- RICHTER, R., 1948: Einführung in die zoologische Nomenklatur durch Erläuterung der Internationalen Regeln. 2. umgearb. Aufl. Frankfurt am Main.
- ROEMER, F., 1885: Lethaea erratica oder Aufzählung und Beschreibung der in der norddeutschen ebene vorkommenden Diluvial-Geschiebe nordischer Sedimentär-Gesteine. *Palaeont. Abh.* Bd 2, H. 5. Berlin.
- Roth, R., 1929: Some ostracodes from the Haragan marl, Devonian, of Oklahoma. *Journ. Pal.* Vol. 3. Menasha.
- VON SIEMIRADSKI, J., 1906: Die Paläozoischen Gebilde Podoliens. 2. Paläontologischer Teil. Mitt. Geol. und Pal. Inst. Univ. Wien, Bd 19. Wien.
- SPJELDNÆS, N., 1951: Ontogeny of *Beyrichia jonesi* BOLL. *Journ. Pal.* Vol. 25. Tulsa (Menasha).
- SWARTZ, F. M., 1932: Revision of the ostracode family Thlipsuridae, with descriptions of new species from the Lower Devonian of Pennsylvania. *Ibidem*. Vol. 6. Menasha.
- 1936: Revision of the Primitiidae and Beyrichiidae, with new Ostracoda from the Lower Devonian of Pennsylvania. *Ibidem*. Vol. 10. Tulsa (Menasha).
- TRIEBEL, E., 1938: Über das Auslesen von Mikrofossilien. *Senckenbergiana*. Bd. 20. Frankfurt am Main.
- 1941: Zur Morphologie und Ökologie der fossilen Ostracoden. Ibidem. Vol. 23.
- ULRICH, E. O., 1891: New and little known American Palaeozoic Ostracoda. Journ. Cincinnati Soc. Nat. Hist. Vol. XII. Cincinnati.
- 1894 (1897): The Lower Silurian Ostracoda of Minnesota. Geol. and Nat. Hist. Survey of Minnesota. Vol. III, Part II. Minneapolis.

- ULRICH, E. O., and BASSLER, R. S., 1908: New American Palaeozoic Ostracoda. U.S. Nat. Mus., Proc. Vol. XXXV. Washington.
- WARTHIN, A. S., 1948: Ostracode genotypes designated by S. A. MILLER. *Journ. Pal.* Vol. 22. Tulsa (Menasha).
- WINKLER, E., 1955: A study of the variation of recent and fossil ostracodes. *Ibidem*. Vol. 29.

ERRATA in ANDERS MARTINSSON: Neue Funde kambrischer Gänge und ordovizischer Geschiebe im südwestlichen Finnland. Bull. Geol. Inst. Uppsala vol. XXXVI No. 5 (Publ. Pal. Inst. Univ. Uppsala No. 8):

In den Erklärungen zu Tafel I, Abb. 3 und 4 (S. 105) sind die Worte "weiblicher" und "männlicher" vertauscht. Die Dimorphen von *Chilobolbina* cf. *umbonata* verteilen sich also folgendermassen: 33 Abb. 3, 5 und 6; 9 Abb. 4.

In the English text to Fig. 9 (p. 97) in stead of E.N.E., read E.S.E.

Palaeontological Institution, University of Uppsala, May 11, 1956.

Explanations of plates

In the plates every single specimen is designated by one number; thus the figures are numbered continuously through the five plates. The components of the figures are designated with the following letters:

- 1 = lateral view, from the left side unless otherwise stated.
- v = ventral view,
- d = dorsal view,
- f = anterior view,
- c = caudal view,
- o = oblique latero-ventral view,
- i = inner side, left or right valve.

The photographical work was carried out at the Palaeontological Institution, Uppsala, by Mr. N. HJORTH and the author. The figures are slightly retouched. Unless otherwise stated, the specimens were whitened with ammonium chloride before photographing. Originals in the Swedish State Museum of Natural History are marked RM; the other originals are in the Museum of the Palaeontological Institution, Uppsala (series G).

Plate I

Beyrichia (Mitrobeyrichia) clavata KOLMODIN. Magnification 20 ×. Fig. 1. Male. KOLMODIN's original, lectotype. No. G 145.

Beyrichia (Beyrichia) dactyloscopia n. sp. Magnification $20 \times$.

Fig. 2. Adult female. Holotype, No. G 146.

Fig. 3. Adult male. No. G 147.

Fig. 4. Subadult female? No. G 148.

Plate II

Beyrichia (Beyrichia) dactyloscopia n. sp. Figs. 6-9, magnification 20 ×.

- Fig. 5. The carapace structure of the inner ventral part of the crumina, with the finger-print pattern, the surface granulosity, and the spines along the edge of the velum. Magnification $40 \times$ (left) and $25 \times$ (right). No. G 149.
- Fig. 6. Adult male. No. G 150.

Fig. 7. Instar (2). No. G 151.

Fig. 8. Instar (2). No. G 152.

Fig. 9. Instar (3), very spinose. No. G 153.

Beyrichia (Beyrichia) subornata n. sp. Magnification 20 ×.

Fig. 10. Female. Holotype, No. G 154.

Fig. 11. Male. No. G 155.

Fig. 12. Male. No. G 156.

Bolbiprimitia inaequalis (JONES). Magnification $20 \times$.

Fig. 13. Female. No. G 157.

Plate III

Bolbiprimitia inaequalis (JONES). Magnification $20 \times$.

Fig. 14. Female. RM No. Ar. 26060.

Fig. 15. Male. No. G 158.

- Fig. 16. Instar (2). No. G 187.
- Fig. 17. Instar (3). No. G 188. Fig. 18. Instar (4). No. G 189.
- Fig. 19. Instar (5). No. G 159.

Clavofabella multidentata MARTINSSON. The ontogeny from instar 4 to adult. Magnification 40 × .

Fig. 20. Adult female. No. G 117.

Fig. 21. Adult male. No. G 160.

- Fig. 22. Subadult female. No. G 161.
- Fig. 23. Instar 2, tecnomorphic. No. G 162.
- Fig. 24. Instar 3. No. G 163.
- Fig. 25. Instar 4. No. G 164.

Clavofabella multidentata MARTINSSON. The difference in shape and size of the two valves. Note the area with seemingly effaced sculpture over the adductorial pit. Magnification $40 \times$. Fig. 26. Left valve. No. G 165.

Fig. 27. Right valve. No. G 166.

Plate IV

Clavofabella incurvata MARTINSSON. The ontogeny from instar 4 to adult. Magnification 40 ×. Fig. 28. Female. No. G 167.

Fig. 29. Male. No. G 168.

Fig. 30. Instar 2. No. G 169.

Fig. 31. Instar 3. No. G 170.

Fig. 32. Instar 4. No. G 171.

Clavofabella reticristata (JONES). The ontogeny from instar 4 to adult. Magnification 40 ×. Fig. 33. Adult specimen with rudimentary dolon; female. No. G 122.

- Fig. 34. Adult female. No. G 172.
- Fig. 35. Instar 2. No. G 173. Fig. 36. Instar 3. No. G 174.
- Fig. 37. Instar 4. No. G 175.

Leiocyamus apicatus n. sp. The differences in shape and size of the two valves.

- Fig. 38. Left valve. Inner side, magnification $55 \times$. Outer side, magnification $40 \times$. No. G 176.
- Fig. 39. Right valve. Inner side, magnification $55 \times$. Outer side, magnification $40 \times$. No. G 177.

Leiocyamus apicatus n. sp. Magnification $25 \times$.

Fig. 40. Female. Holotype, No. G 178.

Fig. 41. Male. No. G 179.

Plate V

Leiocyamus apicatus n. sp. Magnification $25 \times$.

Fig. 42. Larva (instar 2?). No. G 180.

Thlipsurella discreta (JONES). Magnification $40 \times$.

- Fig. 43. Adult. Both left (the centre figure) and right valves depicted. No. G 181.
 - Fig. 44. Instar 2. No. G 182.
 - Fig. 45. Instar 3. No. G 183.
 - Fig. 46. Instar 4. No. G 184.
 - Fig. 47. Adult, hingement and margin of right valve. Not treated with ammonium chloride. No. G 185.
 - Fig. 48. Adult, hingement and margin of left valve. Not treated with ammonium chloride. No. G 186.

Specimens collected by G. LINDSTRÖM and described by T. R. JONES in 1887 and 1888.

- Fig. 49. Thlipsurella discreta (JONES). Syn. Thlipsura v-scripta var. discreta JONES 1888. Right valve, lectotype. RM no. Ar 25726:10. Magnification 40 ×.
- Fig. 50. Bolbiprimitia inaequalis (JONES). Syn. Primitia seminulum JONES 1888, Pl. XXII, Figs. 20a-c. Instar (3), right valve. RM No. Ar 25697:3. Magnification 20 ×
- Fig. 51. Bolbiprimitia inaequalis (JONES). Syn. Entomis inaequalis JONES 1888, Pl. XXII, Figs. 17a-b. Adult female, right valve. Lectotype. RM No. Ar 25697:1. Magnification 20 \times .
- Fig. 52. Primitiops is planifrons var. ventrosa JONES 1888, Pl. XXII, Figs. 19a-c. RM No. Ar 25724:4. Magnification 25 \times .
- Fig. 53. Clavofabella reticristata (JONES). Syn. Primitia reticristata JONES 1888, Pl. XXII, Figs. 15a-b. Female. Lectotype. RM No. Ar 25697:5. Magnification: 53 0 40 ×; 53 l, v, and d $25 \times$.









