

I. Studies on the Ostracode Family Primitiopsidae

By

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ABSTRACT.—A sample of Primitiopsidae from the Mulde marl, probably uppermost Wenlockian of Gotland, is studied. Moulting and growth of *Primitiopsis planifrons* JONES are recorded. A new genus, *Clavofabella*, and two new species, *C. multidentata* and *C. incurvata*, are described. The material as background for a study of population dynamics is briefly discussed. A taxonomic survey of the *Primitiopsidae* is given.

Introduction

This research was started in order to study the pretended trimorphism of *Primitiopsis planifrons* JONES. As far as the material has allowed, however, it has been used to elucidate the ontogeny and taxonomy of this and allied species in the population investigated.

Primitiopsis planifrons was described by JONES (1887) on material from Fröjel, Gotland, collected by G. LINDSTRÖM in a sediment commonly known as the Mulde marl. According to HEDE (1942, p. 19), the Mulde marl probably constitutes the uppermost Wenlockian of Gotland and corresponds in age to the *Cyrtograptus lundgreni* zone of the British graptolite sequence. JONES depicts (op. cit., p. 5) a specimen of the type which has later been considered to be the female, and which is provided with a terminal pouch. HENNINGSMOEN (1954, p. 59) suggests that the specimens of *Primitia valida* JONES & HOLL recorded by JONES from Fröjel (op. cit., p. 4; 1888, p. 405), are identical with the type of *Primitiopsis planifrons* which BONNEMA (1935) suggested to be the male, and in which the terminal pouch is missing.

As a dimorphic species *Primitiopsis planifrons* first appears in ULRICH & BASSLER (1923, pp. 278, 300, Fig. 15) where both sexes are depicted.

In HENNINGSMOEN'S paper quoted above (1954, p. 59) it is stated that *Primitiopsis planifrons* is a trimorphic species. This conception was founded upon the fact that in material from Mulde, which was examined by HENNINGSMOEN, three types of reticulate *Primitiopsidae* were represented, viz. (1) male specimens, corresponding to *Primitia valida* in JONES'S material of 1887 from Mulde and the male specimen of *Primitiopsis planifrons* depicted by ULRICH & BASSLER 1923, (2) female specimens corresponding to the pouch-bearing specimen of *Primitiopsis planifrons* JONES 1887, and (3) specimens with a narrow posterior frill, corresponding to *Primitia reticristata* JONES which was described on material from Fröjel, Gotland (JONES 1887, p. 5; 1888, p. 406, Pl. XXII Figs. 15 a, 15 b, 15 c).

The establishment of trimorphism in fossil ostracodes would, of course, have far-reaching consequences for the limitation of species. Therefore, following a suggestion of Dr. V. JAANUSSON, Uppsala, the author has undertaken this study on *Primitiopsis planifrons*.

Possible causes of trimorphism would in this case be the occurrence of juvenile dimorphic characters in a subadult instar as suggested by HENNINGSMOEN, or the occurrence of parthenogenetic females in a syngamic population—this especially if the dimorphic differences have played a part in the copulation (cf. HESSLAND 1949, pp. 127, 128). A third cause of polymorphism would be the occurrence of different types with different ecological preferences within the sex, as has been demonstrated by FORSMAN (1949 and earlier) and BOCQUET (1953) in the recent asellote isopode *Jaera albifrons* LEACH. It is interesting to note that TRIEBEL (1941, p. 362) discusses ecological differences between the sexes of a species, on the base of actual conditions among recent ostracodes. It is hardly possible, however, that the two latter alternatives would explain the differences in carapace morphology which are exhibited in HENNINGSMOEN'S two female types of *Primitiopsis planifrons*.

With this background it was important to reconstruct the ontogeny of

the species and the appearance of dimorphic characters during the ontogenetic development. Already here it should be anticipated that male types corresponding to HENNINGSMOEN'S subadult female type were recognized already at an early stage of the present investigation. Further examination proved that within this type were contained three related, though clearly distinguished species, forming the new genus *Clavofabella*.

Material and Methods

The material from the Mulde marl used in this study was collected by Dr. V. JAANUSSON at the Mulde brickyard, parish Fröjel, Gotland. Dr. JAANUSSON reports that the marl in the steep slope had evidently been affected by recent solifluction. The sample was not taken for statistical treatment or study of ostracodes at all, but obviously the movements in the marl or the way of collection have not caused any contamination of it. When the present author received the material it consisted of the shelly sand and gravel fractions, while all particles less than 0.125 mm were sifted off.

Material from the same locality has been treated in two of the papers frequently quoted here, SPJELDNAES (1951) and HENNINGSMOEN (1954); furthermore the reticulate *Primitiopsidae* described by JONES (ll.cc.) originated from Fröjel.

Of this material one fourth—mentioned below as “sample Q”—was used for simple statistical treatment to show the moulting stages. To avoid the sampling error—due to sorting—which occurs when decanting an unsorted sand or gravel mass, the material was sifted into 5 fractions, and a fourth of each of these was examined. The shelly sand—the gravel fraction did not contain any ostracodes—was thinly spread over the bottom of a low tray, which was divided into 1 cm² squares, and all ostracodes were picked out under the microscope at convenient magnification. The ostracodes were individually orientated and mounted on a thin strip of plasticine upon a microscopic slide. Three measures were taken of each individual, viz. the total length of the animal parallel to the hinge line, the height of the animal closely behind the adductorial pit and at right angle to the hinge line, and the distance between the centre of the adductorial pit and the extreme anterior end of the animal (the preadductorial distance). The width of the carapaces was not considered, as particularly many of the adult specimens of *Primitiopsis planifrons* were so compressed that the width records were judged to be considerably affected. The measuring was performed at an approximate magnification of 72×. At this magnification the Leitz scale used in the ocular micrometer allowed a technical exactness of $\pm 4.5 \mu$. The size of the ostracodes ranges from 370 μ to 1440 μ . Altogether 922 carapaces or valves were measured to illustrate the ontogeny.

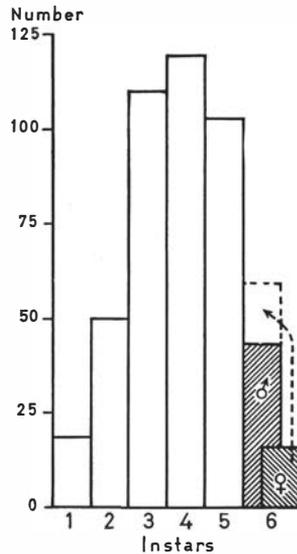


Fig. 1. Distribution of the different instars in the sample of *Primitiopsis planifrons* examined. Dolonate specimens set down as females, non-dolonate adult specimens as males.

The rest of the total sample—mentioned as “sample T” in the diagrams and below—was used for the photographical illustrations and a special study of the female types of the *Clavofabella* species (Fig. 2, C).

The measured animals, represented by entire carapaces or left valves, were plotted on scatter diagrams (Fig. 2). Measurements of right valves have not been considered in diagrams and tables, but the number of right valves in each instar is given in Table 1 to indicate the number of separated carapaces among the complete ones.

As stated above there is no reason to believe that the way of collection, nor the sifting-off of the finest sediment fractions, has made the sample unrepresentative. This assumption is further confirmed by the completed diagram. An instar preceding to the first one in Fig. 2, A would not have escaped representation. The instars are so distinctly limited that there is no reason to suggest allochthonous contamination from another population.

Concerning the representation of the population, however, there are two facts which attract attention. The different instars are represented in proportions which give a curve with its top to the right of the range midpoint. It cannot be excluded that this depicts a normal deposition of moults or dead bodies from an ostracode population, but also a sorting by currents or waves in connection with the original deposition might have given the same results. Secondly, the rate of the traditional male type versus the female is the opposite to what would be expected in most cases where one sex dominates. These facts are illustrated in Fig. 1, and will be further discussed below.

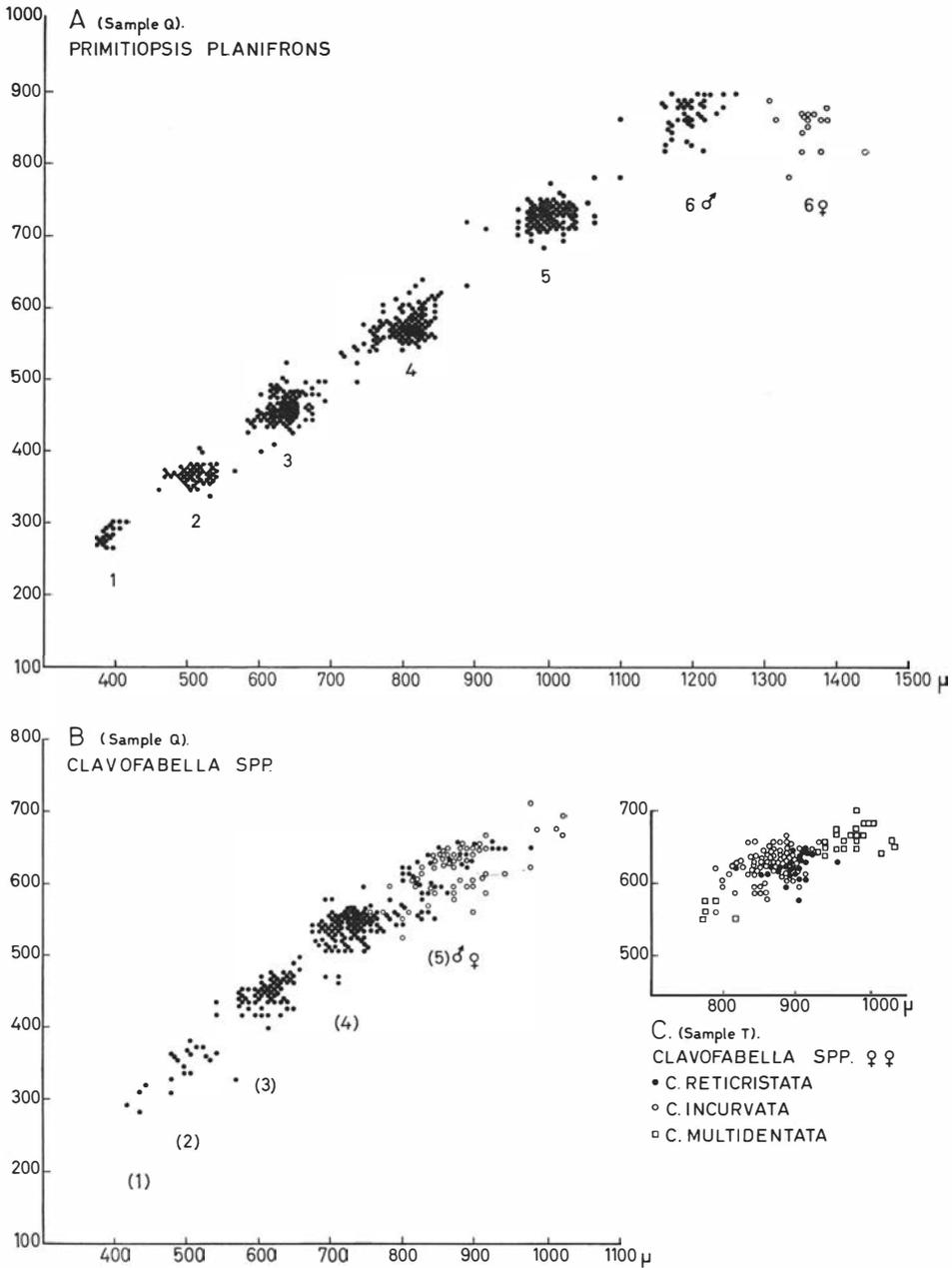


Fig. 2. Diagrams showing size and distribution in instars of the *Primitiopsidae* examined. *A.* *Primitiopsis planifrons*. *B.* The other components of the population of *Primitiopsidae*, i.e. the genus *Clavofabella* n. gen. *C.* Dolonate specimens of the three *Clavofabella* species.

Legend.—In *A* and *B* dolonate specimens are plotted as circlets, non-dolonate as dots. For *C* a special legend is given under the diagram. Established instars are indicated with figures. Dolonate instars set down as females, non-dolonate adult instars as males. Measures in microns; length along the abscissa, height along the ordinate.

The *Primitiopsidae* of the Mulde marl form part of a rich and well-preserved ostracode fauna. In addition to the quoted papers by JONES (1887, 1888), SPJELDNAES (1951), and HENNINGSMOEN (1954), ostracodes from the Mulde and Fröjel marls have been described by KOLMODIN (1869), VON KIESOW (1888, cursorily), CHAPMAN (1901), BOTKE (1916), KUIPER (1916), BONNEMA (1935), and HENNINGSMOEN (1953). HEDE (1917, 1920, 1927 a, b) has described the sediment and listed its fauna.

Terminology

The terminology used in the following discussion and descriptions adheres as much as possible to already established practice. For some details of ostracode carapaces, however, unambiguous and significant terms do not exist. The terms used and proposed in this paper have been discussed or coined in collaboration with Dr. JAANUSSON, at present studying Middle Ordovician ostracodes.

The common terms as *carapace*, *valve*, *hinge line*, *anterior* and *posterior corner*, and *dorsum*, are used in their traditional sense as defined by KESLING (1951 b). The term *domicilium*, introduced by KESLING for the *Primitiopsis*-like genus *Sulcicuneus* (1951 a), is given a more widely applicable sense than in KESLING's terminological paper (1951 b), viz., to signify the part of the carapace enclosing the body of the animal, but excluding any kind of ornamental extensions of the valves, e.g. the *Primitiopsis* pouch. The external pit-like impression of each valve, corresponding to the insertion of the adductor muscles on the inside of the valve, is termed the *adductorial pit*. Where the lateral surface meets the dorsum, an ornamental thickening of the valve is formed, protruding over the hinge line as a *dorsal ridge* (cf. Fig. 3 and HENNINGSMOEN 1953, Fig. 2:5).

The sense of *velar structures* principally follows HESSLAND (1949, definitions also in KESLING 1951 b). Adjectives corresponding to the *velum* should be *velar* (Lat. *velaris*: belonging or referring to the velum) and *velate* (Lat. *velatus*: provided with a velum). To use the latter adjective in both senses, as introduced by HESSLAND (1949), seems to be less advisable linguistically.

In the family treated the velar structures are usually developed as a rather low *velar ridge* along the *free edge* (KESLING 1951 b) of each valve, and separated from this edge by the *subvelar area* as defined below. The part of the velum supplying the dimorphic characters in adult specimens is termed the *dolon* (Lat. *dolo[n]*, from Gr. *δόλον*: a kind of sail). Adjectives: *dolonal*, *dolonate*, *non-dolonate*, etc.

Along the non-dorsal contact line of each valve a row of ornamental *marginal structures* is developed. These structures can be *spines*, *denticles*, or *tubercles* (cf. KESLING 1951 b), or may form a coherent *marginal frill*, developed morphologically as a row of webbed spines.

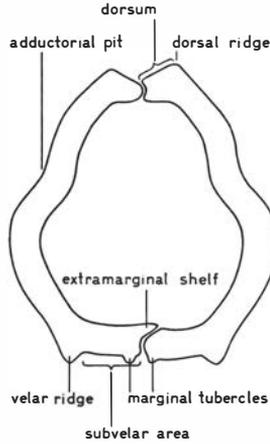


Fig. 3. Schematic transversal section, caudal view, illustrating some morphological terms used in the text.

In the family treated the overlapping part of the right valve covers a narrow shelf of the left valve; as this shelf is situated outside the marginal structure of the single valve, it has been termed the *extramarginal shelf* (Fig. 3).

The area between the velum, or the dolonal part of the velum and the free edge of each valve, is termed the *subvelar* and the *subdolonal* area respectively.

The *lateral outline* of a valve signifies the silhouette of the valve seen in lateral view, marginal structures not included. When the dorsal ridge protrudes over the hinge line, the former thus forms part of the lateral outline. All measurements in this paper are based on points on the lateral outline. As the state of preservation of the marginal structures is very varying in different valves or carapaces, an inclusion of these structures in the conception of the lateral outline is less desirable.

Orientation

The orientation of fossil ostracode carapaces has been subject to much discussion. A representative summary of the general features of this discussion was given by KESLING (1951 b); a very important reconsideration of the value of different morphological characters for determining the orientation, with numerous comparisons with recent forms, was made by TRIEBEL (1941). As far as the discussion has touched upon the *Primitiopsidae* it will be summarized here.

JONES and contemporary palaeontologists generally regarded the thicker and blunter end of the carapace as the posterior. From the pictures of

Primitiopsidae published by JONES (1865, Pl. XIII: 1, 2, 3; 1886, Pl. XIV: 4, 7, 8; 1887, p. 5; 1888, Pl. XXII: 14, 15, 18, 19) can be deduced that he followed this principle in the case of *Primitia* (here *Clavofabella*) *cristata* and *P. reticristata* as well as of *P. tersa* and *P. umbilicata* (obviously non-dolonate types of *Clavofabella cristata*), furthermore in *P. valida* sensu JONES 1887 and *P. grandis* (non-dolonate types of *Primitiopsis planifrons*). The first depicted *Primitiopsis planifrons* was orientated by JONES in the opposite way with the blunter pouched end as the anterior (cf. the specific name *planifrons*). Consequently *Primitiopsis* was regarded as having an anterior dolonal pouch, whilst the dolonal flange of species referable to *Clavofabella* was considered to be posterior. As was later the case in TRIEBEL's (1941) argumentation, JONES (1888, p. 407) founded his conception on an analogy with the recent *Chlamydotheca*.

ULRICH & BASSLER (1923, pp. 298–299) orientated adults of both sexes of *Primitiopsis planifrons* with the blunter end, pouched in the dolonate type, as the posterior. The applicable feature in the principles of orientation in ULRICH & BASSLER (1923, p. 285) is—beside the fact that the carapace is widest behind—the presumption that the dolonal pouch—regarded as a brood pouch—should be associated with the posterior part of the carapace.

In the protracted discussion and polemics between BONNEMA and KUMMEROW on the orientation of ostracodes, *Primitiopsis* was repeatedly discussed. BONNEMA (1933 a, p. 35) regarded the dolonal pouch as a brood pouch, which must be localized at the posterior part of the carapace, “denn sonst würden sie beim Öffnen der Schale wegen der Nähe der Antennulae und Antennae weniger gut für die Aufbewahrung der Brut dienen können”. The insertion of the adductor muscles would, if this orientation is accepted, be situated on the anterior half of the valve. KUMMEROW (1923, p. 425) gave the species the same orientation, but regarded the dolonal space as separated by a wall within the carapace, while BONNEMA (l.c.) emphasized the non-domiciliar character of the pouch. Apart from *P. planifrons*, BONNEMA and KUMMEROW discussed a species named *P. oblonga* (JONES & HOLL) sensu KUMMEROW (1923, p. 424). It was checked by these two authors that they discussed the same species; this can, however, not possibly be identical with the *Primitia oblonga* pictured by JONES & HOLL (1865, Pl. XIII: 14). The interested reader can follow the discussion from a last paper by BONNEMA (1938) and backwards through numerous papers.

In his thorough revision of the orientation of fossil ostracodes, TRIEBEL (1941, p. 358), dealing with *P. oblonga* sensu KUMMEROW (l.c.), came to the conclusion that the *Primitiopsis* pouch is anterior. This thought was founded on analogies with *Chlamydotheca rudolphi* TRIEBEL, which has an anterior pouch. But on applying the general principles for orientation given by TRIEBEL (op. cit.), as the adductor attachment and the swing of the carapace the pouch must be regarded as posterior.

HESSLAND (1949, pp. 239, 240) adopted JONES's and TRIEBEL's idea of an anterior pouch. KESLING (1951 b, p. 104; cf. GEIS 1932, p. 153) stated a posterior dimorphism. HENNINGSMOEN (1953, p. 230) adds the essential observation that during the ontogenetic development the adductor pit migrates towards the non-dolonate end, as the adductor muscle scar migrates forwards in recent ostracodes.

For the illustration of this migration, the present author has used a *preadductorial index*, expressing the preadductorial distance as percentage of the total length. The results are given in a column of Table 1. Closely similar methods have been used by KESLING (1951, Chart 1) on the recent *Cypridopsis vidua*, and by SPJELDNAES (1951, p. 754) on *Beyrichia jonesi*. In contrast to CLAUS (1872), KESLING (l.c.), and the present author, SPJELDNAES (l.c.) obtained an allometric and increasing index, the latter due to his premise that the brood pouches of *Beyrichia* are situated posteriorly. On the evidence of this sulcal migration, in addition to the arguments in TRIEBEL (op. cit.), *Beyrichia* ought to be orientated opposite to what has been done by SPJELDNAES (op. cit., except Pl. 103:7; cf. HENNINGSMOEN 1953, p. 196; 1954, p. 18).

From the preceding discussion it can be concluded that the dolon of the *Primitiopsidae* is posterior. The increase of the blunter post-adductorial part of the carapace, which most probably contained, *inter alia*, the voluminous reproductive organs, is illustrated by the decreasing preadductor index. To this should be added the evidence of the forward swing of the anterior part of the lateral outline. The hydrodynamic probability of a posterior location of the rudder- or pouch-like dolon ("gerichteter Fortsatz" in the widest sense of TRIEBEL 1941), however, cannot be considered as a reliable argument for orientation in this case, as the dolon is situated anteroventrally in most related forms. For connection of the orientation with other fossil forms, the existence of a rudimentary preadductorial node may be helpful (see discussion in the taxonomic chapter).

Larval Development and Growth Factors

The results of the measurements are given in Fig. 2.

In the material 6 instars of *Primitiopsis planifrons* have been proved to exist (Fig. 2, A). The diagram suggests that an instar preceding the youngest one indicated would not have escaped representation in the material.

Specimens diverging from *Primitiopsis planifrons*, comprising the type which suggested to HENNINGSMOEN (1954) the belief in a trimorphism of the species, were recorded separately. Due to the reticulation of the carapace and to the development of the dolon, these types seem indeed on cursory examination to form a homogeneous population with *Primitiopsis planifrons*. Also the non-

Table 1.

Growth of *Primitiopsis planifrons* JONES. All calculations based on values in scale divisions (113 sc.d. = 1 mm) which are not included in the table. Sizes of the instars are given in the text. Values affected by the presence of the dolonal pouch are given in brackets.

Instar	Number		Linear growth factors				Pre-adductorial index	Increase of post-adductorial distance %
	Entire carapaces and left valves	Right valves (not considered in growth calculations)	Length		Height			
			Mean	Median	Mean	Median		
1	19	1	—	—	—	—	53.2	—
2	50	0	1.30	1.30	1.26	1.29	51.4	4
3	110	6	1.24	1.26	1.24	1.25	51.0	1
4	119	13	1.26	1.26	1.20	1.24	49.8	2
5	103	6	1.14	1.23	1.32	1.29	48.7	2
6 ♂	43	0	1.19	1.19	1.19	1.20	47.5	2
6 ♀	16	2	(1.36)	(1.36)	1.17	1.17	(41.6)	(11)
Total	460	28	—	—	—	—	—	—

dolonate types are, however, easily distinguished from *Primitiopsis planifrons*. The development of the dolon and of the velar ridge refers these specimens to a distinct genus, *Clavofabella*. The specimens in question are plotted on a scatter diagram (Fig. 2, B). The dots are distributed in five groups. As the first of these groups contains only four specimens, the possible existence of a smaller instar cannot be excluded.

The measuring of the dolonate *Clavofabella* types proved these to be divided into three units, with a good co-variation in the development of dorsum, velar ridge, marginal structure, and certain features in the ornamentation within each unit. A special sample of 123 specimens proved a good co-variation also in size (Fig. 2, C). Also the non-dolonate types were distinguished. The three species, *Clavofabella reticristata*, *C. multidentata*, and *C. incurvata*, will be treated below.

PRZIBRAM (1931, p. 26) supposed a doubling in weight of each arthropode instar, corresponding to a linear increase in size for each moult of 1.26. This rule has been applicated to several populations of recent ostracodes (see summary in SOHN 1950, p. 430; cf. SKOGSBERG 1920; KESLING 1951 c; KEY 1954). For fossil populations the growth factor has been calculated by COOPER (1945), SOHN (l.c.), SPJELDNAES (1951), and KESLING (1952 a). Generally the empiric results correspond to PRZIBRAM's theoretical ones ("BROOKS's law"). SOHN (op. cit., p. 429, requotation) was of the opinion "that there can be molting without growth, growth without molting" (*sic*), and that he "would guess that in fossil ostracodes there probably were molt stages after maturity was reached".

The present material furnishes no evidence that moulting has occurred with growth rates differing considerably from PRZIBRAM's value. Specimens falling considerably outside the concentrated groups of dots were often obviously monstrous. To avoid the bias of such specimens, also the median linear growth of each instar, based on values read from the primary large-scale diagrams, is recorded in Table 1.

This single series permits no opinion on the possible significance of the sudden decrease of length growth preceding instar 5, corresponding to an increase of the growth in height. The increase in size preceding the adult instar 6 is slightly less than in the younger instars (1.19; height increase in dolonate specimens 1.17).

Dimorphism

The dimorphic character of the *Primitiopsidae* is the posterior dolon. In the genus *Clavofabella* the dolonal edges of the two valves are free, while in *Primitiopsis* they are in close contact with each other, so that a pouch is formed.

This pouch has generally been regarded as a brood pouch. Inside the pouches formed by the domiciliar wall in *Beyrichia*, carapaces of small specimens, regarded as brood, have been found (HESSLAND 1949, p. 124, Pl. XIV: 9; SPJELDNAES op. cit.). In a few sections made through the *Primitiopsis* pouch by the author only calcite crystals were to be seen.

If there has existed an extradomiciliar brood care in *Primitiopsis*, this can hardly have functioned without any structures in addition to those which have been fossilized. As TRIEBEL (1941, p. 351) has pointed out, the mere fact that the brood would fall out when the carapace was opened, is an argument against the concept of a brood pouch. But provided that the brood would reach the pouch, the possibilities of adherence or active clinging hardly seem to be excluded.

In the present material adult specimens of *Primitiopsis planifrons* have been sufficiently numerous for the establishment of a sex quotient. In doing so 43 non-dolonate "males" have been found against 14 dolonate "females" (see Table 1 and the histogram in Fig. 1). If these proportions are representative for the species, they call for a revision of the traditional concept of the dolonate specimens as the females. I abstain, however, from basing any conclusion on this single sample. In the figures dolonate specimens are entered as females, non-dolonate ones as males. It should be added that the brittle dolonate specimens are more likely to be destroyed than the non-dolonate ones, thus becoming under-represented in the sediment. It is not probable that the dolonate specimens are the result of a moulting without increase in size of the non-dolonate adult specimens (cf. previous discussion). The risk of sorting of the sediment, as mentioned above, is also to be considered in this connection.

It has been suggested that in mature ostracodes no moulting takes place (cf. summary in SOHN 1950). Against this conception SOHN (1950) has raised objections.

HENNINGSMOEN (1954) suggested—which was one of the starting-points for this study—that subadult females could be distinguished in *Primitiopsis planifrons*. As has been anticipated above, these females have proved to be *Clavofabella* species.

Among the present material no specimens have been found which show transitions to the dimorphic characters of the adult ostracodes. No suggestions of post-adult moulting have been indicated. In *Primitiopsis planifrons*, *Clavofabella incurvata*, and *C. reticristata* all dimorphic specimens belong to the last instar indicated.

On the other hand there are among the material specimens which show all characters of dolonate specimens of *Clavofabella multidentata*, apart from the size which closely corresponds to the last but one instar. The increase in size between these specimens and the adult dolonate specimens corresponds to an empiric growth factor of 1.25, thus corresponding almost exactly to the theoretical values quoted above. The phenomenon can hardly be explained otherwise than as a realization of the trimorphism—taken in HENNINGSMOEN'S very wide sense of the word—which was suggested by HENNINGSMOEN for *Primitiopsis planifrons*. As the two groups of dolonate specimens are essentially alike, except in size, I hesitate to use the word trimorphism in this case. Dimorphic specimens of a size corresponding to the last but one instar were reported also by SPJELDNAES (1951, p. 751) in *Beyrichia jonesi*.

Without knowing whether the subadult dimorphic specimens have been fossilized as carapaces shed in moulting or as dead bodies, it is impossible to assert whether or not they were destined to moult once more in order to reach adult size.

Population Dynamics. Animal Necrocoenoses and Arthropode Pseudocoenosis

With regard to what has been dealt with above some aspects of the fossilization of an ostracode population ought to be briefly discussed.

In the two existing investigations of fossil ostracode populations which are based on a very large material, viz. that of *Beyrichia jonesi* (SPJELDNAES 1951), and that of *Primitiopsis planifrons* by the present author, the instars are represented in essentially different ways. *Beyrichia jonesi* shows a high number of individuals of the youngest instars—except the very youngest ones which were observed in brood pouches or were supposed to have been destroyed—and a gradually decreasing number of the following. In *Primitiopsis planifrons*, on the other hand, the youngest and oldest instars are considerably scarcer than the intervening ones.

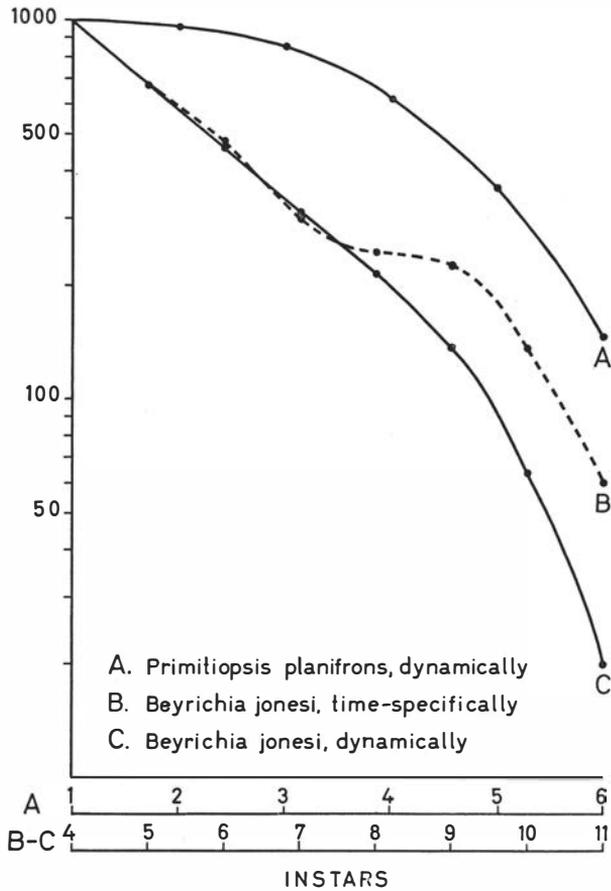


Fig. 4. Survivorship curves for the ostracodes *Primitiopsis planifrons* and *Beyrichia jonesi* as contained in samples from the Mulde marl. Discussion in the text. Data for the curves B and C from SPJELDNAES 1951 and KURTÉN 1953.

In his discussion of the *Beyrichia* population from Mulde SPJELDNAES (op. cit., pp. 750-751) draws a parallel between his material and an application of recent *Limulus* moulting to fossil Merostomata, made by STØRMER (1934, p. 57). This proves that dead specimens are to a great extent destroyed by scavengers, while the well preserved exuviae are left intact. SPJELDNAES therefore came to the conclusion that the fossil complete carapaces are likely to represent mainly exuviae.

KURTÉN (1953; 1954) has introduced the study of population dynamics into palaeontological work, especially with respect to mammals. In these papers, SPJELDNAES' *Beyrichia* population is discussed and compared with mammalian populations.

As a descriptive background for the study of population dynamics life tables and survival curves are constructed. KURTÉN (1953, p. 47) refers to

three different ways of constructing a life table. The *dynamic method* summarizes survival and mortality of a given cohort over a period of years (horizontal life table of DEEVEY 1947). The *time-specific* (= vertical) *life table* is established on census data from a single period of observation. The *composite life table* is drawn up dynamically or time-specifically after census or mortality data for different periods or different populations. The data are recalculated to an original cohort of e.g. 1000 or 100 individuals, and the numbers of survivors in the age groups are plotted as a semilogarithmic survivorship curve (Fig. 4). In the treatment of the *Beyrichia* population it was presupposed that age is expressible by moults. KURTÉN (1953, p. 51) points out that if the *Beyrichia* specimens largely consist of exuviae, a time-specific interpretation seems to be the correct one. In the survivorship curve the age along the abscissa would also be expressed as percentual deviation from mean longevity (cf. KURTÉN 1954, Fig. 1).

Only the dynamic curve can suit a distribution like the present one of *Primitiopsis*. Such a curve is plotted in the diagram (Fig. 4) for comparison.

Although the curve published by SPJELDNAES (1951, Fig. 2 A) corresponds to what would be logically expected for every way in which an autochthonous fossilization of the ostracodes has taken place, the other few curves published, based on fossil ostracode populations, are of the same type as that given here, with the maximum in an intermediate instar (cf. COOPER 1945, Fig. 1; SPJELDNAES 1951, Fig. 2 B-D; KESLING 1952 b; furthermore SKOGSBERG'S Mediterranean collection of *Krithe* sp., 1920, p. 144, where empty valves and living specimens were considered; and the collection of dead *Payenborchella* in KEY 1954. In all these investigations there has been an urgent interest to examine as many specimens as possible for each instar). Though we must presume a dominant probability that the curves are not representative for the production of fossilizable carapaces or valves in the different populations, an opportunity is given to discuss briefly the fossilization of an animal community.

A *vertebrate biocoenosis* is represented as fossils by the fossilizable parts of animals perishing at different ages. In KURTÉN'S papers the possibilities of determination of the absolute age in fossil mammals are beautifully demonstrated. In order to obtain the original cohort of a population—whether for a simple or a composite life-table—we must sum up the animals perishing in the different age intervals. If these are available as fossils, we have, in principle, material for a dynamic treatment, provided that “normal” factors have caused the death. If a population has perished simultaneously (cf. KURTÉN 1953, p. 48) the dead animals represent the animals living at the very moment of the catastrophe, and consequently a time-specific curve should be used.

In the sense of WASMUND (1926), the preserved remains of a biocoenosis constitute or form part of a dead community, termed *thanatocoenosis*. HESSLAND (1943) in his

paper on the marine shell deposits of Bohuslän used the term *necrocoenosis*, stressing that the fossils concerned originated from dead bodies. This is always the case as far as the communities are constituted by vertebrates, echinoderms, brachiopods, molluscs, corals, etc.

The fossils from an *arthropode biocoenosis* would also represent dead animals of different age intervals, a *necrocoenosis* proper. An autochthonously fossilized ordinary population would theoretically afford material for a dynamic analysis; as in the case of vertebrates a simultaneous death of the population would supply material for a time-specific treatment (for ostracodes this has been suggested to be the case e.g. in connection with the ash-rains of bentonite sedimentation; cf. THORSLUND 1948, pp. 346, 356–357). But, in addition, the exuviae from each moult are likely to be fossilized, which in many papers is regarded as the most important way of arthropode fossilization. The fossils formed in this way do not constitute a necrocoenosis, but a fictitious image of a biocoenosis which may be termed a *pseudocoenosis*.

A necrocoenosis—either autochthonous or allochthonous—is thus constituted by individuals, while the pseudocoenosis is constituted by parts shed by the individuals during life. The consequences for every work on arthropode palaeosociology, which is based on quantitative calculations, are evident. The thanatocoenosis in the sense of WASMUND seems to cover both kinds of fossil communities.

Optimally an arthropode individual may be fossilized pseudocoenotically as many times as it moults. The pseudocoenosis sums up in a composite picture all living specimens which have existed in all the different instars during the space of time covered by the biocoenosis which is contained in the sediment in question. In contrast to the necrocoenosis, the pseudocoenosis thus offers material for a time-specific treatment.

This has to be taken into consideration when constructing the descriptive basis for further study of population dynamics. In most cases, unfortunately, it is extremely difficult to determine whether the arthropode fossils have been preserved necrocoenotically or pseudocoenotically. In SPJELDNAES's paper on *Beyrichia jonesi* the latter case was supposed; consequently the time-specific presentation, as favoured by KURTÉN (1953, p. 51), ought to be given preference.

These considerations concern the ordinate in a diagram of arthropode survivorship. Concerning the abscissa, i.e. the age of the animals, some notes should be added.

In the exquisitely made determinations of age in fossil mammals (KURTÉN 1953) essentially absolute age is obtained. In the treatment of ostracodes (KURTÉN 1953, p. 51) or other arthropodes, relative age, indicated by moulting stages, seems to be useful as a substitute. This is also the case as far as the animals are to be grouped in age intervals without respect to the relations of duration of the different instars.

During the ontogeny of arthropodes, however, the intervals between moultings increase continually. The example of the lobster is well known from every handbook; for ostracodes the same is demonstrated e.g. by ERNA SCHREIBER (1922, p. 506; unfortunately in as long units as days) and ELOFSON (1941, pp. 395–397). Presuming that the death rate of the population is constant throughout time—which is certainly very seldom the case—e.g. in a population of *Cypris incongruens* (figures from SCHREIBER l.c.), four times as many specimens die in the last larval instar as in the first; in the last instar dies the rest, the adult specimens, without further moulting, after shorter or longer time. In any comparison with a population, the absolute age of which is considered, there will be a heavy over-representation in the older groups.

In a mammal, e.g. *Homo sapiens* (though his survivorship curve is biased in many respects by civilization), the climax of the life span is reached after a more or less lengthy adolescence, and death mostly ensues after a considerable period of senescence. In an arthropode, on the other hand, the climax—i.e. reproduction—may fall within the last instar, as is the case with the ostracodes or, more extremely still, with most insects, the last instar of which often comprises a very short portion of the life. This gives *a priori* an altered meaning to the terms “mean longevity” and “expectation of life” when used about arthropodes instead of about mammals.

These facts must be considered when establishing a descriptive frame for the study of fossil arthropode population dynamics, especially if comparison is made with populations with essentially different life rhythms. Within this frame all the death factors, constant, varying with time or size, or setting in suddenly during the life span of the populations, may be considered. The possibilities of theoretical construction are innumerable. As investigations concerning fossil ostracode populations, except those considered here, are still lacking, no base for further analysis is available.

Finally, the sample which is taken out of a fossilized population may cover a period which comprises less than one, or a few, generations, or it may contain a long sequence of generations. In the former case occasional situations in populations with periodical fluctuations (cf. KURTÉN 1953, p. 48) will be depicted in a population curve, in the latter case an equalization will have taken place. Here another unknown factor presents itself, the rate of sedimentation.

In an ostracode necrocoenosis we thus get a curve with a heavy over-representation in the latter instars, which may be supposed in certain cases to dominate the curve. In a pseudocoenosis—or a combination of a necrocoenosis and pseudocoenosis—the curve is likely to drop from a maximum in the first instar.

Most certainly the greater part of the animals dying before maturity are victims of predation, and are withdrawn from fossilization. One instar we

know to be preserved necrocoenotically, i.e. the adult one, in which moulting is not known in ostracodes (cf. previous discussion).

Although there is a slight possibility that the *Primitiopsis planifrons* curve would fit a necrocoenotic concept of deposition, there are no indications that the moults are not included as fossils. It is hardly to be expected that the younger instars of this thick-shelled species should be considerably less capable of preservation. Though there is no base for a conclusion, the curve seems to have been affected by sorting in some way.

Taxonomy

Order *Ostracoda* LATREILLE 1802

Suborder *Palaeocopa* HENNINGSMOEN 1953

Superfamily *Beyrichiacea* ULRICH & BASSLER 1923

Family *Primitiopsidae* SWARTZ 1936

The diagnosis given by SWARTZ (1936, p. 555) fits well the present concept of the family. The reservation that the terminal dolonal flanges may not meet is here applied on the genus *Clavofabella* n. gen.; SWARTZ's reservation applied to *Primitiopsis oblonga* sensu KUMMEROW 1923 (cf. p. 19). At first HENNINGSMOEN (1953, pp. 231, 263, with diagnosis) ranked the *Primitiopsidae* as a subfamily (*Primitiopsinae*), later as a family (1954, pp. 52, 59).

DIAGNOSIS.—Posterior velar dimorphism, characterized by dolonal flanges, which may or may not meet to form a closed chamber. No other adventral structures present. One valve overlapping. Hingement simple.

GENERA.—The definition given here covers the known genera *Primitiopsis* JONES 1887, *Clavofabella* n. gen., and *Sulcicuneus* KESLING 1951.

REMARKS.—Immediately in front of the adductorial pit of *Primitiopsis* and *Clavofabella* a marked impression is situated upon the inner side of the valve, and not discernible on the outer side (Fig. 6). In many other palaeocope ostracodes a preadductorial node (presulcate node, HESSLAND 1949) on the outer side of the valve corresponds to a similar interior impression, giving another basic argument for orientation.

HESSLAND (1949, p. 207), accepting the analogies and the principles of orientation of *Primitiopsis* given by TRIEBEL (1941, p. 358) rejects, under such circumstances not without consistency, the high taxonomic value of the dolonal pouch. These arguments lose their meaning with the opposite orientation of the carapace, without respect to the possible function of the dolonal pouch.

Beside *Primitiopsis* and *Clavofabella* a few other genera have been referred to the family *Primitiopsidae*. KAY (1940, p. 262) includes the genus *Primitiella*, which does not, however, show the characteristic dimorphism of the family.

KAY favoured the concept of an anterior pouch in *Primitiopsis* and consistently applies the same orientation in *Primitiella* (cf. discussion in HESSLAND 1949, pp. 207, 240, where the fact that HESSLAND orientates *Primitiopsis* and *Primitiella* in different ways has led the discussion to a paradox; as HESSLAND, however, touches upon, the existence of a terminal [= posterior in the present paper] dolon, the essential criterion of the *Primitiopsidae*, is not demonstrated for *Primitiella*).

The Devonian genus *Sulcicuneus* was referred to the family by KESLING (1951 a). It shows great resemblance in dimorphism to the *Primitiopsidae* treated here. HENNINGSMOEN (1953, p. 230) interpreted the "extraneous chamber" in KESLING's description as a marginal structure. To judge from KESLING's abundant illustrations (op. cit., Pls. I-III) it seems, however, to be velar. For this reason the present author is strongly inclined to follow KESLING's incorporation of *Sulcicuneus* in the family. In addition to the similar dimorphism there are some minor differences, such as a larger left valve, the presence of a sulcus, and obviously some differences in marginal contact and morphology of the adductor insertion. At the present state of our knowledge none of these differences has a higher taxonomic value than the criterion supplied by the dimorphism.

Signetopsis (HENNINGSMOEN 1954, p. 61) was tentatively assigned to the *Primitiopsidae*, due to the suspicion of a posterior velar dimorphism in the genus. This has not yet been established. Though there are transitions from the richly lobated *Signetopsis* species to the non-lobated *Primitiopsis* (e.g. *Signetopsis malornata* HENNINGSMOEN op. cit., p. 64), and though wide variations in lobation within small units are not foreign to ostracode taxonomy, the inclusion of *Signetopsis* in the family is not immediately given.

The *Primitiopsidae* are known from Silurian (*Primitiopsis*, *Clavofabella*) and Devonian (*Sulcicuneus*) deposits. Concerning an Ordovician species, named *Primitiopsis bassleri* HARRIS, cf. p. 19.

The Silurian *Primitiopsidae* from Gotland, the Oslo region, and England, consist of closely related *Primitiopsis* and *Clavofabella* species. In addition to the characters given in the diagnosis such common features should be mentioned as the absence of lobes and sulci, the presence of dorsal ridges, a tendency towards formation of reticulation, the presence of a row of marginal tubercles or denticles, overlapping right valve, and similar features in the marginal contact of the valves. Many of these additional features are regarded as unreliable characters in taxonomic work (concerning ornamentation, cf. KESLING 1954, also for the following discussion).

Dr. HENNINGSMOEN has kindly placed some of his original specimens from the Oslo region at the author's disposal. They have proved to contain *Clavofabella* species, the taxonomy of which cannot be elucidated without investigation of further material.

Genus *Primitiopsis* JONES 1887

TYPE SPECIES.—*Primitiopsis planifrons* JONES 1887, p. 5.

DIAGNOSIS.—Dolonal flanges meet posteriorly to form a closed chamber. Dolon continues forwards in a slight velar bend. Right valve overlapping.

SPECIES.—Only one species known, *Primitiopsis planifrons* JONES 1887.

REMARKS.—Besides the species treated in this paper, a number of different ostracodes have been referred to this genus. The five Devonian species, *P. eifliensis* KUMMEROW, *P. ornatus* PÉNEAU, *P. pisciformis* GÜRICH, *P. punctulifera* (HALL), and *P. ? unicornis* VAN PELT, have not been considered here. The Ordovician species *Primitiopsis bassleri* HARRIS (1931, p. 91, Pl. XI Fig. 2, Pl. XIV Fig. 2) was described as exhibiting a dimorphism which is closely similar to that in *Clavofabella* n. gen., but from HARRIS's pictures it cannot even be judged if it is velar in origin. The hingement has proved to be very different from that in *Primitiopsis* and *Clavofabella*, with teeth and sockets at the end of the hinge line. LEVINSON (1950, p. 67) who established this fact, concluded that the dimorphism is anterior (op. cit., p. 68, Fig. 4). This does not seem to be disproved.

Primitiopsis oblonga sensu KUMMEROW (1923, p. 424) which—though it was orientated in the same way by the two authors—was one of the recurrent motives in the discussion between BONNEMA and KUMMEROW on orientation and brood care, is not possibly identical with *Primitia oblonga*, described by JONES & HOLL (1865, p. 423, Pl. XIII: 14). Even if the inner part of the valve was not accessible to JONES & HOLL, the very broad dorsum and the strongly marked dorsal ridge cannot have escaped their notice. The discussed species *Primitiopsis oblonga*, beautifully pictured by BONNEMA (1938, Figs. 1–19) shows all the characteristics of the *Primitiopsidae*, except in lateral outline. A velar structure cannot, however, be traced from the dolon and forwards. The right valve is strongly overlapping. Most certainly the species should constitute a genus of its own within the family, as pointed out by SWARTZ (1936, p. 555) and HESSLAND (1949, p. 240). As the species is known from glacial drift in Germany and in the Netherlands, type locality and access to further material are unavailable.

KUMMEROW (1923, p. 425) refers to *Primitiopsis* yet another species, which he mentions as *Primitia obsoleta* JONES & HOLL. There is no reason to assume an identity with *Primitia obsoleta* as described by JONES & HOLL 1865, p. 423, Pl. XIII: 12. The only relation between the two species lies in the fact that they are both described from glacial drift in northern Germany. KUMMEROW has not depicted the species. *Primitiopsis obsoleta* sensu KUMMEROW (*Aparchites obsoletus* KRAUSE, cf. p. 27) is inevitably a blind alley in taxonomy.

Primitiopsis dorsoPLICATA HENNINGSMOEN 1954, finally, has a dolon which extends forwards to the foremost part of the ventral side of the carapace.

Whether the species is to be referred to a genus of its own within the *Primitiopsidae*, cannot be established without examination of the original material.

Primitiopsis planifrons JONES 1877

Plate I, Figs. 1-9; Plate II, Fig. 23.

- 1887 *Primitiopsis planifrons* n. sp.—JONES, p. 5, Fig. p. 5.
 1887 *Primitia valida* JONES & HOLL—JONES, p. 4.
 1887 *Primitia grandis* n. sp.—JONES, p. 4.
 1888 *Primitiopsis planifrons* JONES—JONES, p. 406, Pl. XXII: 18.
 1888 *Primitia grandis* JONES—JONES, p. 405, Pl. XXII: 14.
 1888 *Primitiopsis planifrons* JONES—LINDSTRÖM, p. 5.
 1888 *Primitia valida* JONES (*sic*)—LINDSTRÖM, p. 5.
 1888 *Primitia grandis* JONES—LINDSTRÖM, p. 5.
 1901 *Primitiopsis planifrons* JONES—CHAPMAN, pp. 154, 159.
 1901 *Primitia valida* JONES & HOLL—CHAPMAN, pp. 147, 158.
 1917 *Primitiopsis planifrons* JONES—HEDE, pp. 24, 29.
 1921 *Primitiopsis planifrons* JONES—HEDE, pp. 49, 98.
 1921 *Primitia valida* JONES & HOLL—HEDE, pp. 49, 98.
 1923 *Primitiopsis planifrons* JONES—KUMMEROW, p. 425.
 1923 *Primitiopsis planifrons* JONES—ULRICH & BASSLER, p. 300, Fig. 15: 7-8.
 1927 *Primitia valida* JONES & HOLL—HEDE 1927 a, p. 54.
 1927 *Primitiopsis planifrons* JONES—HEDE 1927 b, pp. 20, 21, 56.
 1927 *Primitia valida* JONES—HEDE 1927 b, pp. 21, 55.
 1933 *Primitiopsis planifrons* JONES—BONNEMA 1933 a, p. 34, Figs. 26-28.
 1933 *Primitiopsis planifrons* JONES—BONNEMA 1933 b, p. 151.
 1934 *Primitiopsis planifrons* JONES—BASSLER & KELLETT, pp. 17, 465, Figs. 6: 7-9.
 1934 *Primitia valida* JONES & HOLL—BASSLER & KELLETT, p. 458.
 1934 *Aparchites grandis* JONES—BASSLER & KELLETT, p. 158.
 1935 *Primitiopsis planifrons* JONES—BONNEMA, p. 84, Fig. 3.
 1936 *Primitiopsis planifrons* JONES—KUMMEROW, p. 466.
 1936 *Primitiopsis planifrons* JONES—SWARTZ, p. 555, Pl. 83: C: 1.
 1938 *Primitiopsis planifrons* JONES—BONNEMA, p. 104.
 1940 *Primitiopsis planifrons* JONES—KAY, p. 261.
 1940 *Primitiella planifrons* sine auctore—KAY, *ibidem*.
 1949 *Primitiopsis planifrons* JONES—HESSLAND, p. 239.
 1950 *Primitiopsis planifrons* JONES—LEVINSON, p. 67.
 1951 *Primitiopsis planifrons* JONES—KESLING 1951 a, p. 222.
 1953 *Primitiopsis planifrons* JONES—HENNINGSMOEN, p. 230.
 partim 1888 *Primitia valida* JONES & HOLL—JONES, p. 405.
 partim 1954 *Primitiopsis planifrons* JONES—HENNINGSMOEN, p. 59.
 non 1954 *Primitiopsis* cf. *planifrons* JONES—HENNINGSMOEN, p. 60, Pls. 6: 16-19.

NEOTYPE.—The lectotype designated by HENNINGSMOEN (1954, p. 60), i.e. the pouch-bearing valve figured by JONES (1887, p. 5), has been reported not to be found among JONES's original specimens in the British Museum (Nat. Hist.). As neotype is designated here the dolonate specimen in Pl. I, Fig. 1 (Mus. Pal. Inst., Uppsala, No. G 101).

DIAGNOSIS.—Original diagnosis given by JONES 1887, p. 5:

“Oblong with rounded ends; bearing a faint sulcus, together with the subcentral pit which is normal in *Primitia*; also another slight furrow is observable along the ventral region, as is usually the case with *Primitiae* of the group to which *P. umbilicata*, *P. valida*, and their allies belong; and the ventral convexity, overhanging the margin, hides the continuous row of denticles which border each valve. The surface is reticulate except at the anterior end. The interior of each valve has a thin cross wall in the anterior region, dividing off about an eighth of the length of the valve from the rest of the interior. This constitutes the generic distinction. The narrow crescentic area of surface, corresponding to the separate portion of the interior, being destitute of ornament, and therefore smooth, gives the specific name.”

The animal should be given the reverse orientation, and the extradomiciliar origin of the dolonal pouch should be established.

DESCRIPTION.—Reticulate; reticulation almost regular towards the velar bend. Dorsum very narrow, dorsal ridge low, in the postadductorial half protruding over the hinge line. Anterior corner with smooth triangular area. Ventral and, often, dorsal part of the dolon slightly overlapping; minute longitudinal linear structures sometimes observable on the dolon (Pl. I, Fig. 2). Tubercles 26–32 per mm along the ventral part of the free margin of the left valve, closer along the corresponding margin of the right valve. In the non-dolonate specimens the subvelar area of the right valve is folded over towards the left valve, so that only the marginal structure of the left valve is visible. In the non-dolonate specimens the anterior part of the marginal structure is often preserved as a marginal frill.

Adductorial pit corresponds to a slight eminence on the inner side of the valve; in front of this eminence the valve bears an internal impression. Muscle scars not observed. Extramarginal shelf of left valve continued by the overlapped part of the subdolonal domiciliar wall; marginal part of the right valve forms a transition to the overlapping part of the subdolonal domiciliar wall (Pl. II, Fig. 23).

Six instars established. The essential features of ornamentation may be followed starting from the first instars. In the younger instars a sulcus-like impression of the area over the adductorial pit. Adductorial pit migrates forwards during ontogeny. Dolonate types, tentatively regarded as females, observed only in the sixth instar.

Size in microns:

Instar	1	2	3	4	5	6 ♂	6 ♀
Length	380–420	460–570	590–700	710–860	880–1050	1090–1250	1280–1440
Height	260–310	330–410	400–530	510–640	680–790	800–900	780–900
Width						715–760	760–860

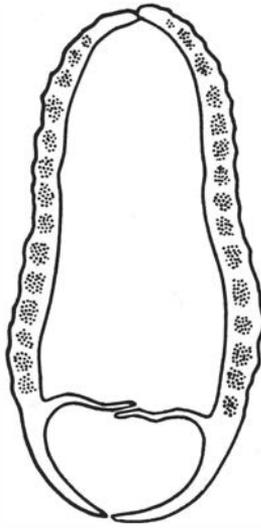


Fig. 5. Horizontal section through a dolonate specimen of *Primitiopsis planifrons*, exhibiting the thin subdolonal part of the domiciliar wall and the thicker dolon. Overlap of the right valve shown. Drawn from thick microscopic section, magnification $\times 50$. The sections studied give no further explanation about the structure of the carapace wall.

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian of Gotland.

TYPE LOCALITY.—Mulde, parish Fröjel, Gotland. LINDSTRÖM's collection locality is named "Fröjel" in the original description by JONES and cannot be restricted to a smaller unit than the parish with the same name. Though there are other marl localities in the parish, the author has chosen the brickyard of Mulde, which has given the name to the sediment and afforded much material for other studies. This remark also concerns the neotype of *Clavofabella reticristata*.

REMARKS.—Due to its central position in the palaeocope system, *Primitiopsis planifrons* has been frequently dealt with in literature. Several papers in the synonymy list concern orientation or morphological details, the correct interpretation of which is essential to taxonomy. The dolonate type has been recognized by all authors; BONNEMA (1935, p. 84) first pointed to the necessity of incorporating JONES's *Primitia valida* from Mulde within *Primitiopsis planifrons*, as was done later by HENNINGSMOEN (1954). This species and *Primitia grandis* are beyond doubt non-dolonate types of *Primitiopsis planifrons*. JONES (1888, p. 405) points out that his *Primitia valida* from Mulde is different from the species described one year earlier by JONES & HOLL (1886, p. 409); a possible identity—which would give priority to the specific name *valida*—can only be checked on JONES's original specimen in London.

The preadductorial impression in *Primitiopsis planifrons* was observed by BONNEMA (1933, p. 34), who believed it to indicate the position of paired eyes.

As pointed out above, minute linear structures are observed on the dolon. The striae in LILJEWALL's picture (JONES 1887, p. 5), however, are certainly due to the woodcut technique (cf. HENNINGSMOEN 1954, p. 59).

In *Primitiopsis planifrons* from Mulde the ornamentation is very seldom affected by weathering. On the other hand the specimens are often laterally or dorsoventrally compressed. In the latter case the specimens assume the shape of the variety *ventrosa* (JONES 1887, p. 6). The hingement is then mostly depressed and the subdolon wall cracked outwards, as may be observed in isolated valves.

The material of ostracodes described by HENNINGSMOEN 1954 as *Primitiopsis* cf. *planifrons* does not seem to contain specimens of this species. HENNINGSMOEN's dolonate specimens (op. cit., Pl. 6, Figs. 18, 19) show *Clavofabella* valves. The internal mould (l.c., Fig. 19) beautifully shows the internal preadductorial impression. A preadductorial node, which is foreign to the *Primitiopsidae* treated here, is discernible in the non-dolonate valves (l.c., Figs. 16, 17).

Genus *Clavofabella* n. gen.

DERIVATION OF NAME.—From Latin *fabella*, diminutive of *faba*, bean, and *clavus*, rudder, alluding to the rudder-like posterior dolonal flanges.

TYPE SPECIES.—*Clavofabella incurvata* n. sp.

DIAGNOSIS.—Dolonate flanges do not meet posteriorly. Dolon continues forwards in a velar ridge or a velar bend. Right valve overlapping.

SPECIES.—*Clavofabella multidentata* n. sp., *C. cristata* (JONES & HOLL 1865), *C. incurvata* n. sp., *C. borussica* (KUMMEROW 1923), and *C. reticristata* (JONES 1888).

REMARKS.—The *Clavofabella* species form a well limited unit. Excepting the different organisation of the dolonal flanges they show a close resemblance to *Primitiopsis* in almost every detail, including ornamentation. It is common to the *Clavofabella* species that the dorsum and the subvelar area are broader than in *Primitiopsis*. As to HENNINGSMOEN's *Primitiopsis* cf. *planifrons* see above.

Although it is possible to follow the larval development of the different *Clavofabella* species from young instars this has not been done here, as the diagram Fig. 2, B was compounded before the species were distinguished. For the genus five instars have been established. The existence of a still younger instar with a length of 380–390 μ does not seem improbable, as the youngest of the established instars is represented by only four specimens.

REMARKS ON *C. CRISTATA* (JONES & HOLL) AND *C. BORUSSICA* (KUMMEROW).—Beside the *Clavofabella* species recorded by HENNINGSMOEN (1954, p. 60) from the Oslo area two other *Clavofabella* species are found in literature.

Clavofabella cristata was described in 1865 as *Primitia cristata* JONES & HOLL (1865, p. 420, Pl. XIII: 1). The figure quoted depicts a smooth dolonate

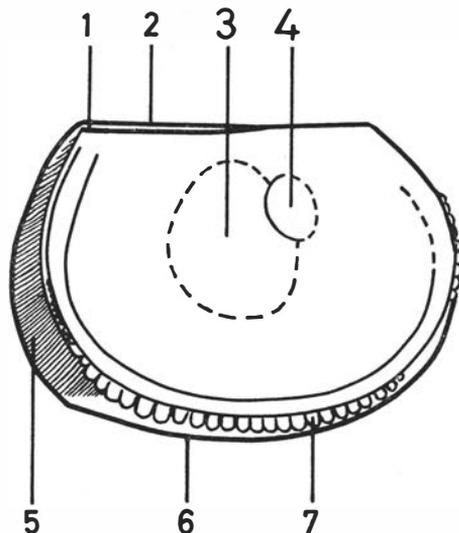


Fig. 6. Left valve of *Clavofabella reticristata*, from the inner side, showing marginal structures and the interior preadductorial impression. Magnification $\times 35$.

Legend.—1. Hinge line. 2. Dorsal ridge. 3. Bulge corresponding to the adductorial pit. 4. Preadductorial impression corresponding to the preadductorial node in other ostracodes. 5. Dolon. 6. Velar bend. 7. Marginal tuberculation.

Clavofabella specimen (British Museum [Nat. Hist.] No. I. 2088). The second specimen in the same plate, *Primitia umbilicata* JONES & HOLL (op. cit., p. 420; British Museum [Nat. Hist.] No. I. 2089) is certainly a non-dolonate specimen of the same species, and it is not improbable that the same remark refers to the third species, *Primitia tersa* JONES & HOLL (op. cit., p. 421; British Museum [Nat. Hist.] No. I. 2075). All the species depicted are from the Wenlock limestone of Malvern. Later (1886, pp. 410, 411) JONES & HOLL write about reticulate varieties of the two latter species. This seems to require a special study.

Primitia cristata is recorded in several fossil lists from Gotland (HEDE 1921, pp. 49, 98; 1927, p. 53; BONNEMA 1935, p. 83, from the Mulde marl).

BOUČEK (1936) refers *P. cristata* in the above sense (*Primitia cristata* and *P. tersa*, but not *P. umbilicata*) to the genus *Laccoprimitia* ULRICH & BASSLER 1923. HESSLAND (1949, pp. 230, 231) has followed this recommendation, but stresses the heterogeneity of *Laccoprimitia* in this sense, and points out that a velar structure is obviously lacking in the type specimen *Laccoprimitia centralis* ULRICH (1890, p. 130, Pl. 10: 1, 2). The anterior view given by ULRICH (op. cit., Pl. 10, Fig. 2 b) shows that the carapace is broadest dorsally and that it seems to have a marginal structure, while no velar structure is present. The genus has no characters common with the *Clavofabella* species referred to it.

A *Clavofabella* species, found in a glacial drift boulder in Northern Germany, had earlier been referred to *Laccoprimitia*, viz. *Laccoprimitia borussica* KUMMEROW (1923, p. 422, Pl. 20 [numbered 21], Fig. 20). Length values given by KUMMEROW (l.c.) for two specimens are 1.01 mm and 0.99 mm, and height values 0.75 mm and 0.74 mm respectively, thus somewhat higher than *Clavofabella multidentata*. It is not impossible that some of the specimens of *Clavofabella borussica* in the same boulder were non-dolonate (KUMMEROW, op. cit., p. 433: "Vielleicht ist an Geschlechtsdimorphismus zu denken").

Clavofabella multidentata n. sp.

Plate I, Figs. 10–12; Plate II, Figs. 13, 17, 18, 24.

DERIVATION OF NAME.—From Latin *multidentatus*, alluding to the dense marginal tuberculation.

HOLOTYPE.—The dolonate specimen in Plate I, Fig. 10 (Mus. Pal. Inst., Uppsala, No. G 110).

DIAGNOSIS.—Velar ridges well developed, parallel or subparallel on the ventral side. Dense marginal tuberculation; 25–32 tubercles/mm on the ventral part of left dolonate valve. Reticulate. Size of adult dolonate type, left valve: length 920–1030 μ , height 630–700 μ . Dorsum very broad, dorsal ridge acute.

DESCRIPTION.—Reticulation almost regular towards the velar ridge (Pl. II, Figs. 17, 18). With very few exceptions, the ornamentation in the adult dolonate type is missing between the smooth anterior corner and the adductor pit. Marginal tuberculation on the right valve closer than on the left. Very fine marginal tuberculation along the overlapping right subdolonate wall. Internal preadductorial impression observed.

In the non-dolonate type the posterior third of the right subvelar area is commonly stretched over the left (Pl. II, Fig. 12). In both types an anterior marginal frill is often preserved.

Dolonate specimens observed in the oldest and the oldest but one instars. Except in size the subadult and adult dolonate specimens are essentially alike. In these subadult specimens the smooth preadductorial field is seldom observed.

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian of Gotland.

TYPE LOCALITY.—Mulde, parish Fröjel, Gotland.

REMARKS.—This species is likely to have been included in *C. reticristata*. This is probably the case in BONNEMA 1935 (Fig. 2). If the scale in this figure is approximately exact—and Fig. 3 in the same paper suggests that it is—the species is most probably *C. multidentata*. Anyhow the relative width of *C. reticristata* is considerably greater.

Clavofabella incurvata n. sp.

Plate II, Figs. 14-16, 19, 20, 25.

DERIVATION OF NAME.—From Latin *incurvatus*, alluding to the ventrally incurved velar ridges of the dolonate type.

HOLOTYPE.—The dolonate specimen in Plate II, Fig. 14 (Mus. Pal. Inst., Uppsala, No. G 114).

DIAGNOSIS.—Velar ridges strongly developed, in the dolonate specimens considerably incurved on the ventral side. Reticulate. Sparse marginal denticulation or tuberculation; 13-22 denticles or tubercles/mm on the ventral part of the left dolonate valve. Size of dolonate type, left valve: length 790-930 μ , height 580-650 μ . Dorsum broad, dorsal ridge acute.

DESCRIPTION.—Reticulation almost always longitudinally extended towards the velar ridge and often towards the dorsum (Pl. II, Figs. 19, 20). Marginal tuberculation closer on the right valve than on the left. Fine marginal tuberculation along the overlapping right subdolonal wall. Interior preadductorial impression observed.

Velar ridge in the non-dolonate specimens not incurved. The right subvelar area, particularly the posterior half, shows a marked tendency to be folded out over the left. In both types an anterior marginal frill is often preserved.

Dolonate specimens observed in the adult instar only.

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian of Gotland.

TYPE LOCALITY.—Mulde, parish Fröjel, Gotland.

Clavofabella reticristata (JONES 1888)

Pl. II, Figs. 21, 22, 26.

- 1887 *Primitia reticristata* n. sp.—JONES, p. 5, not pictured.
 1888 *Primitia reticristata* JONES—JONES, p. 406, Pl. XXII: 15.
 1888 *Primitia reticristata* JONES—LINDSTRÖM, p. 5.
 1901 *Primitia reticristata* JONES—CHAPMAN, pp. 149, 158.
 1921 *Primitia reticristata* JONES—HEDE, pp. 49, 98.
 1927 *Primitia reticristata* JONES—HEDE 1927 a, p. 54.
 1927 *Primitia reticristata* JONES—HEDE 1927 b, pp. 21, 55.
 1934 *Primitia reticristata* JONES—BASSLER & KELLETT, p. 454.
 1936 *Primitia reticristata* JONES—KUMMEROW, p. 466.
 1936 *Primitia reticristata* JONES & HOLL—SWARTZ, p. 558, in illustration text.
 1938 *Primitiopsis reticristata* JONES—BONNEMA, p. 104.
 1949 *Primitiopsis reticristata* (JONES & HOLL)—HESSLAND, p. 240.
 partim 1935 *Primitiopsis reticristata* JONES—BONNEMA, p. 83 (? non Fig. 2).
 partim 1954 *Primitiopsis planifrons* JONES—HENNINGSMOEN, p. 59.

NEOTYPE.—The dolonate specimen in Plate II, Fig. 21 (Mus. Pal. Inst., Uppsala, No. G 121). After inquiry at the British Museum (Nat. Hist.) it

has been reported that the original specimen is not to be found in JONES's collections, nor any other specimens from the type locality collected or determined by T. R. JONES.

DIAGNOSIS.—Velar structure developed as a velar bend, continuing the dolon forwards. Coarsely reticulate, or rather pitted. Dorsum broad, dorsal ridge rounded.

DESCRIPTION.—Size of dolonate type, left valve: length 810–970 μ , height 570–650 μ . Reticulation or pits mainly somewhat longitudinally extended towards the margin (Pl. II, Figs. 21, 22). Close marginal tuberculation, 31–40 tubercles/mm on the ventral part of the left valve, on the right valve denser; very fine tuberculation along the overlapping right subdolonal wall. Interior preadductorial impression observed.

No marginal frill observed.

Dolonate specimens observed in the adult instar only.

TYPE STRATUM.—Mulde marl, probably uppermost Wenlockian of Gotland.

TYPE LOCALITY.—Mulde, parish Fröjel, Gotland.

REMARKS.—There is no doubt that JONES's picture (1888, Pl. XII: 15) represents the same species as the neotype. As pointed out above, the three *Clavofabella* species treated here seem to have been included in *C. reticristata*. A "partim" might therefore be added to most of the references in the list of synonyms, as has been done for BONNEMA 1935. It should be stressed that BONNEMA (op. cit.), due to his clear understanding of the orientation and his correct homologization of the velar structures, earlier than anybody else realized the close relationship between *Primitiopsis planifrons* and the group of species which here forms the genus *Clavofabella*. There seems to be no doubt that KRAUSE (1891, p. 495, Pl. XXX: 8, 9) has seen *Clavofabella* spp.; from his pictures of *C. reticristata* it cannot possibly be decided to what species his specimens belong (in the same paper, Pl. XXX: 1, 2, we also find the first pictures of *Aparchites* (?) *obsoletus* and *A.* (?) *oblongus*, later referred to *Primitiopsis* by KUMMEROW 1923).

Without further reference BASSLER & KELLETT (1923) report *C. reticristata* from the Yeringian of Cave Hill, Lilydale, Victoria, Australia.

Conclusions

The examined population of *Primitiopsidae* contains four species, viz. *Primitiopsis planifrons*, *Clavofabella multidentata*, *C. incurvata*, and *C. reticristata*.

In *Primitiopsis planifrons* six instars are known, and the existence of younger free instars does not seem probable. In the genus *Clavofabella* five instars are suggested; the existence of a still younger instar cannot be excluded.

The *Primitiopsidae* should be orientated with the more voluminous end as the posterior. The anterior part of the lateral outline then makes a slight forward swing. The anterior corner forms a triangular area without ornamentation. During ontogeny the adductorial pit migrates towards the anterior end. A rudimentary preadductorial node is obviously present.

The growth factors obtained in *Primitiopsis planifrons* correspond essentially to the value 1.26, corresponding to a doubling of volume as known from earlier investigations. A slightly lower growth factor is observed only for the last moulting.

The dimorphic character is supplied by an extended part of the velar ridge, the dolon, which in the *Primitiopsidae* is posteriorly situated. In *Primitiopsis* the dolonal margins lie in contact, and a pouch is formed; in *Clavofabella* the dolonal margins are free. Although the function of the dolonal pouch is not known, the dolonate and non-dolonate types may traditionally be termed females and males respectively. In *Clavofabella multidentata* dolonate types are found in the two last instars; in the other species investigated such types have been observed only in the last instar.

If a fossil ostracode or other arthropode population is to be used for a study on population dynamics, the compilation of essential life data is associated with certain difficulties, which have not presented themselves in corresponding studies on fossil mammals. The absolute age of the individuals cannot be ascertained, nor the relative age in equivalent units, as the moults do not correspond to equal intervals of time. The fossilization may take place in two essentially different ways, as a *necrocoenosis* or a *pseudocoenosis*, which ought to be treated with different methods. *A priori* the population curve would be expected to be dominated by pseudocoenotic components; a single investigation of *Beyrichia* quoted sustains this conception, while further empiric material of this kind is lacking. The large component of adults in the present curve, which must be regarded as truly necrocoenotic as moulting is not known in adults, suggests, however, a considerable necrocoenotic element in the curve. Although a heavy representation in the older instars may find an explanation, the distribution curve and the sex quotient obtained in this investigation are strongly suggestive of not representing the original population.

In a group like the ostracodes, the recent species of which have very similar carapaces and are determined on characters which have not been preserved in the fossils, it would be expected that a "palaeontological species" contains many species as defined in zoological taxonomy. This investigation has touched that problem, although the investigated species of reticulate *Primitiopsidae* have proved to contain good fossilized morphological characters. The desirability of an abundant material when defining a fossil species is obvious.

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Through Dr. R. BAKER photographs of original specimens in the British Museum have been placed at the author's disposal. Mr. N. HJORTH has made all photographs published; Mrs. I. THOMASSON has redrawn diagrams and other illustrations; further technical assistance has been given by Mrs. E. EKLIND and Mrs. M. LINDELL at the Palaeontological Institution.

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The papers by CLAUS (1872) and PRZIBRAM (1931) have not been seen in the original.

Explanation of Plates

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

- l* = lateral view of left valve,
- v* = ventral view,
- d* = dorsal view,
- c* = caudal view,
- o* = oblique latero-ventral view.

The photographic work was carried out by Mr. N. HJORTH, Palaeontological Institution, Uppsala. All specimens were whitened with NH_4Cl before photographing.

The numbers in brackets refer to original specimens in the Museum of the Palaeontological Institution, Uppsala.

Plate I

Primitiopsis planifrons JONES, adult specimens and larval instars. Magnification $\times 25$.

- Fig. 1. Adult dolonate specimen. Neotype (No. G 101).
- Fig. 2. Adult dolonate specimen (No. G 102).
- Fig. 3. Adult non-dolonate specimen, with well-developed marginal frill (No. G 103).
- Fig. 4. Adult non-dolonate specimen (No. G 104).
- Fig. 5. Instar 1 (No. G 105).
- Fig. 6. Instar 2 (No. G 106).
- Fig. 7. Instar 3 (No. G 107).
- Fig. 8. Instar 4 (No. G 108).
- Fig. 9. Instar 5 (No. G 109).

Clavofabella multidentata n. sp. Magnification $\times 25$.

- Fig. 10. Adult dolonate specimen with marginal frill and area without reticulation between the anterior corner and the adductor pit. Holotype (No. G 110).
- Fig. 11. Subadult dolonate specimen (No. G 111).
- Fig. 12. Adult non-dolonate specimen (No. G.112).

Plate II

Clavofabella multidentata n. sp. Magnification $\times 25$.

- Fig. 13. Adult non-dolonate specimen with marginal frill (No. G 113).

Clavofabella incurvata n. sp. Magnification $\times 25$.

- Fig. 14. Adult dolonate specimen with marginal frill. Holotype (No. G. 114).
- Fig. 15. Adult dolonate specimen with marginal frill (No. G 115).
- Fig. 16. Adult non-dolonate specimen (No. G 116).

Clavofabella mutidentata n. sp. Oblique view showing velar ridge, marginal tuberculation, and the almost regular reticulation towards the velar ridge. Magnification $\times 25$.

- Fig. 17. Adult dolonate specimen (No. G 117).
- Fig. 18. Adult non-dolonate specimen (No. G 118).

Clavofabella incurvata n. sp. Oblique view showing velar ridge, marginal denticulation, and the extended reticulation towards the velar ridge. Magnification $\times 25$.

Fig. 19. Adult dolonate specimen (No. G 119).

Fig. 20. Adult non-dolonate specimen (No. G 120).

Clavofabella reticristata (JONES). Magnification $\times 25$.

Fig. 21. Adult dolonate specimen. Neotype (No. G 121).

Fig. 22. Adult non-dolonate specimen (No. G 122).

Valves showing inner side with the interior preadductorial impression (seen in Figs. 24–26). Magnification $\times 35$.

Fig. 23. Postadductorial half of right valve of *Primitiopsis planifrons* JONES.

Fig. 24. Right valve of *Clavofabella multidentata* n. sp. Groove along the hinge line (No. G 124).

Fig. 25. Left valve of *Clavofabella incurvata* n. sp. (No. G 125).

Fig. 26. Left valve of *Clavofabella reticristata* (JONES) (No. G 126).

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