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# ON TWO HOLLINID OSTRACODE GENERA FROM THE UPPER CARBONIFEROUS OF NORTHWESTERN SPAIN

BY

M. J. M. BLESS *

## ABSTRACT

This paper describes some features of the carapace of two hollinid ostracode genera: *Hollinella* and *Jordanites*. The carapace of these ostracodes consists essentially of the same layers as modern ostracodes, with exception of the velar structures.
A survey on the ontogeny of species of *Hollinella* and *Jordanites* reveals that this is very similar to the ontogeny of other palaeocopid ostracodes.
It is suggested that *Hollinella* and *Jordanites* were marine near-bottom swimmers. The velum probably served to prevent the animal from sinking too deeply into a soft substrate.
Five species of *Hollinella*, including three new species, and three species of *Jordanites* are described. All species are restricted to the Upper Carboniferous of NW Spain.

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## INTRODUCTION

When Coryell established the genus *Hollinella* in 1928 he will hardly have expected that forty years later about 120 species from all over the world would be assigned to *Hollinella*. In 1929, less than one year after Coryell's publication, Kellett described five new species of *Hollinella* and assigned five species, previously placed in *Hollina*, to this genus. In 1934 Bassler & Kellett reported 44 species of the genus in their "Bibliographic Index of Paleozoic Ostracodes". Kesling and his co-workers described many new species from the Middle Devonian of North America between 1950 and 1958. Numerous species were described from the Devonian, Carboniferous and Permian of North America (e.g. Cooper, 1946), Russia (e.g. Pozner, 1951; Yegorov, 1953), Europe (e.g. Latham, 1932; Kummerow, 1953; Blumenstengel, 1965), China (e.g. Patte, 1935) and Japan (Ishizaki, 1964). Jordan (1964) even mentioned a species from the Upper Silurian of Germany.
Notwithstanding the continuous attention the genus received in these forty years, knowledge of the structure of the carapace and the velum is still inadequate. Several contradictory opinions about the structural elements of the carapace can be encountered in literature, especially with regard to the velum (cf. Pokorny, 1951, and Scott: Treatise, 1961). During an investigation on the presence of ostracodes in the Carboniferous of NW Spain new data have been recognized, which may throw some light on the structure and the ontogeny of the velum of hollinid ostracodes. These data will be discussed in the present paper. At the same time other aspects of the carapace have been studied in some detail.
The ontogeny of four species is treated in detail in the present paper. Because the juveniles of different species of hollinid ostracodes are often very similar it is usually impossible to assign juvenile forms to a species. In the samples collected from fossiliferous beds in Palencia and Asturias, however, often only one species was present with both adults and juveniles. Because all the adult forms in these samples belong to one single species, it seems reasonable to assume that the juvenile forms recognized in the same sample also belong to that species. No indications were found that this supposition is false.
Although the ostracodes from the Spanish Carboniferous are usually poorly preserved in shales, which are often pyritous, the number of specimens encountered seems to be large enough to get reliable results. Attempts were made to free the ostracodes from the shales. This appeared however to be impossible. All the specimens described in this paper

* Geologisch Bureau v.h. Mijngebied, Heerlen.

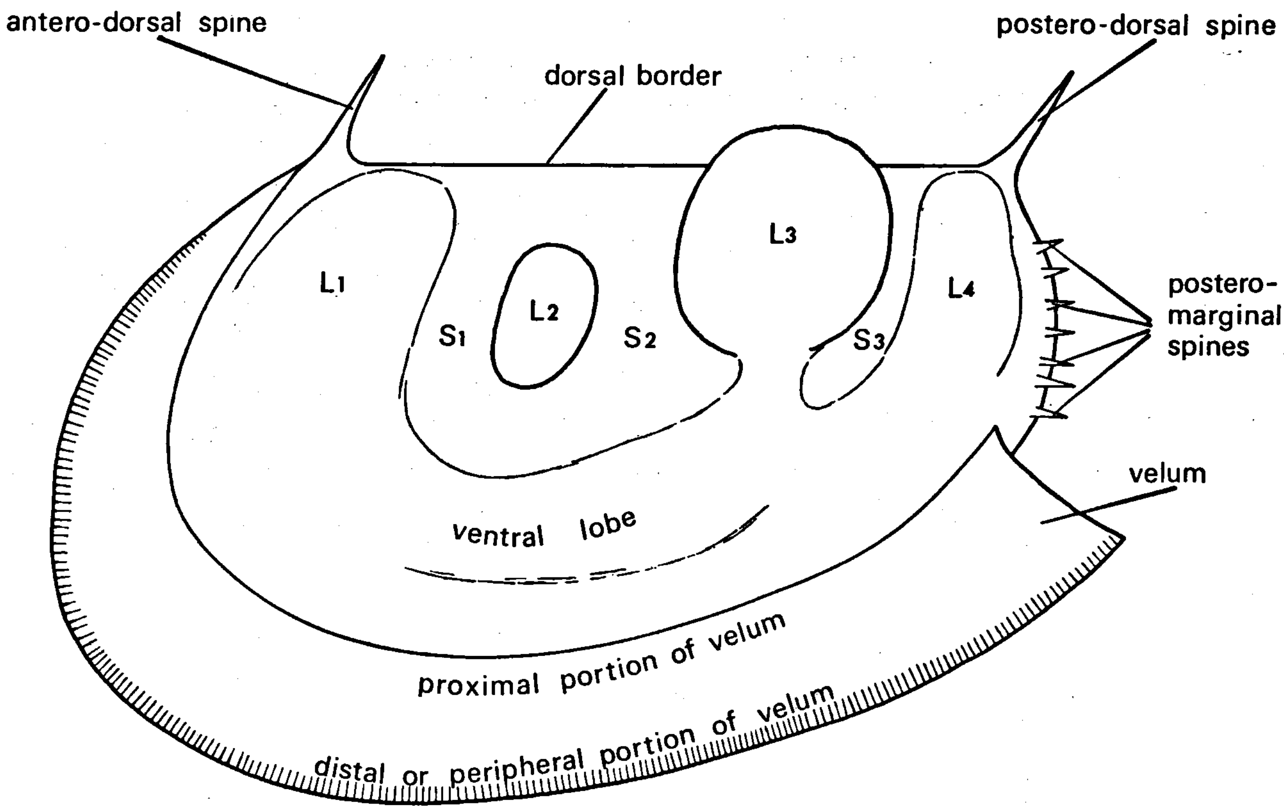


Fig. 1. Nomenclature of external features of a typical hollinid ostracode (LV).

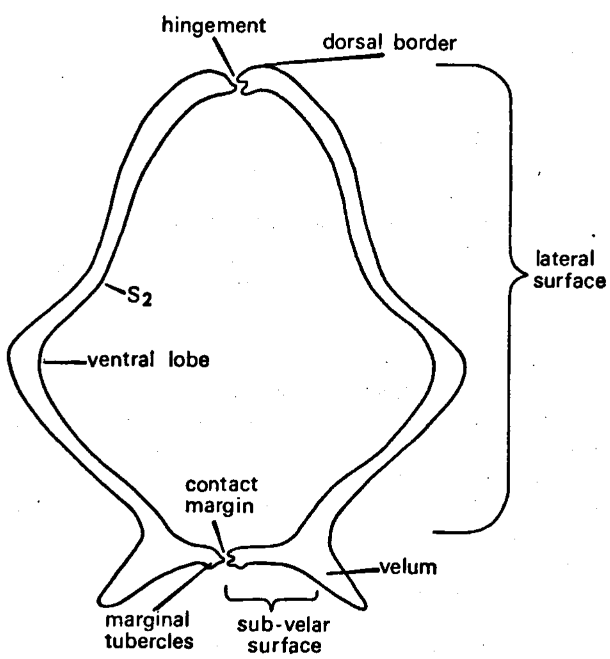


Fig. 2. Nomenclature of carapace structure of a typical hollinid ostracode (thin section).

(with the exception of *H. camoni*, which were found in limestone) were studied still partly embedded in the shale.

The terminology used is largely adapted from Kesling & McMillan (1951). Figures 1 and 2 show the terminology used in this paper.

All the ostracodes have been stored with the collection of the Department of Stratigraphy and Paleontology of the University of Leiden.

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## STRATIGRAPHY

The hollinid ostracodes described here have been collected from the Barruelo Formation in the Redondo Coal Basin of Palencia and from the Lena and Sama formations in the northern part of the Central Carboniferous Basin of Asturias. The stratigraphy of the Redondo Coal Basin has been treated in detail by several authors (Nederlof & de Sitter, 1957; Nederlof, 1959; van Ginkel, 1965; de Sitter & Boschma, 1966) and the reader is referred to their publications for further information. Little detailed information exists about the Lena and Sama formations (and especially the latter) in the Central Carboniferous Basin of Asturias with the mining centres "Mieres — Pola de Lena" in the south and "Sama de Langreo — Pola de Laviana" in the north. Of course, the economic importance of the mining districts has attracted a number of geologists since the beginning of the past century, but the very complicated structure of the basin made a detailed subdivision of the approximately three thousand meters of sediments almost impossible up to the present time. Because it seems useful to give at least an indication of the stratigraphic level from which the ostracodes have been collected, a provisional summary of the stratigraphy of the northern part of the Asturian basin is given with special reference to the Sama Formation.

In the beginning of the previous century the first papers on the geology of this region were published, among which especially those of Schulz (1837, 1838, 1844) should be mentioned. Later studies of special interest are those of Barrois (1882), Adaro (1926), Delépine (1932, 1943) and Madariaga Rojo (1932, 1933), and in the last few years of Llopis Llado (1952, 1954, 1955) and Martínez Alvarez (1962, 1965). The latter author gives an excellent bibliography of all studies of the Asturian Basin up to 1965. However, the publication "La cuenca central hullera asturiana" (Anonymous, 1948; commissioned by the Jefatura de Minas??) demonstrates that the problem of the correlation of coal beds within the basin still exists.
A survey of the stratigraphic sections of the Sama Formation, made by mining engineers and by the present author, reveals an alternation of shales, sandstones and coal layers, with sporadically an intercalation of a limestone bed or a conglomerate. These sediments formed the criteria for the subdivision into members (Calizas — Oscura) of the productive coal measures in Asturias. With exception of the Calizas Inferiores coal member all members form part of the Sama Formation. The practical use of this subdivision was rather poor because lateral changes in the sediments occur frequently and within short distances. Sandstones considered characteristic in the section of one mine disappear in the section of another. Notwithstanding, these sediments formed the basis for the subdivision into members and the "tramos" Hullero inferior, medio, supramedio and superior (fig. 2a). As can be readily understood nowadays, the result was a subdivision which outside of the region of Langreo, where the type-sections were located, could not be applied using those criteria, because even "safe criteria" such as the "calizas gonfoliticas" (conglomerates of limestone pebbles frequently recognized in the upper part of the Sama Formation) disappeared laterally whereas other "calizas gonfoliticas" appeared abruptly in other stratigraphic sections.
Looking for new ways to solve this problem, Madariaga (1932, 1933) published two papers on marine levels in the coal mines "Fondon" (Langreo) and "Soton" (Sotrondio) in order to use these levels as better guides for correlation of coal seams. This investigation was stopped for unknown reasons when it had just started. Afterwards the subject was abandoned, perhaps because the direct economic importance of this kind of investigations had not been recognized by the mining engineers in those times. The crisis in the coal mining industry in the last few years led to the formation of new companies comprising many of the older ones and the problem of detailed correlation between all the mines in the basin has become urgent in order to enable an investigation of the yield of these mines in the future. It is hoped that such an investigation will be started before many coal mines are closed down, which would mean the loss of a great deal of important data. In order to study the possibility of a detailed correlation of the coal beds throughout the entire basin, the author visited the coal mines of "Pumerabule", "Mosquitera", "Sta. Eulalia", "Llascaras", "Fondon" and "Sorriego", measuring twelve stratigraphic sections in detail (Enclosure 1). The provisional results are the recognition of new tools for a detailed correlation between the coal members, a better definition of the limits between the same, a more detailed subdivision of the Sama Formation into "subtramos" or "mega-rhythms" and the recognition of a new coal member at the top of the Sama Formation, the "Sorpresa coal member".

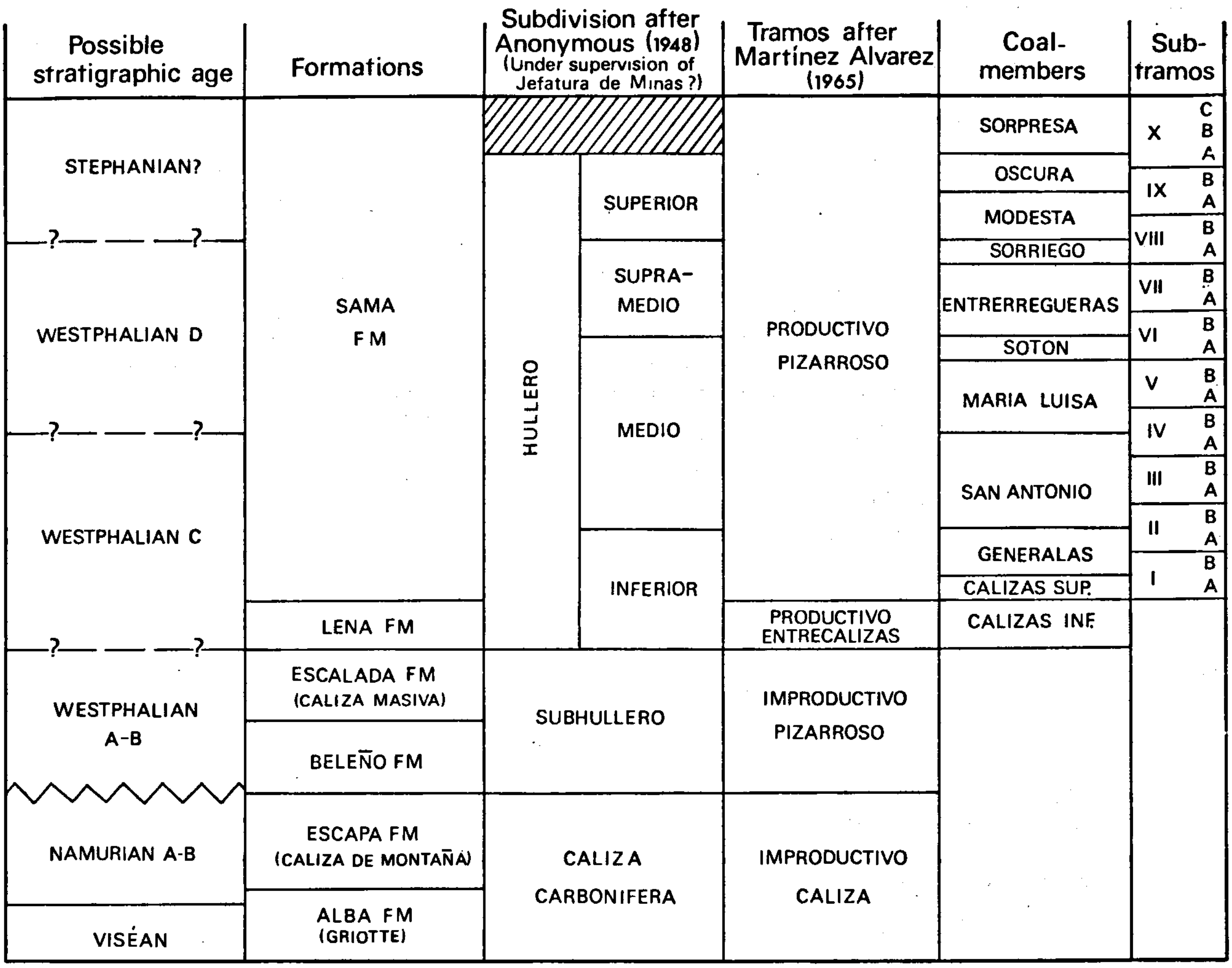



Fig. 2a. Subdivision of the Carboniferous in the Central Carboniferous Basin of Asturias.

An analysis of the sections shows that they consist of a number of cyclothems. The concept of cyclothems has been elaborated by Weller (1930) and many others as well. Each cyclothem consists of a series of beds deposited during a single sedimentary cycle. The number of beds and their character may vary in each region since they are dependent on local conditions. They also vary within the stratigraphic column of one region if the conditions in that region changed during the time involved. In the sections discussed three types of cyclothems have been recognized (fig. 2b). They may be composed of ten different members, which are described below.

*Member 1.*—Coarsely grained sandstones with well rounded pebbles, which may form real conglomerates. Sometimes in place of pebbles, large fragments of carbonized trunks may be present. Conglomerates of limestone pebbles in a matrix of sandstone or limestone are called "calizas gonfoliticas". Lateral and vertical changes in these beds are frequent and often very abrupt.

*Member 2.*—Finely to coarsely grained sandstones with cross-bedding.

*Member 3.*—Parallel laminated, finely grained sandstones, often micaceous and with high shale content. Plant fragments may be abundant.

*Member 4.*—Homogeneous shaly sandstones with trunks and rootlets "in situ".

*Member 5.*—Underclay (Span.: fusca, tierra, esquistera) with high carbon content, sometimes even workable. This member has been recognized in more than 50 % of the coal beds with a thickness of more than 15 cm and in more than 30 % of the coal beds of 1 cm or more.

*Member 6.*—Coal bed.

*Member 7.*—Greyish-black shale, sometimes with ferruginous concretions, often with high pyrite content or slightly calcareous. May be very fossiliferous. Fauna represents in most cases a marine environment, rarely a brackish-water environment.

*Member 8.*—Greyish or black marine limestones, very fossiliferous, especially at the base.

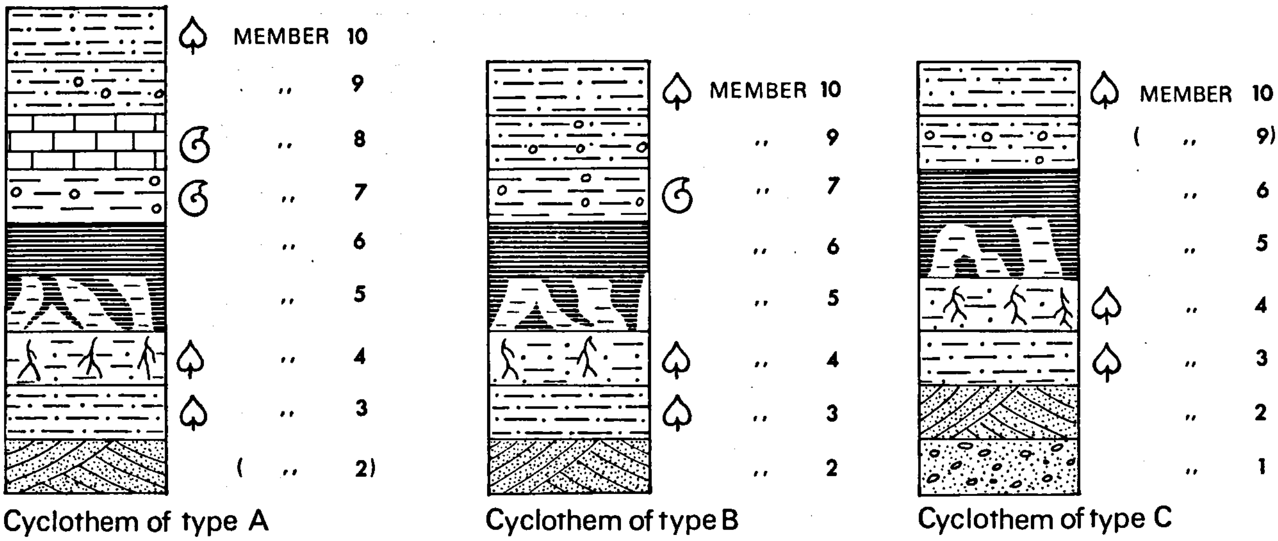



Fig. 2b. Cyclothems frequently recognized in the Upper Carboniferous of the Central Carboniferous Basin of Asturias.

*Member 9.*—Arenaceous shales and siltstone with parallel lamination. Thickness of laminae 1—50 mm. Often laminae of shale (siltstone) alternated with laminae of very fine sandstone. Reddish concretions parallel to bedding plane have frequently been observed.

*Member 10.*—Arenaceous shales, sometimes micaceous and with plant fragments. Parallel lamination.

The limits between these members are usually not well-defined. A gradual transition between members of one cyclothem is quite frequent. Before the deposition of the sediments of a new cyclothem a period of erosion often affected part of the former cyclothem. Therefore the limit between two cyclothems is usually abrupt and easily discernable.

The members 1—6 are assumed to represent limnic environments, the members 7 and 8 a brackish or marine environment. The members 9 and 10 have been deposited in an unknown environment. Maybe they represent a brackish or deltaic facies.

Cyclothems of type A are characterized by the members (2) — 3 — 4 — 5 — 6 — 7 — 8 — 9 — 10, cyclothems of type B by the members 2 — 3 — 4 — 5 — 6 — 7 — 9 — 10, and cyclothems of type C by the members 1 — 2 — 3 — 4 — 5 — 6 — (9) — 10. The marine influence disappears completely from cyclothems of type A to cyclothems of type C.

One might feel the temptation, analysing the cyclothems of types A, B and C, to reconstruct from them the ideal cyclothem, consisting of the members 1—10. However the distribution of the cyclothems of types A, B and C in the sections considered and also in the stratigraphic sections measured by others (especially by Martínez Alvarez, 1962) do not support the hypothesis that such an ideal cyclothem may ever have been possible, because the cyclothems of type A are clearly restricted to the lower part of the sections in the Asturian basin (Calizas Inferiores and Calizas Superiores coal members), and cyclothems of types B and C, instead of being irregularly distributed in the stratigraphic sections, are found to follow a rather peculiar pattern (Enclosure 2). Apparently a group of cyclothems of type B (or type A in the lower part of the sections studied) is followed by a group of cyclothems of type C. Or, in other words, a group of cyclothems,characterized by marine transgressions, is followed by a group of cyclothems apparently without marine transgressions. This suggests that other rhythms of major scale ("mega-rhythms") (Enclosure 2) were superimposed upon the sedimentary rhythms ("micro-rhythms") which formed the cyclothems recognizable today. A detailed study of the sediments might solve this problem. Provisionally the mega-rhythms are defined here as a lower section of cyclothems with distinct marine influence and an upper section of cyclothems consisting of exclusively non-marine beds. The fact that these mega-rhythms can easily be followed through all the stratigraphic sections studied suggests that they have a regional value for correlations. Following the idea of Martínez Alvarez (1962, 1965), who subdivided the Carboniferous in Asturias into five "tramos", it is convenient to subdivide his "tramo productivo pizarroso" (productive shale series) which includes all the coal members in the basin (with exception of the Calizas Inferiores coal member) into ten "subtramos", corresponding to the ten mega-rhythms recognized here. Each "subtramo", just as each mega-rhythm, should be divided into a lower and upper part, thus permitting a subdivision of the Sama Formation which is much finer than the subdivision into coal members used until now.

These "subtramos" are indicated here by the numerals I — II — III — IV — V — VI — VII — VIII — IX — X. The lower part of each "subtramo" is indicated by the letter "A", the upper part by the

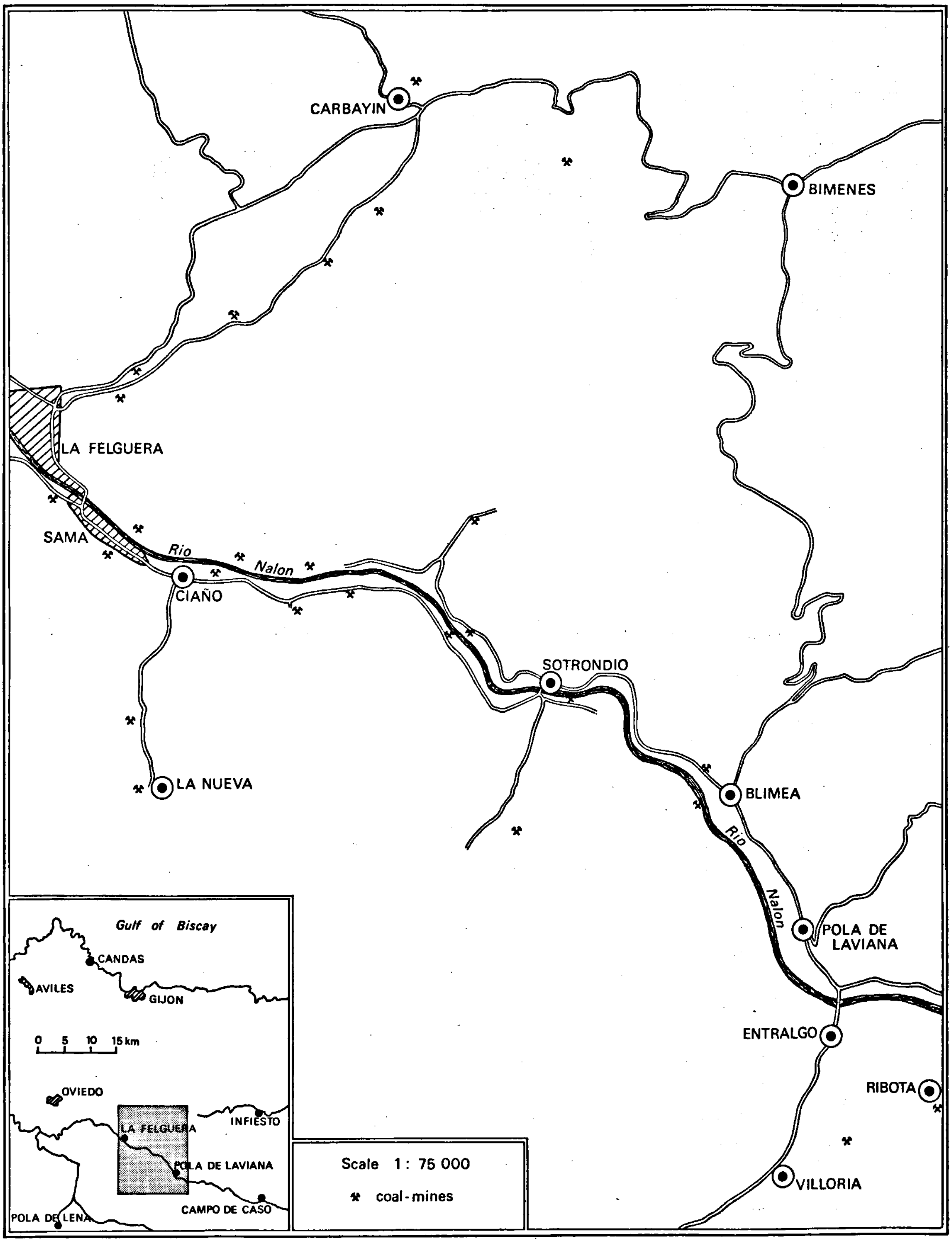



Fig. 2c. Geographic map of northeastern part of the Central Carboniferous Basin of Asturias.

letter "B". The "subtramo" X is subdivided provisionally into three parts, the part indicated "XC" probably representing a new "subtramo" (Enclosure 2). It should be noted that the limit between the lower and upper part of a single "subtramo" is often difficult to define and therefore somewhat arbitrary. The boundary between two "subtramos", however, is always easily recognizable.
It is interesting to observe that the boundary between two coal members defined by previous authors (fig. 2a; Enclosure 2) always coincides with either the limit between two "subtramos" or the limit between the lower and upper parts of a "subtramo". At the same time it should be noted that the stratigraphic value of the "calizas gonfoliticas" is greatly reduced. In the Mine Mosquitera the first "calizas gonfoliticas" appear in the Sorpresa coal member, in the Fondon and Sorriego mines they are already present in the Sorriego coal member (Enclosure 1). After finishing the correlation of the stratigraphic sections it was surprising to find in the Mosquitera section above the Oscura coal member an unknown coal member, representing the major part of the "subtramo X". This coal member, erroneously considered to represent the Sorriego coal member is named here the "Sorpresa coal member".

The coal seams (workable and unworkable) are located rather irregularly in the stratigraphic sections. On the other hand, however, they do have a slight tendency to concentrate in the upper parts of the "subtramos", this means in the exclusively continental part of these "subtramos". The same tendency has been recognized considering only the worked and workable coal seams (at least in the sections studied). On the other hand there seems to be no difference in thickness or regularity of the coal seams between the upper and lower parts of these "subtramos".

## LOCALITIES

Hollinid ostracodes belonging to the genera *Hollinella* and *Jordanites* have been collected from almost all marine beds in the Upper Carboniferous coal basins of Redondo in Palencia and of Asturias. Only those localities yielding the ostracodes described in this paper are listed below. All samples were collected by the author from beds immediately overlying the coal seams indicated in the localities.

*Locality in Redondo Coal Basin of Palencia*

Re20: Coal Mine "Pepe", about 1 km north of the village of Santa Maria de Redondo. Redondo coal beds. Stephanian A.

*Localities in Central Carboniferous Basin of Asturias*

Fr1—Fr104: Coal Mine "Villoria", near the village of Villoria (mine closed in 1967). Capa Cuarta coal. Calizas Inferiores coal member.

Fr105—Fr116: Coal Mine "Ribota", near the village of Ribota (mine closed in 1967). Capa Segunda coal. This coal bed has been correlated with the Capa Cuarta coal. Calizas Inferiores coal member.

Fe130: Coal Mine "Barredos, zona Blimea", tercera planta, near the village of Sotrondio (mine closed in 1967). San Luis coal. Maria Luisa coal member.

Fe249: Coal Mine "Pozo Venturo", segunda planta, near Sotrondio. San Antonio coal. Sorriego coal member.

Fe361: Coal Mine "Pozo Mosquitera primero", tercera planta, in the village Mosquitera. Adolfa coal. Modesta coal member.

La391: Coal Mine "Llascaras", tercera planta del pozo antiguo, near La Felguera. Venon coal. Sorriego coal member.

La393: Coal Mine "Llascaras", tercera planta del pozo antiguo, near La Felguera. Serradero coal. Sorriego coal member.

La412: Coal Mine "Pozo Pumerabule", sexta planta, near the village of Carbayin Bajo. Adolfa coal. Modesta coal member.

La422: Coal Mine "Pozo Pumerabule", sexta planta, near Carbayin Bajo. Carbonero Maroma coal. Sorriego coal member.

Fe455: Coal Mine "Pozo Fondon", septima planta, near Sama de Langreo. Segundo San Luis coal. Entrerregueras coal member.

As473: Coal Mine "Pozo Carbones Asturianos", quinta planta, primera rama, near the village of Ciaño. Capataz coal. Soton coal member.

As475: Coal Mine "Pozo Carbones Asturianos", quinta planta, selunda rama, near Ciaño. Capataz coal. Soton coal member.

Nu484: Coal Mine "Pozo San Luis", quinta planta, near the village of La Nueva. Coal 21 meters below the coal seam 15. Soton coal member.

Fe494: Coal Mine "Mina Modesta", piso primero, near Sama de Langreo. Coal layer 10 meters above the Seiz coal. Soton coal member.

m1004: Coal Mine "Llascaras", planta 375, near La Felguera. First coal above Dos Vetas coal. Soton coal member.

m1004a: Coal Mine "Llascaras", planta 375, galeria izquierda, near La Felguera. First coal above the Dos Vetas coal. Soton coal member.

m1013: Coal Mine "Llascaras", planta 325, near La Felguera. Serradero coal. Sorriego coal member.

m1023: Coal Mine "Pozo Pumerabule", sexta planta, near Carbayin Bajo. Estefania coal. Modesta coal member.

m1030: Coal Mine "Pozo Pumerabule", sexta planta, near Carbayin Bajo. Second coal above the Sucia coal. Sorriego coal member.
m1031: Coal Mine "Pozo Pumerabule", sexta planta, near Carbayin Bajo. First coal above the Sucia coal. Sorriego coal member.
m1044: Coal Mine "Pozo Pumerabule", sexta planta, near Carbayin Bajo. Raposa coal. Sorriego coal member.
m1050: Coal Mine "Santa Eulalia", decima planta, near La Felguera. About 45 meters above Escribana coal. Maria Luisa coal member.
m1053: Coal Mine "Santa Eulalia", decima planta, near La Felguera. Second coal above Angelita coal. San Antonio coal member.
m1055: Coal Mine "Santa Eulalia", decima planta, near La Felguera. First coal below Angelita coal. San Antonio coal member.
m1070: Coal Mine "Pozo Mosquitera segundo", tercera planta, in the village of Mosquitera. Coal about 97 meters above San Guillermo coal. Sorpresa coal member.
m1075: Coal Mine "Pozo Mosquitera segundo", tercera planta, in the village of Mosquitera. Coal about 108 meters above the San Guillermo coal. Sorpresa coal member.
m1081: Coal Mine "Pozo Mosquitera segundo", cuarta planta, in the village of Mosquitera. About 40 meters above Septima coal. Oscura coal member.
m1090: Coal Mine "Pozo Mosquitera segundo", cuarta planta, in the village of Mosquitera segundo", cuarta planta, in the village of Mosquitera. Adolfa coal. Modesta coal member.
m1091: Coal Mine "Pozo Mosquitera segundo", in the village of Mosquitera. First coal below the Adolfa coal. Modesta coal member.
m1093: Coal Mine "Pozo Mosquitera segundo", cuarta planta, in the village of Mosquitera. Cantera coal. Modesta coal member.
m1100. Coal Mine "Pozo Fondon", septima planta, near Sama de Langreo. First coal above the Falsa coal. Entrerregueras coal member.

## THE CARAPACE

In modern ostracodes (Podocopida and Myodocopida) the carapace is secreted by epidermal cells during the moulting process (cf. Van Morkhoven, 1962, pp. 29—30; Kesling in Treatise, 1961, p. Q19). The carapace consists of an outer and an inner lamella, which are fused by a chitin strip in the peripheral zone of the valves, the "zone of concrescence". Both the inner and outer lamella usually contain three layers. An outer chitin layer, a middle calcareous layer and an inner chitin layer can be distinguished. The calcareous layer may be only weakly developed (e.g. in many Myodocopida). In other ostracodes more than one calcareous layer seems to be present. In the genus *Cavellina* (Podocopida) four to nine layers have been recognized (Levinson in Treatise, 1961, p. Q73). A number of pore canals are present in the outer lamella and in the zone of concrescence. They have not been noted in the inner lamella. It is supposed that the carapace of Paleozoic ostracodes of the orders Leperditicopida and Palaeocopida was also secreted by epidermal cells, just as in recent forms. The presence of an inner lamella, characteristic of the Podocopida has not been observed in Paleozoic ostracodes, with the possible exception of the genus *Geisina* (cf. Sohn in Treatise, 1961, p. Q182).

In ostracodes of the suborder Beyrichicopina of Palaeocopida, adventral extensions are present on the carapace which are unknown in Podocopida and Myodocopida. These adventral extensions of the carapace are called "carina", "histium" or "velum" (cf. Jaanusson, 1957; Treatise, 1961). In accordance with the terminology of the Treatise (1961), the term "velum" is used here for the adventral extensions of the carapace of that section of the genera studied.

The term "domicilial wall" is applied to the carapace without adventral extensions.

The domicilial wall in the genera *Hollinella* and *Jordanites* is essentially layered as in most recent Podocopida.

In the velum two calcareous layers have been distinguished; these layers are a continuation of the single calcareous layer in the domicilial wall. An attempt is made to give a satisfactory explanation for this phenomenon.

In contradiction to the opinion of earlier authors, it is suggested here that juvenile specimens of *Hollinella* and *Jordanites* already had a well-developed velum. Thus, the presence of a velum in the genera *Hollinella* and *Jordanites* is not indicative of the adult state.

### THE DOMICILIAL WALL

The domicilial wall in the genera described here consists of one calcareous layer and two chitin layers (fig. 3). We can distinguish:

a) internal chitin layer, coating the interior of the domicilial wall
b) calcareous layer
c) external chitin layer, coating the exterior of the domicilial wall

A number of pore canals are present in both the lateral and subvelar part of the domicilial wall (fig. 4).

#### *Internal chitin layer*

This layer is usually not preserved in the ostracodes. In only a few specimens can a thin, opaque layer of pyrite be observed in thin sections "lining" the domicilium interiorly (fig. 4). This layer is assumed to be a pyritized chitin layer, since it occupies the same

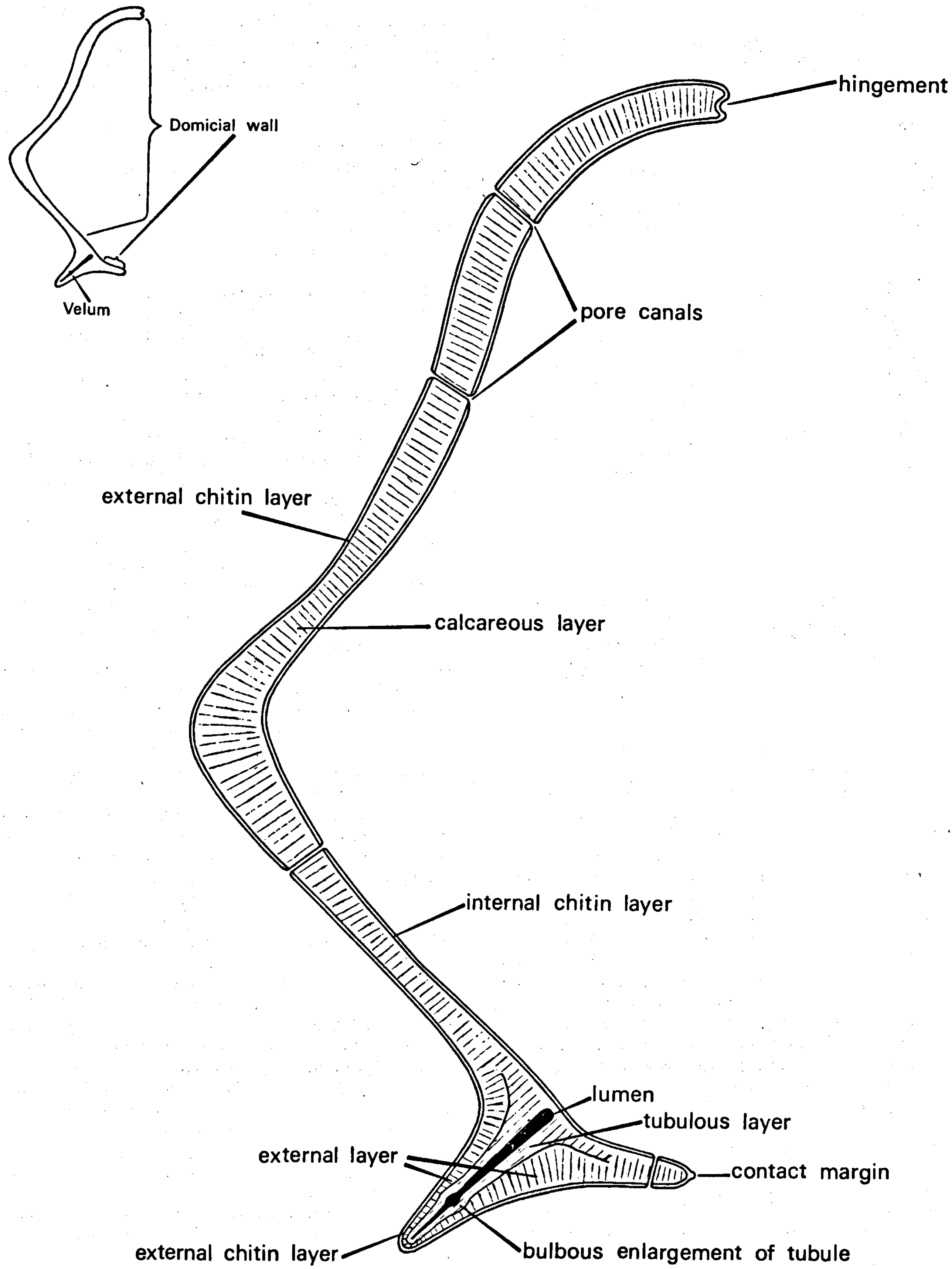



Fig. 3. Diagrammatic section through valve of adult hollinid ostracode.

Fig. 4. Thin section through *Hollinella camoni.* Re20-Hol.c. Chitin layers and part of calcareous layers pyritized. (175×)

position as the chitin layer in recent ostracodes. It does not seem reasonable to assume that this layer might also have been calcareous, because the calcareous layer is still present in some specimens with an unaltered microstructure.

A dark layer in place of the internal chitin layer has been noted in a large number of Paleozoic ostracodes by several authors. Kummerow (1933, pp. 43—44) described a dark inner layer in a species of *Primitia.* He suggested that it was a fossilized chitin layer. Hessland (1949) published some photos as thin sections through palaecopid ostracodes which show a distinct dark line occupying the same position as the internal chitin layer of recent ostracodes. Jaanusson (1957, pp. 192—193) maintained that this dark line,which also may be present in the velum as a "bisecting line", originated from the "inner chitin layer".

Scott (in Treatise 1961, p. Q24) stated that "sections of *Beyrichia* show that the velum is a downfold lined with the inner chitin layer. Even in *Hollinella* where the two sides of the velum are in contact, a dark line representing the infolded inner chitin layer is preserved."

Martinsson (1962, p. 356) questioned, however, Scott's statements. He did not find any evidence that an inner chitin layer was present in Paleozoic ostracodes.

The presence of an infolded internal chitin layer in the velum of *Hollinella* could not be proved in the thin sections studied here. The specimen shown (fig. 4) distinctly shows a dark (pyritic) line sealing off the lumen of the tubules from the domicilium. This line is certainly not infolded into the velum. Maybe the dark line mentioned by Scott represented a tubule in the velum or merely the contact of the two sides of the external layer in the velum.

*Calcareous layer*

In the genera *Hollinella* and *Jordanites* only one calcareous layer has been recognized in the domicilial wall. This layer consists of calcite prisms perpendicular to the outer surface of the carapace. The layer is thickest in the S2 and the ventral portions of the carapace. The domicilial wall is much thinner in juvenile specimens than in adults, especially in the ventral part of the carapace. Apparently the carapace was less calcified in the earlier moultings than in the last moulting when the animal reached maturity. The very thin calcareous layer in the domicilial wall of juvenile instars corresponds with the absence of an external (calcareous) layer in the velum.

Kesling (1954, p. 18) gave examples of hollinid ostracodes with two calcareous layers, usually each with a different ornamentation. He suggested that "the thin outer layer may be the replacement of chitin by calcium carbonate during fossilization."

*External chitin layer*

A thin outer layer of pyrite has been recognized in specimens of *H. camoni.* The calcareous layer here is well-developed and coated with a thin layer of pyrite on both sides. In recent ostracodes we find a thin chitin layer on both sides of the calcareous layer and it seems reasonable to suppose that this outer pyrite layer is a pyritized chitin layer.

In juvenile specimens an external chitin layer also seems to have been present, since indications have been found that the velum in juveniles contained an external chitin layer.

## THE VELUM

The velum in the genera *Hollinella* and *Jordanites* is a lateral extension of the domicilial wall running subparallel to the free margin, beginning at the anterior cardinal corner and lying below the ventral lobe. The greatest width lies antero-ventrally. In the posterior section of the carapace the velum may be small or absent. The velum is a three-layered structure (fig. 3), although in juveniles of *Jordanites* and *Hollinella* only two layers are developed. It should be noted that in this paper the term "velum" is also applied to the velar structure, which is present in juvenile stages. In the velum of an adult *Hollinella* (or *Jordanites*) we distinguish:

a) tubulous layer, being the lateral extension of a part of the calcareous layer of the domicilial wall
b) external layer, being the lateral outfold of a part of the calcareous layer of the domicilial wall

c) external chitin layer, being the lateral outfold of the domicilial wall.

The external layer is not developed in juvenile specimens.

*Tubulous layer*

The tubulous layer in adult ostracodes is covered by the external layer and the external chitin layer. In juveniles, however, this layer can be studied easily, since the external layer has not developed and the external chitin layer has disappeared.

In juvenile specimens of *H. cristinae* the tubules composing the tubulous layer are relatively large and therefore are most appropriate for a detailed examination (fig. 5). The tubules lie with some interspacing in a single row. In the four juvenile instars recognized in this species, the relative distance between the tubules decreases slightly from the fifth instar through the eighth instar. The tubules in a specimen of the fifth instar are approximately 0.1 mm long, or about one fourth of the total height of the carapace. In a specimen of the eighth instar they are approximately 0.12 mm long or about one-fifth of the total height of the carapace. The width of the tubules for a specimen of the eighth instar is about 0.04 mm at their proximal end and 0.002 mm at their distal end, where the tubules are multi-furcated. The tubules were originally hollow and have filled with sediment or with secondary clear calcite. They are open at their proximal end in juvenile instars and communicate with the interior of the domicilium. There does not seem to be any connection with the exterior at the distal end. The tubules are a continuation of at least a part of the calcareous layer of the domicilial wall. This can be seen in an interior view of the carapace (fig. 6).

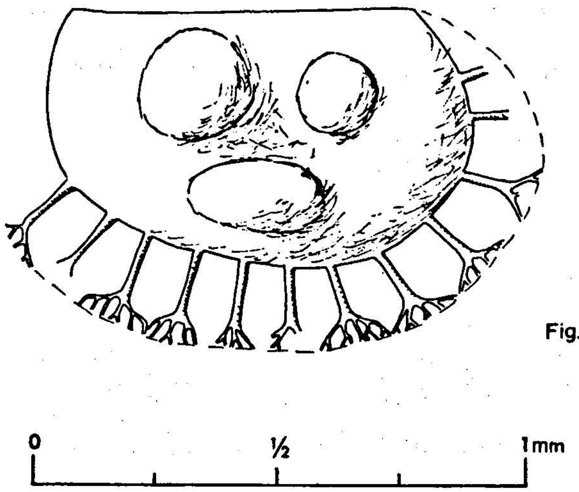



Fig. 5a

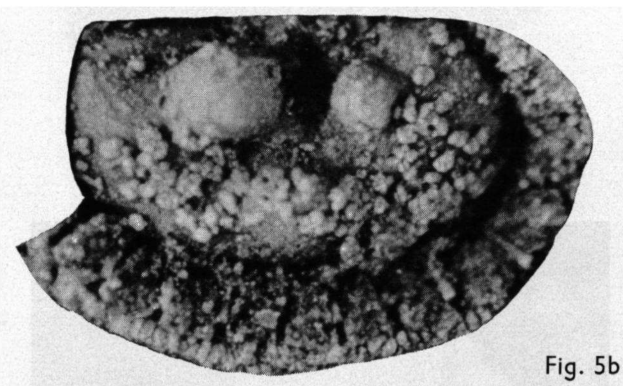


Fig. 5b

Fig. 5a-b. RV of juvenile specimen of *Hollinella cristinae* (eighth instar). Note well-preserved tubulous layer. Fr8-26.

Fig. 6. Interior view of LV of juvenile specimen of *Hollinella cristinae* (eighth instar). Fr116-2.

In adults the tubules are closed and no communication with the interior of the domicilium has been found. In adults the tubules are placed in two rows. In each row they are separated by a distance equal to their own diameter. The tubules of both rows intercalate near the peripheral margin of the velum. This has been observed in several species of *Hollinella* (fig. 7).

In other species of *Hollinella* (e.g. *H. camoni*) and *Jordanites* (e.g. *J. rawihinggili*) the tubules are extremely thin (usually less than 0.01 mm at their proximal end).

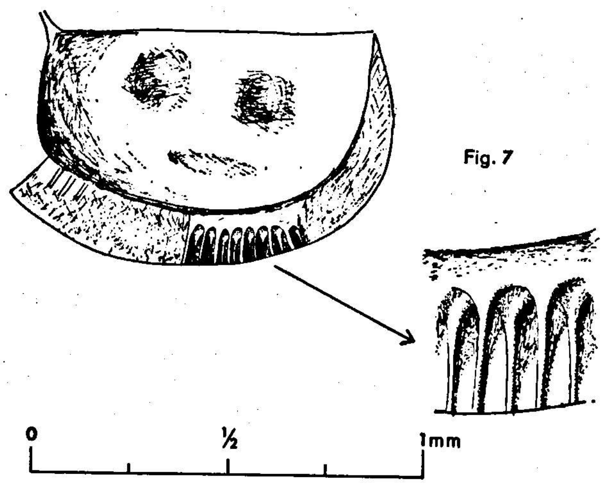



Fig. 7

Fig. 7. LV of adult specimen of *Hollinella* sp. (interior view). Tubulous layer partly visible because external chitin layer and external layer have been removed by selective weathering. B1493-47.

They are distinctly hollow, as in *H. cristinae*. This can be easily observed when the tubules are broken (fig. 8). In juvenile forms they may open into the interior of the domicilium. In adults, no connection with the

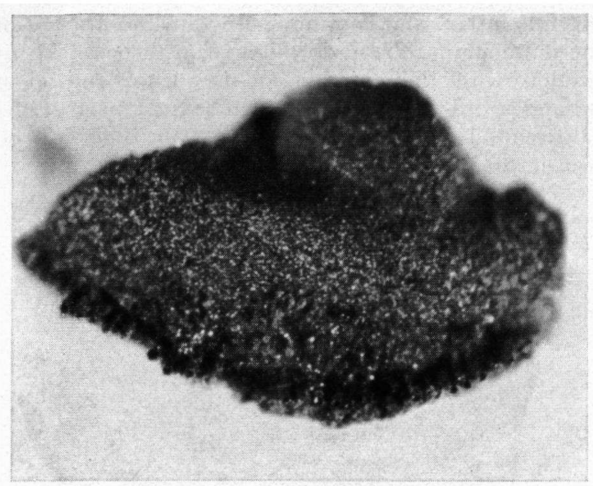


Fig. 8. Fragment of juvenile specimen of *Hollinella camoni*, showing lumen in the tubules. Re20-18.

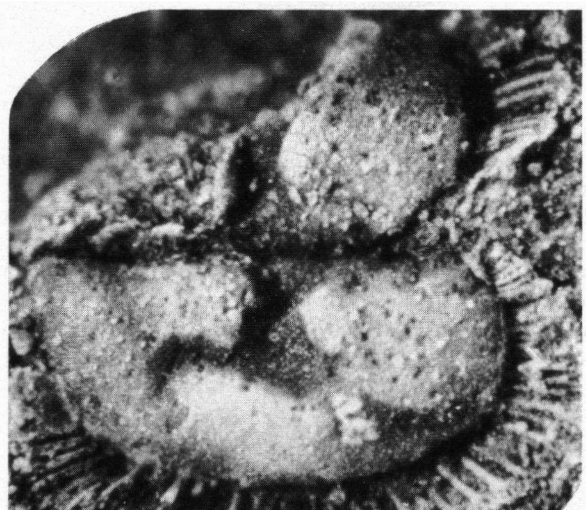


Fig. 9a. RV of juvenile specimen of *Jordanites rawihinggili* (eighth instar). Fe361-18.

interior of the domicilium was ever found. The tubules always seem to be furcated at the distal end. The number of furcations and their shape appear to vary in some species within one instar, and even for one specimen (fig. 9). In one species (*H. camoni*), the tubules show a bulbous enlargement near the distal end, just before the furcations (fig. 10).
The micro-structure of these tubules could not be identified. They seem to have been originally calcareous. Possibly they consist of calcite prisms, just as the calcareous layer.

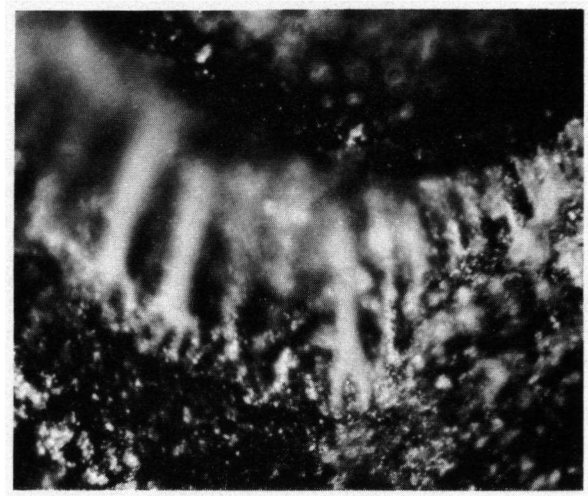
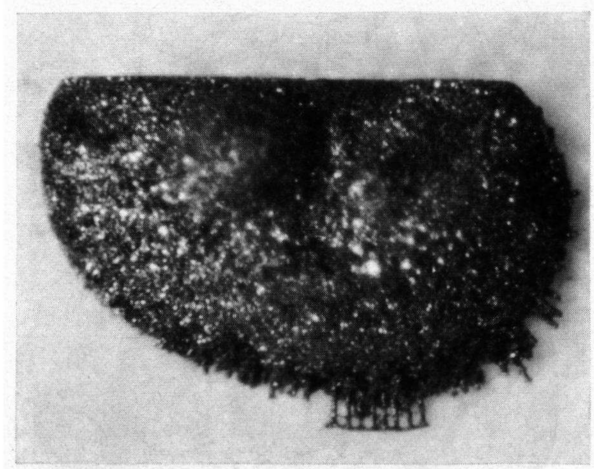


Fig. 9b. Magnification of anteroventral part of velum of same specimen as Fig. 9a, showing different types of furcation.

The tubulous layer is not restricted to the velum of *Hollinella* and *Jordanites*.
Kesling (1955, p. 269) described a similar structure in the velum of adults of *Oepikium tenerum* (Opik, 1935).



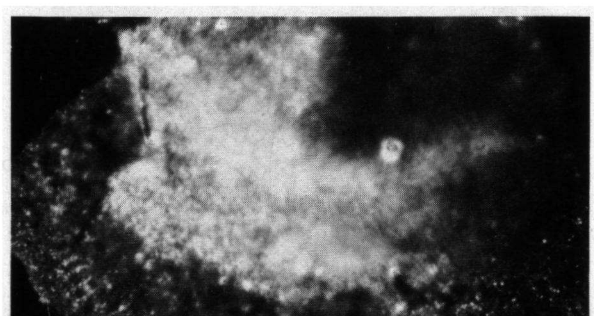


Fig. 10a-b. RV and fragment of juvenile specimens of *Hollinella camoni* (eighth instar). Tubules showing bulbous enlargement. Re20-12 & Re20-13.

In this species the tubules are comparable with those described here for *H.cristinae*. Some tubules are furcated at their distal end. In *O. tenerum* the tubulous layer is also covered by a thin layer, comparable with the external layer described in this paper.
In *Piretella reticulata* (Krause, 1891) a velar structure with a tubulous layer was noticed by Kummerow (1933, p. 48). The tubules are hollow and communicate with the interior of the domicilium. Each tubule has one or more bulbous enlargements, similar to *H. camoni*. In a specimen of *Bollia granulosa* Krause, 1891, shown by Kummerow (1939, pl. 7, fig. 13), some distinctly furcated tubules can be distinguished in the weathered posterior part of the velum.
Tubules in velar structures of adult specimens of Middle Devonian hollinid ostracodes have been recognized by Melik (1966) in species of *Adelphobolbina*, *Falsipollex*, *Hollinella* and *Ruptivelum*. He stated (p. 240) that "the tubules neither communicate with the interior of the carapace, nor reach the outer edge of the frill. They were probably sealed off from the interior of the carapace by secretions of the hypodermis."
Jaanusson (1957, p. 230) described a layer of narrow radial tubules, surrounded by an external layer, in the eurychilinid frill. He noticed that "in specimens of *Oepikella tvaerensia* Thorslund, 1940, immersed in some liquid, narrow tubules give the impression to pierce the contact area between the domicilium and the velum, and thus open probably in the interior." He stated that "the presence of internal openings of the tubules in other eurychilinid genera is less certain. A peripheral opening of the tubules has not been observed so far in any specimen. In order to obtain absolute certainty in respect to such minute details of the construction of the frill exceptionally favourable preserved specimens are needed, which have not been available." Jaanusson noted that the pore space in some tubules was filled with secondary clear calcite, pyrite or hematite. He did not mention whether the tubules in these cases were broken in order to allow a mineral solution to enter the pores and subsequently to crystallize, or whether they had any openings to the interior of the carapace.
Martinsson (1962) noted tubules in the velum of beyrichiids. He never found any communication of the tubules with the domicilium. He believed (op. cit., p. 72) they were formed by "a differentiation of the epithelium, the processes of the epithelium being retracted or resorbed before the calcification of the carapace was completed." He recognized one (juvenile??) specimen (op. cit., fig. 20) in which the tubules have a distinct communication with the interior of the carapace. He supposed that this was an adult specimen in which the calcification was not completed.
Spjeldnaes (1951, p. 753) stated that tubules in the velum of *Beyrichia jonesi* Boll, 1856, consist of calcite prisms with their c-axes parallel to the direction of elongation of the tubules. This could be neither proven nor disproven with the thin sections of the specimens studied here.
It should be noted that the tubulous layer is extremely fragile. Usually the tubules are broken and a row of small tubercles or spinelets remains. Sometimes the tubules are broken at their base and the carapace seems smooth where the tubulous layer should be. This seems to be the case in most of the American specimens shown by earlier authors.

*External layer*
In the genera *Hollinella* and *Jordanites* the external layer has been recognized only in adult specimens. Because the external layer is a continuation of a part of the calcareous layer of the domicilial wall, it is quite understandable that the domicilial wall is thin in juvenile specimens where the external layer is absent and relatively thick in adults where the external layer is well-developed. The external layer is a lateral outfold of part of the calcareous layer of the domicilial wall and covers the tubulous layer completely. The external layer consists of calcite prisms perpendicular to the outer surface of the velum (fig. 3). In *H. cristinae* and *H. hispanica*, the external layer becomes extremely thin in the peripheral part of the velum and the tubulous layer below it is visible in the form of a row of radial striae in the peripheral part of the velum. For instance, in *H. camoni* the tubules of the tubulous layer are thin and the external layer is relatively thick. Here the velum appears practically smooth. The external layer was described by Jaanusson (1957, p. 230) as a "layer, covering a layer of narrow, radial tubules in the eurychilinid frill". He concluded that the "external layer is continuous with a thin layer of the domicilial wall." This conclusion is in accordance with the present writer's observations.

*External chitin layer*
It is supposed that the velum and the carapace were coated originally by an external thin chitin layer. This layer has not been preserved in any specimen studied. However, in a number of juvenile specimens of a.o. *J. rawihinggili*, *H. cristinae* and especially in *H. hispanica*, a faint imprint in the shale between the rather widely spaced tubules of the velum has been recognized and is believed to have been caused by the external chitin layer (fig. 11). It is suggested here that this external chitin layer was present in all species and both in juveniles and in adults. If this interpretation is true, the velum of juveniles of *Hollinella* and *Jordanites* was an essentially uninterrupted structure, similar to that of adults of these genera.
Spjeldnaes (1951) showed juvenile specimens of *Beyrichia jonesi* with an uninterrupted velum.
Martinsson (1962) showed juvenile instars of *Craspedobolbina* (*Mitrobeyrichia*) *clavata* (Kolmodin, 1869) which have an uninterrupted velum, just as the adults of that species.
Sohn (pers. comm.) recognized a *Hollinella* species in the Permian of Texas, in which a juvenile instar has

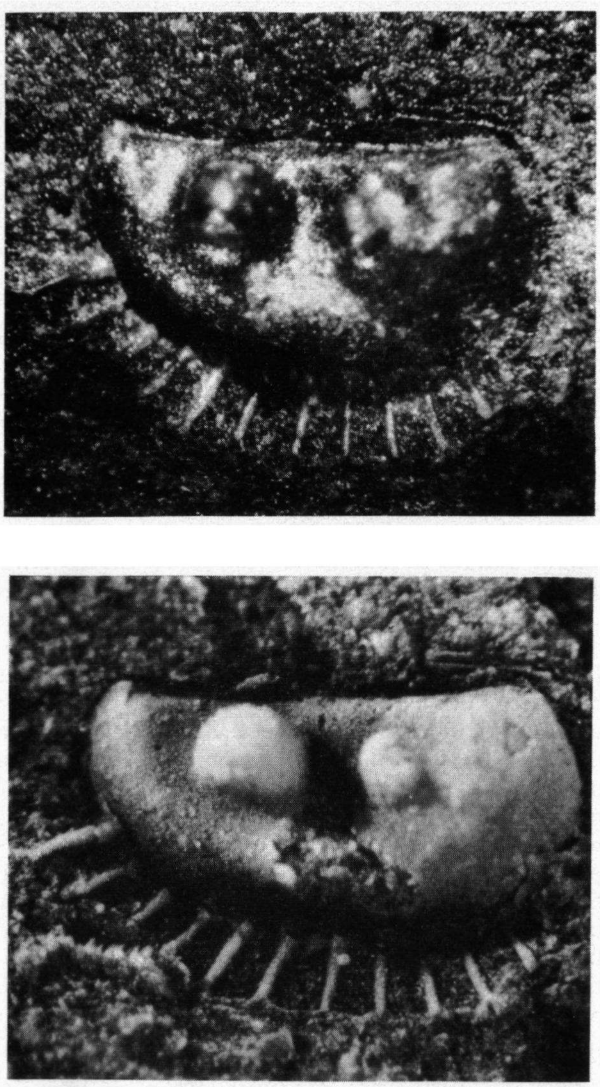


Fig. 11a-b. LV of juvenile specimen of *Hollinella hispanica* (eighth instar). Note imprint of external chitin layer between the tubules. m1004a-9. (fig. 11b coated with ammonium chloride)

the same velar structure as the adults. This might be a specimen with the external chitin layer of the velum preserved.

The observations described above can be summarized as follows. The domicilial wall in the genera *Hollinella* and *Jordanites* was three-layered (fig. 3). In the velum of adults the calcareous layer is differentiated into the external layer and the tubulous layer. In juvenile specimens the external layer in the velum is not developed. The tubulous layer in these juveniles is already well-developed. The tubules of the tubulous layer in the velum may communicate with the interior of the domicilium in juvenile instars. In adults, no trace of any communication between the domicilium and the tubules could be detected.

It is suggested here that the secretion of the carapace by the epidermal cells in the Palaeocopida studied was similar to that of the modern Podocopida. First the external chitin layer was secreted. Subsequently the calcite prisms of the calcareous layer of the domicilial wall and the external layer of the velum were formed. When the external layer in the velum was calcified completely the epidermal cells in the velar zone differentiated and the tubules of the tubulous layer were calcified, whereas the secretion of calcite prisms of the calcareous layer in the domicilial wall may have continued. Finally a new chitin layer secreted, coating the interior of the domicilium. In juvenile specimens the differentiation of the epidermal cells in the velum occurred immediately after the secretion of the external chitin layer and no external layer was formed.

*Function of the velum*

The function of the velum is not fully understood. Kellett (1929, pp. 197—198) distinguished three forms in the genus *Hollinella*. An unfrilled form with a row of small spinelets or tubercles, which should represent males and juveniles; a narrow frilled form and a wide frilled form. These frilled forms were supposed to be nonproductive and productive females, respectively. She suggested that the space between the frills was a place for temporary lodging and protection of the brood.

Blake (1930, pp. 297—298) pointed out that recent ostracodes are not known to moult after reaching maturity and thought it "certainly unreasonable to suppose that the Beyrichiidae [= Palaeocopida in the present paper] differ essentially in this respect from recent Podocopida." Blake suggested that the velum "may have served to protect the appendages when projected from the valves. Second, and more likely, they may have served as outriggers to prevent the animal from sinking deeply into the soft mud, on the surface of which many forms live. It is, of course, possible that the frill subserved no function whatever."

Kummerow (1939, p. 48) suggested that the tubules in the velum of *Piretella* contained eggs.

Cooper (1946, pp. 88—89) was the first to state that the forms described by Kellett in 1929 represent juveniles, females and males respectively. He pointed out that the narrow frilled forms have a larger domicilium than the wide frilled ones. Since the females of recent ostracodes, for instance the Podocopida, have a larger domicilium than the males this might also be the case for Palaeocopida. Pozner (1951, pp. 46—47) used the term "pore canal frill" in his description of *Hollinella avonensiformis* Pozner, 1951 and *H. sokolovi* Pozner, 1951 (cf. Catalogue of Ostracoda by Ellis and Messina, supplement 3, 1965). Apparently he thought that the tubules in the velum had the same function as the (radial?) pore canals in Podocopida.

Kesling (1951, pp. 166—167) gave examples of species of *Hollinella* in which the wide frilled forms are, according to him, the females. Spjeldnaes (1951, p. 754) also stated that the tubules in the velum communicated with the interior of the domicilium as well as with the exterior. He supposed they were pore canals. This was denied by Martinsson (1962, p. 72). Jaanusson (1957, p. 205) suggested that the narrow frilled forms of *Hollinella* might be males and the wide frilled specimens females. In the Treatise (1961, p. Q137) Kesling considered the narrow frilled forms of *Hollinella* males and the wide frilled ones females.

The suggestions of Kummerow and of Pozner and Spjeldnaes that the tubules in the velum of Palaeocopida might have served as a deposit for eggs and as pore canals, respectively, do not seem tenable since they have no communication with the interior of the domicilium in at least a large number of species.
The hypothesis presented by Cooper that the narrow frilled individuals of *Hollinella* represent females is contradicted by Kesling and by Jaanusson, who supposed that they are males. This author believes that Cooper's idea is supported by the fact that in the narrow frilled specimens of *H. camoni*, the L3 is twice as large as in the wide frilled forms. An inflation of the posterior part of the domicilium has also been noted for the females of recent Podocopida and in the supposed females of Kloedenellacea. Moreover these narrow frilled specimens of *H. camoni* also have a larger domicilium than the wide frilled ones. It should be noted that in other species of *Hollinella* the size of the L3 is not as distinctly different for both dimorphs. If the hypothesis of Cooper is true and the narrow frilled forms should represent females, then the idea that the velum served as a place for temporary brood care as suggested by Kellett is no longer tenable. The first suggestion by Blake that the velum served to protect the appendages when protruded from the carapace is not tenable in those cases where the velum is orientated in an almost lateral direction (e.g. *H. camoni*). This was already explained by Jaanusson (1957, p. 201). The only hypothesis which seems reasonable, at least with the present state of our knowledge, is the second suggestion by Blake: that the velar extensions served as outriggers to prevent the animal from sinking too deeply into a soft substrate. The fact that a velum was already developed in juvenile instars of all Palaeocopida investigated so far is thought to support this idea. The tubulous layer might be explained as a reinforcing skeleton, especially for the rather fragile lateral extensions of the juvenile carapace.

## ONTOGENY

Ostracodes have a discontinuous growth. Since they, like other crustaceans, have an ectodermal skeleton (the carapace), increase in size and weight can only occur when the external hard parts encasing its body are shed (moulting). Before a new carapace is formed, the ostracodes increase their volume and add new organs and appendages to their anatomy.
Thus the ostracode ontogeny consists of a fixed number of stages in which growth occurs (moultings) and a fixed number of stages in which the form and shape of the animal are constant (instars). The number of instars has been investigated for several recent and fossil ostracode species. Within one species, the number of instars seems to be constant (cf. Kesling, 1953). In most species nine instars have been detected. The first instar is the youngest stage after the ostracode has hatched from the egg. The ninth instar is the adult stage. Only one adult stage is known for ostracodes (cf. Müller, 1912, p. 5; Klie, 1926, p. 16—47; Elofson, 1941). Species with a different number of instars are known (cf. Spjeldnaes, 1951). For fossil ostracodes the number of instars is virtually unknown. It seems, however, useful to suppose that fossil ostracodes also went through nine instars. This is confirmed by reports of among others Cooper (1945) and Martinsson (1962). The adult forms are then placed in the ninth instar and the juvenile forms in the successively younger instars. This has been done by Kesling (1952a) in his study on *Ctenoloculina cicatricosa* (Warthin, 1934). In the present paper this example is followed.
According to Przibram (1931) ostracodes double their size during each moulting. Several investigations on ostracode growth (e.g. Kesling, 1952a; Martinsson, 1957) confirmed Przibram's theory. Kesling (1952b, p. 773) calculated that when the size of the carapace doubles, the linear dimensions of the carapace increase exactly 1.25992 times the dimensions of the former instar, if the shape of the animal and the carapace remained constant from one instar to the next. This is in accordance with the hypothesis of Fowler (1909, p. 229) that ostracodes increase their length in each growth stage by a fixed percentage. This percentage should be approximately constant for a given species. Kesling (1952a) applied this hypothesis to *Ctenoloculina cicatricosa* and found a mean value of 1.26 for the linear growth factor. This is very close to the theoretical value he calculated.
Spjeldnaes (1951) in his study on *Beyrichia* (*Mitrobeyrichia*) *clavata* Kolmodin, 1869, found values for the linear growth factor varying between 1.21 and 1.30. In the last moulting the linear growth factor was, however, distinctly lower (about 1.14).
Martinsson (1957) in his paper on the ontogeny of Silurian ostracodes reported values for the linear growth factor in species of *Beyrichia* of 1.20 to 1.30. In the last moulting the linear growth factor was lower: 1.12 to 1.21. He explained that "this low linear growth does not correspond to an equally small volume growth, as the voluminous brood pouches are developed in this (last) instar." In the present investigation, the results of the authors

mentioned above are roughly confirmed. The linear growth factor in the earlier moultings varies between 1.20 and 1.34. In the last moulting low values of 1.10 to 1.16 have been calculated although a distinct increase in the size of the L3 could be determined (e.g. *H. camoni*). A value of 1.26 for the linear growth factor in the last moulting has been calculated for *Jordanites rawihinggili* where the shape of the adult carapace remained the same as that of the juvenile instars. The increase in height is lower than the increase in length in most cases. This was also concluded by Martinsson (1957, p. 8) for beyrichiids.

The shape of the carapace changes during each moulting. In the last moulting when the animal reaches maturity, the change in the shape of the carapace is more pronounced than in the previous moultings.

The development of some features is very gradual. This was also concluded by Martinsson (1957, p. 8) for the surface ornamentation. In the present study the same conclusion has been made.

Kellett (1929) noticed that the ventral lobe is further developed than the L2 and L3 in early juvenile instars of *Hollinella*. In later instars the L2 and L3 become the most prominent features of the carapace. This is also true for the Spanish species of *Hollinella*. The S2 gradually becomes broader and deeper during ontogeny.

The velum, too, develops gradually during the ontogeny. Martinsson (1957) reached the same conclusion for species of *Beyrichia*. In the present study this was noted for *Hollinella* and *Jordanites*. In the younger instars the tubulous layer develops more tubules at every moulting. Pokorny (1950, p. 582) supposed that this process was extended to such a degree that a continuous velum in *Hollinella* "is often formed by the fusion of a row of spines, as may be seen in the young stages of the genotype, *Hollinella dentata* Coryell, 1928." This hypothesis appeared to be untenable in the present study.

In the last moulting the external layer is secreted. The secretion of the external layer corresponds to the development of a thicker calcareous layer in the domicilial wall.

In contrast to the gradual development of the features mentioned above, dimorphic characteristics appear suddenly in the last moulting. The width and shape of the velum in the adults may vary considerably in both sexes. This has been noted in many hollinellid species (cf. Cooper, 1946; Kesling, 1953; Kesling & Weiss, 1953; Kesling & Peterson, 1958; Weiss in Melik, 1966). In the Spanish *Hollinella camoni*, the L3 is also different in males and females. This is the first species of the genus where the lobes show dimorphic features. In *Jordanites rawihinggili*, the dimorphism is perhaps found in the ventral part of the carapace. In the presumable females this is much wider than in presumable males.

One feature of the carapace appears to be restricted to juvenile instars and disappears in the last moulting. Martinsson (1957, 1962) described spinelike extensions at the cardinal corners of the right valves of a *Beyrichia* species in juvenile instars. He called them the "larval processes." He noted that the larval processes disappear gradually during ontogeny and are absent in adult specimens. In the genus *Hollinella* some species have similar spines on the cardinal corners. They show a progressive development during the juvenile instars and disappear suddenly in the last moulting. In e.g. *Hollinella camoni* and *Hollinella hispanica* they have been recognized in the left valves of juvenile specimens (fig. 12). The spine on the anterior cardinal corner (antero-dorsal spine) is completely absent in adults. The spine on the posterior cardinal corner (postero-dorsal spine) appears to be relatively thinner and smaller in adults. In *Hollinella cristinae* and *Jordanites rawihinggili*, only a postero-dorsal spine has been recognized in juvenile specimens. The presence of an antero-dorsal spine is, however, not excluded. In both species the postero-dorsal spine is smaller for adults. In *J. rawihinggili* this spine is practically completely reduced and only visible in very well preserved specimens. The function of these larval

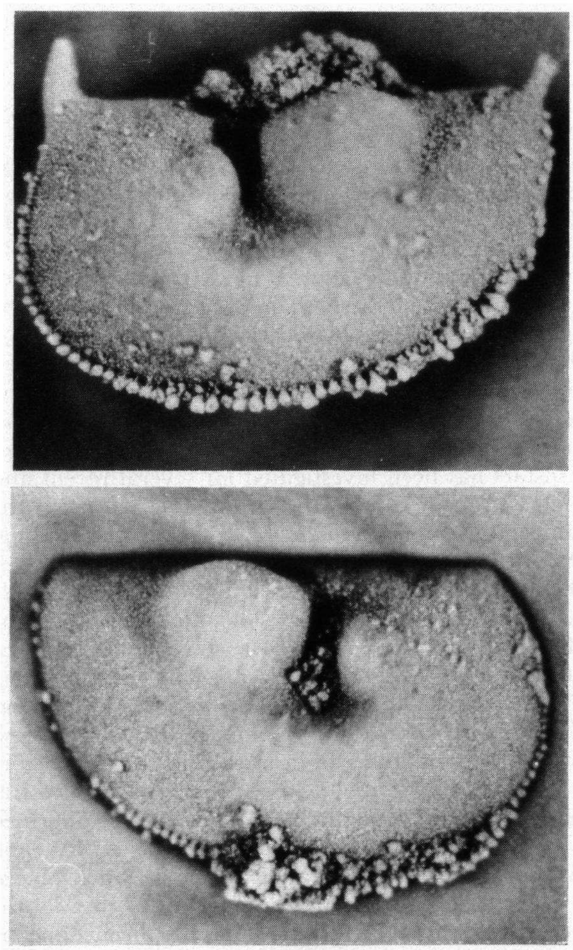


Fig. 12a-b. LV and RV of juvenile specimens of *Hollinella camoni* (eighth instar). Note larval processes in left valve. Re20-14 & Re20-15.

processes is not known. Martinsson (1957) suggested they might have served, in some way, the brood pouches of the females of the beyrichiids. In the genus *Hollinella* such brood pouches are, however, unknown. Moreover they become better developed in older instars before their sudden disappearance in the last moulting. This is in contrast to the observations of Martinsson for beyrichiids.

## PALEOECOLOGY

The genus *Hollinella* had a world-wide distribution. Species have been described from Europe, North America, Asia and Australia. All species lived in a full-marine habitat as far as is known. They have been recognized in association with articulate brachiopods, marine lamellibranchs, bryozoans, corals and trilobites. Kremp & Grebe (1955) described them from marine environments from the Lower Westphalian of Germany. Lane (1964) considered the ostracodes of this genus typical indicators for marine deposits. Calver and Hecker recognized species of *Hollinella* only in marine sediments from the Carboniferous of England and the USSR respectively (pers. comm.). Bless (1965, 1967a) described species of *Hollinella* and *Jordanites* from marine strata in the Westphalian and Stephanian of NW Spain. Patte (1935) recognized *Hollinella* in Permian strata of China in association with marine lamellibranchs.

As far as is known, species of these genera have a relatively short stratigraphic range. Therefore they should be excellent index fossils. Their practical use is, however, reduced by their restricted geographic distribution. This may indicate that they had no planctonic stages during their lives. This hypothesis is supported by the fact that in the samples studied from the Upper Carboniferous of Spain, juvenile and adult specimens of the same species frequently are found in close association. In a single locality, a bed as thick as two meters may contain only one or two species throughout the entire bed. In another bed only a few meters higher in the stratigraphic sequence a different species may be present, also with both adults and juveniles. Because the sequences, in which the ostracode beds have been recognized, are characterized by continuous transgressions and regressions it is suggested here that the animals invaded an environment only during the transgressive period and remained there during the regressive period. Apparently no other species later invaded the same environment after the transgression had stopped. If these ostracodes were planctonic in their early juvenile stages they might also have invaded the environment later.

The most prolific faunas of hollinid ostracodes have been noted in beds where marine lamellibranchs predominate over other fossils. In beds where brachiopods are the only macro-fossils present they are practically absent, unless pectinids can be recognized. In brachiopod beds, the non-velate, presumably creeping and burrowing ostracodes are common (Bless, 1968). Because brachiopods are not vagrant in contrast to many lamellibranchs (e.g. pectinids), it is suggested that brachiopods and presumably creeping and burrowing ostracodes needed other environmental conditions than lamellibranchs and hollinid ostracodes. It is supposed that the substrate was one of the most important controlling factors for brachiopod/non-velate ostracode distribution as well as for lamellibranch/velate ostracode distribution. Those conditions of the substrate favourable for the brachiopods were apparently not suitable for the hollinid ostracodes. This implies that the hollinid ostracodes lived in immediate contact with the substrate. According to Hartmann (1964, p. 36) the shape of these ostracodes seems to favour a swimming mode of life. He compared the shape of Palaeocopida with that of recent ostracodes. If this is true, *Hollinella* and *Jordanites* may have been near-bottom swimmers. During the sixth International Carboniferous Congress in Sheffield (1967) several papers were presented which support this suggestion.

## SYSTEMATICS

Order PALAEOCOPIDA Henningsmoen, 1953
Sub-order BEYRICHICOPINA Scott, 1961
Super-family HOLLINACEA Swartz, 1936

*Diagnosis:* The super-family Hollinacea in this paper is defined in the same way as in the Treatise (1961). The families included show distinct velate structures in at least one of the dimorphs in adults. Jaanusson (1957) distinguished between Eurychilinacea and Hollinacea, because he supposed that the adventral extensions of the carapace in these super-families were of different origins. It seems, however, that this is not tenable, since the adventral structures in both the Eurychilinacea and in the Hollinacea may have been similarly formed. The velum in *Hollinella*, *Jordanites* and *Oepikium* is quite similar to that of the Eurychilinidae according to the description by Jaanusson (1957, pp. 230—231).

Family HOLLINIDAE Swartz, 1936

*Diagnosis:* The family Hollinidae is composed of a rather variable group of genera, which are characterized by different types of lobation, sulcation, velate structures and dimorphism. The family was characterized by Kesling (in Treatise, 1961, p. Q133) as follows. "Carapace slightly inequivalved, with strongly developed lobation, including bi-, tri- and quadrilobate types. L3 large and bulbous in many genera; velar structures more or less prominent, restricted to

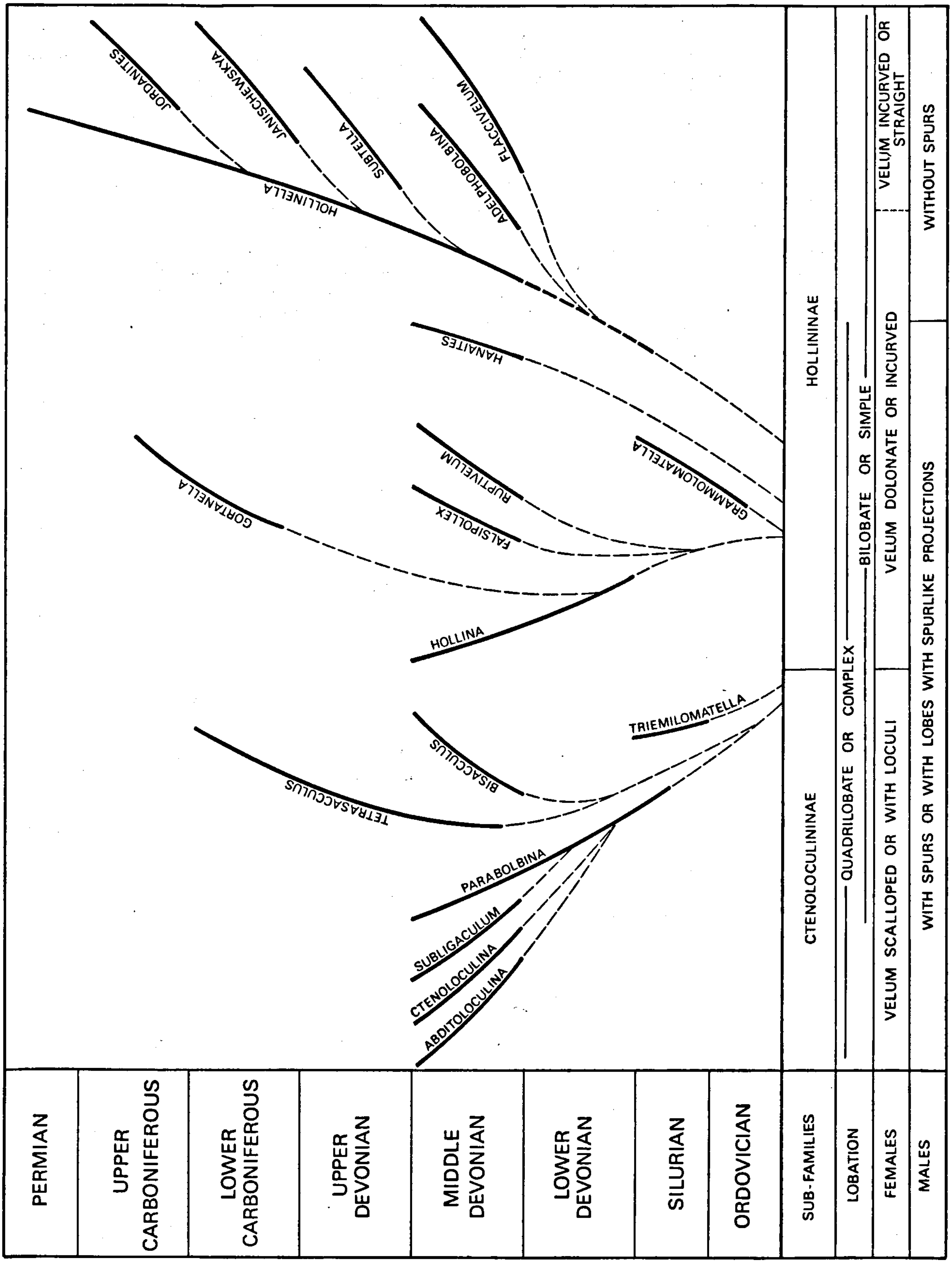



Fig. 12c. Generic relationships of 21 hollinid genera (after data of a.o. Kesling, 1952c and Kesling & McMillan 1951; modified).

anterior and ventral parts of free border. Dimorphism distinct, shown primarily by form of velar structures. Surface commonly papillate (Kesling, 1952, Swartz, 1936)."

Jaanusson (1957) denied the velate nature of the adventral structures and considered them of histial origin. As stated above this is not tenable since the velum in at least some genera is quite similar to that of Eurychilinidae, which possess a distinct velum, (cf. Jaanusson, 1957, pp. 230—233).

Sub-families HOLLININAE Swartz, 1936
CTENOLOCULININAE Jaanusson & Martinsson, 1956.

Jaanusson & Martinsson (1956) and Jaanusson (1957) proposed a subdivision of the Hollinidae into two sub-families. This subdivision is supported by investigations on the generic relationships of Hollinidae from the Devonian by Kesling (1952c) and Kesling & McMillan (1951).

The Hollinidae are characterized by "unisulcate to quadrilobate hollinids lacking the loculi in heteromorphs (= females). Dorsal part of L1 and L3 often bulbous, but not produced into a spine" (Jaanusson, 1957, p. 409). The Ctenoloculininae are characterized by "unisulcate to quadrilobate Hollinidae with locular dimorphism" (Jaanusson & Martinsson, 1956, p. 402). The Ctenoloculininae are not further discussed here.

Sub-family HOLLININAE Swartz, 1936
Genera ADELPHOBOLBINA Stover, 1956
FALSIPOLLEX Kesling & McMillan, 1951
FLACCIVELUM Kesling & Peterson, 1958
GORTANELLA Ruggieri, 1966
GRAMMOLOMATELLA Jaanusson, 1957
HANAITES Pokorný, 1950
HOLLINA Ulrich & Bassler, 1098
HOLLINELLA Coryell, 1928
JANISCHEWSKYA Batalina, 1924
JORDANITES Bless, 1967
RUPTIVELUM Kesling & Weiss, 1953
SUBTELLA Zaspelova, 1952

*Grammolomatella* is the oldest genus known. It has been recognized in the Ordovician and Silurian. *Adelphobolbina, Falsipollex, Hanaites, Hollina* and *Ruptivelum* are restricted to the Devonian. *Hollinella* ranges from the Middle Devonian into the Middle Permian but may already be present in the Upper Silurian (cf. Jordan, 1964, p. 61). *Janischewskya* is restricted to the lower part of the Lower Carboniferous. *Gortanella* and *Jordanites* are restricted to the Upper Carboniferous, though Ruggieri (1966) suggested that *Gortanella* may have had a wider range through the entire Carboniferous.

The phylogenetic relationships of those genera are poorly understood. Kesling & McMillan (1951) and Kesling (1952c) made an attempt to reconstruct the phylogeny of hollinid ostracodes. The results of their investigations are reflected in the subdivision of the Hollinidae into two sub-families as stated above (fig. 12c). *Hollinella, Jordanites* and *Adelphobolbina* have adults with a continuous velum. All other genera possess one or two ventro-lateral spines in at least one of the dimorphs.

*Janischewskya* and *Gortanella* show a quite baroque ornamentation. Lobation is simple in *Flaccivelum, Jordanites, Adelphobolbina* and *Hanaites*, but rather pronounced in the other genera. The ontogeny of *Hollinella* and *Jordanites* is very similar and juveniles of these genera are sometimes difficult to distinguish. Juveniles of *Falsipollex, Gortanella* and *Hanaites* have been shown by several authors. They differ distinctly among each other and also from *Hollinella* and *Jordanites*. Juveniles of other genera have not been described so far. A complete survey of their ontogeny is needed before a further subdivision of the Hollininae can be made. It seems, however, possible that *Hollinella, Jordanites* and *Adelphobolbina* will be separated from the other genera into a separate group because of the similarity in their velar structures.

Genus HOLLINELLA Coryell, 1928

*Type species:* By original designation *Hollinella dentata* Coryell, 1928.

*Synonyms:* *Basslerina* Moore, 1929
*Hollites* Coryell & Sample, 1932.

*Diagnosis*

*Adults:* Small, nearly equivalved, straight-backed, preplete, lobate, sulcate and velate ostracodes.

L2 and L3 developed as nodes or bulbs, the L3 being distinctly larger than the L2. L1 and L4 usually inconspicuous, but they may have developed as small, vertically elongate lobes in some species. Ventral lobe conspicuous, mostly as inflated ridge below median sulcus, sometimes as a prominent node. S2 always well developed. S1 and S3 sometimes present, but then poorly developed in comparison with S2. Greatest height before the S2. Greatest width at L3. Velum sub-parallel to anterior and ventral parts of the free margin. Sub-parallel to posterior part of free margin, the velum may have a continuation in the form of a row of short spines. In the sub-velar surface one or more rows of stout, low tubercles parallel to the free margin may be present. A postero-dorsal spine is usually noted on the left valve. An antero-dorsal spine may sometimes also be recognized. The surface of the domicilium may be smooth, granulose, spinose, papillose, punctate or reticulate. The velum is usually smooth or ornamented with concentric striae. Radial markings caused by the tubulous layer may be present. The hingement seems to be quite variable (cf. Melik, 1966). Often a simple bar and groove hingement is noted (fig. 13), but more complicated forms have been recognized. The contact margin of one valve is usually rabbeted to accomodate the contact margin of the other valve. Sometimes both contact margins are rabbeted.

The dimorphism may be conspicuous. In species where dimorphism can be observed the presumable females have a domicilium with slightly larger dimensions than that of presumable males. Their velum is, however, smaller than that of the males.

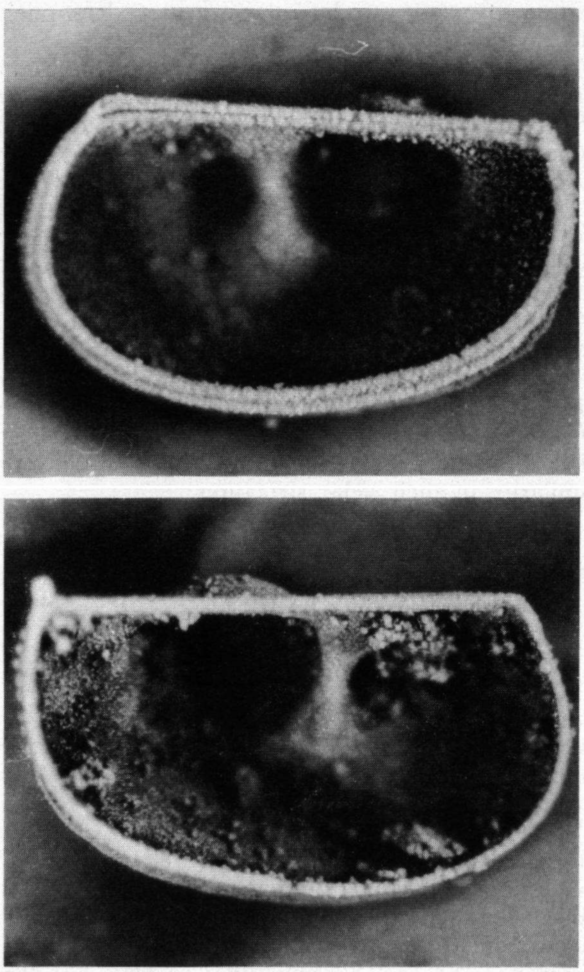


Fig. 13a-b. LV and RV of adult specimens of *Hollinella camoni* (interior view), showing hingement structures. Re20-16 & Re20-17.

Lobate dimorphism is developed in a few species. The L3 in the presumable females is almost twice as large as in the presumable males. In case of lobate dimorphism, the other dimorphic characteristics described here are also recognized.

*Juveniles:* General shape of domicilium similar to adult males. L2 and L3 proportionately smaller than in adults. Antero-dorsal spine may be well-developed in left valve. It is supposed that this spine was present in all species in juvenile instars. Postero-dorsal spine always present in left valve. Velum lacks external layer. External chitin layer seems to have been present. Tubules of tubulous layer well-developed. The domicilial wall is relatively thin in comparison with that of adults.

*Remarks:* The holotype of *Hollinella dentata* Coryell, 1928 (the type-species of the genus) is a juvenile instar with all the tubules of the tubulous layer in the velum broken almost at their base.

In 1929 Kellett recognized the specific relationship between some frilled species of *Hollina* and unfrilled species of *Hollinella*. She assigned both forms to the genus *Hollinella*, considering the frilled forms females and the unfrilled forms males and juveniles of the same species. At the same time R. S. Moore (1929), unaware of the relationship of these forms, described a new genus: *Basslerina*, the types of his species being adult specimens of *Hollinella* species. In 1932 Coryell & Sample founded a new genus: *Hollites*. The type species of this genus was a juvenile specimen of a *Hollinella* species. In 1934 Bassler & Kellett in their "Index of Paleozoic Ostracodes" considered *Basslerina* and *Hollites* synonyms of *Hollinella* and placed them together in the genus *Hollinella*. Cooper (1946) redescribed the type species *H. dentata* and gave description and illustrations of both adult and juvenile specimens "from the same formation near the type locality". Cooper concluded (pp. 90—91) that the holotype is a "next-to-last instar of the moult series". He suggested (p. 89) that "no species should be founded on immature or unfrilled specimens". The present study revealed, however, that juvenile instars of *Hollinella* already have a velum. The American material seems badly preserved in this respect and the velum has not been preserved. The supposition that velate forms should be adults led to the description of two new species (cf. Bless, 1965) which in fact represented the adult and juvenile forms of only one species. Bassler & Kellett (1934), Pokorny (1950), Brayer (1952), Kesling & Weiss (1953) and Yegorov (1953) assigned hollinid ostracodes to the genus *Hollinella* which have two ventro-lateral spines instead of a continuous velum. These spines may be present in one of the two adult dimorphs or in juvenile specimens. They are excluded here from the genus *Hollinella*. This feature is common in other hollinid genera, for example *Falsipollex, Gortanella, Parabolbina.* Hollinid ostracodes with ventro-lateral spines may belong to these genera.

Hollinellid-like ostracodes with an interrupted velum were placed by Kesling & Weiss (1953) in the genus *Ruptivelum* Kesling & Weiss, 1953. *Hollinella hamata* Kummerow, 1953, from the Middle Devonian of Poland, is assigned here to that genus, since it also has such an interrupted velar structure.

*Ecology:* All species of *Hollinella* described so far are supposed to have been marine near-bottom swimmers (see p. 173).

*Geographic distribution:* Species of *Hollinella* have been recognized in North America, Europe, Asia and Australia (see p. 173).

*Stratigraphic distribution:* Silurian?; Middle Devonian — Middle Permian.

*Hollinella camoni* nov. spec.

Figs. 14—19; pl. 1—2, figs. 50—56.

*Holotype:* Re20-1

*Paratypes:* Re20-2
Re20-3
Re20-4
Re20-5
Re20-6
Re20-7
Re20-8

*Locus typicus:* Coal Mine "Pepe" (locality Re20), near Santa Maria de Redondo (Palencia, Spain).
*Stratum typicum:* Stephanian A, Redondo coal beds.
*Material:* About 100 valves and complete carapaces, partly damaged.

*Description*

*Female:* Sub-oblong *Hollinella* with large, bulbous L3 and small velum. L2 little node, partly fused with L1. L3 prominent, large bulb, reaching distinctly above dorsal border. Ventral lobe in the form of low ridge, confluent with L2 and L3, bordering S2 ventrally. S2 deep, widest at mid-height just before center of carapace. Some marginal spines on posterior part of carapace. Postero-dorsal spine present on left valve, absent on right valve. Surface smooth or with a few scattered, low spines. Velum small, running subparallel along almost the entire free margin. Velum with external layer covering tubulous layer. Some faint, radial striae may be visible externally on the velum. Dimensions: see table IA.

*Male:* Sub-oblong with large L3 and wide velum. L2 little node, partly fused with L1. L3 bulbous, reaching slightly above dorsal border. Diameter of L3 about three-fourth the diameter of L3 in females. Velum about twice as wide as in females. Other characteristics as females. Dimensions: see table IA.

*Eighth instar:* General shape and form as that of adult male, but velum lacking external layer. L2 little node, L3 bulbous, reaching dorsal border. L3 proportionately smaller than L3 in adult male. Antero-dorsal and postero-dorsal spines in left valves well-developed. Posterior marginal spines present. Surface smooth or with a few scattered, very small spines. Velum with well-developed tubulous layer. Tubules evenly placed with little interspacing, three-furcated terminally. In some specimens a bulbous enlargement in the distal part of the tubules is present. External layer absent. Dimensions: see table IA.

*Seventh instar:* Valves with general shape and form as those in eighth instar. L3 not prominent. Dimensions: see table IA.

*Sixth instar:* The only carapace recognized has same shape and form as those of seventh instar. Ventral lobe is most prominent feature of carapace. Dimensions: see table IA.

*Fifth instar:* Only one carapace has been recognized with same shape and form as the carapace of the sixth instar. L2 and L3 small and inconspicuous. Ventral lobe most prominent feature of carapace. Dimensions: see table IA.

*Type-description*

Holotype is female left valve with all characteristics of female.

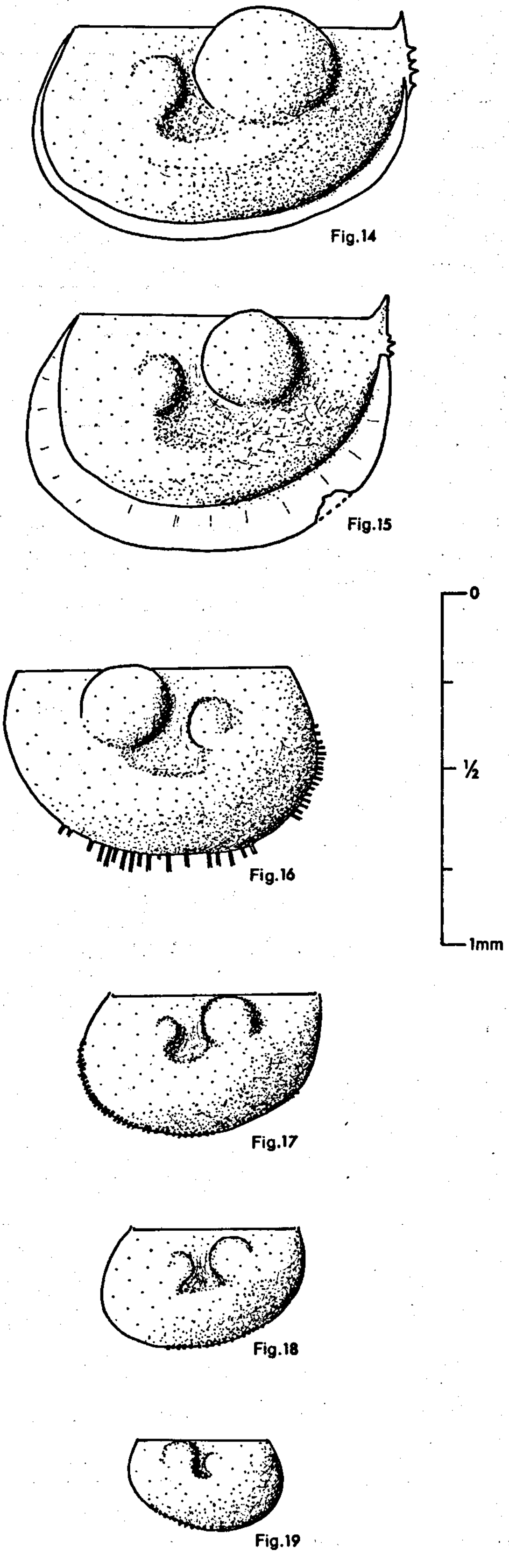



Fig. 14—19: *Hollinella camoni* nov. spec.

Fig. 14. LV of adult female specimen. Holotype. Re20-1.
Fig. 15. LV of adult male specimen. Paratype. Re20-2.
Fig. 16. RV of specimen of eighth instar. Paratype. Re20-3.
Fig. 17. LV of specimen of seventh instar. Paratype. Re20-4.
Fig. 18. LV of specimen of sixth instar. Paratype. Re20-5.
Fig. 19. RV of specimen of fifth instar. Paratype. Re20-6.

Table IA. Mean dimensions of *Hollinella camoni* nov. spec.

| INSTARS | Number of specimens | Height «domicilium» in mm | Mean height «domicilium» in mm | Length «domicilium» in mm | Mean length «domicilium» in mm | Width of velum in mm | Mean width of velum in mm | Linear growth-factor of height | Linear growth-factor of length | H/L - ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| FEMALES | 24 | 0.50-0.57 | 0.542 | 0.90-1.10 | 1.013 | 0.03-0.08 | 0.054 | 1.042 | 1.143 | 0.535 |
| MALES | 32 | 0.48-0.60 | 0.528 | 0.85-1.05 | 0.956 | 0.10-0.18 | 0.114 | 1.015 | 1.079 | 0.553 |
| ADULTS (Males and Females) | 56 | 0.48-0.60 | 0.534 | 0.85-1.10 | 0.982 | x | x | 1.026 | 1.108 | 0.543 |
| EIGHTH INSTAR | 15 | 0.47-0.53 | 0.520 | 0.80-0.92 | 0.886 | x | x | 1.274 | 1.303 | 0.586 |
| SEVENTH INSTAR | 7 | 0.40-0.43 | 0.408 | 0.60-0.70 | 0.680 | x | x | 1.275 | 1.236 | 0.600 |
| SIXTH INSTAR | 1 | 0.32 | 0.32 | 0.55 | 0.55 | x | x | 1.280 | 1.222 | 0.581 |
| FIFTH INSTAR | 1 | 0.25 | 0.25 | 0.45 | 0.45 | x | x | | | 0.555 |

x Tubules of tubulous layer in velum broken or width not measured

Height: 0.56 mm
Length: 1.05 mm
Width of velum: 0.05 mm

Paratype Re20-2 is a male left valve. Velum partly broken postero-ventrally.

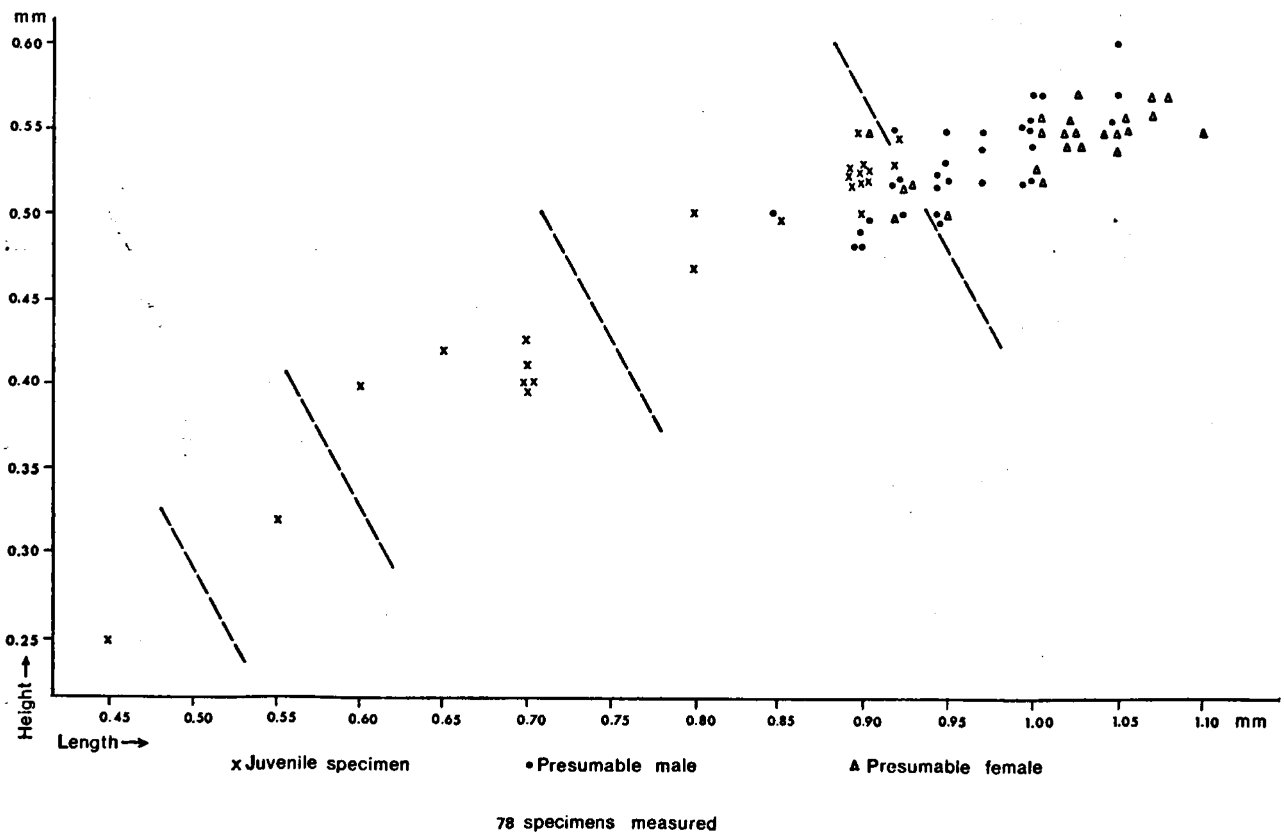
Height: 0.55 mm
Length: 0.95 mm
Width of velum: 0.125 mm

Paratypes Re20-3 — Re20-6 are juvenile instars with characteristics of juveniles. The tubules of the velum are all broken.

Paratype Re20-7 is a female right valve, paratype Re20-8 is a male right valve.

*Remarks:* Four juvenile instars have been recognized. They show a regular increase in length and height (table IB). They are distinguished from adults by the

Table IB. Height vs. length diagram for *Hollinella camoni* nov. spec.



absence of the external layer in the velum and by the presence of an antero-dorsal spine on their left valve. The linear growth factor is about 1.265. The linear growth factor is distinctly less for the last moulting, but the L2 and especially the L3 increase proportionately more in diameter (and thus in volume) than in the earlier moultings. The H/L ratio slightly decreases in older instars. Adults of this species are distinguished by their form and shape from other species of *Hollinella*. The sexual dimorphism is prominent in *H. camoni*.
*Occurrence in Spain:* Localities Re20 (Type-locality), La 391.

*Hollinella cristinae* Bless, 1965
Figs. 20—24; pl. 3—4, figs. 57—63.

*Hollinella cristinae* Bless, 1965. Leidse Geol. Med., Deel 33, p. 178, figs. I, III, IV. ——— Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, figs. 8—11.
*Hollinella fraderae* Bless, 1965. Leidse Geol. Med., Deel 33, pp. 179—180, fig. II. ——— Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, fig. 12 (not fig. 13).

*Material:* About 150 valves, partly damaged.

*Description*
*Adults:* Sub-oblong, hollinellid ostracodes with strongly developed lobation. L2 node. L3 large bulb. Ventral lobe prominent. S2 deep and wide, extending to dorsal border. Cardinal angles well-defined; anterior cardinal angle obtuse; posterior cardinal angle obtuse to rectangular. Surface finely to coarsely granulose. Postero-dorsal spine present. Junction of velum with domicilium distinct. Velum wide, curved outwards in the anterior part. Velum restricted to anterior, ventral and postero-ventral parts of free margin. Velum with faint, concentric striae and some radial markings. In the distal part of the velum the external layer is very thin and the velum appears radially striated, because the tubules of the tubulous layer become visible. Tubules of tubulous layer placed in two rows at their base, intercalating at their distal ends. Dimorphism not observed. Dimensions: see table IIA.
*Eighth instar:* Domicilium with same characteristics as adults, but L3 proportionately smaller. Velum lacks external layer. Tubules of tubulous layer placed in one row with some interspacing. Tubules long and relatively wide, communicating with the interior of the domicilium. Tubules multi-furcated.
Dimensions: see table IIA.
*Seventh instar:* Valves with general shape and form as those of eighth instar, but tubules in velum placed with relatively wider interspacing.
Dimensions: see table IIA.
*Sixth instar:* Valves with general shape and form as those of seventh instar, but tubules in velum placed with relatively wider interspacing.
Dimensions: see table IIA.
*Fifth instar:* Valves with general shape and form as those in sixth instar, but tubules in velum placed with relatively wider interspacing. Surface smooth.
Dimensions: see table IIA.
*Remarks:* Four juvenile instars have been recognized

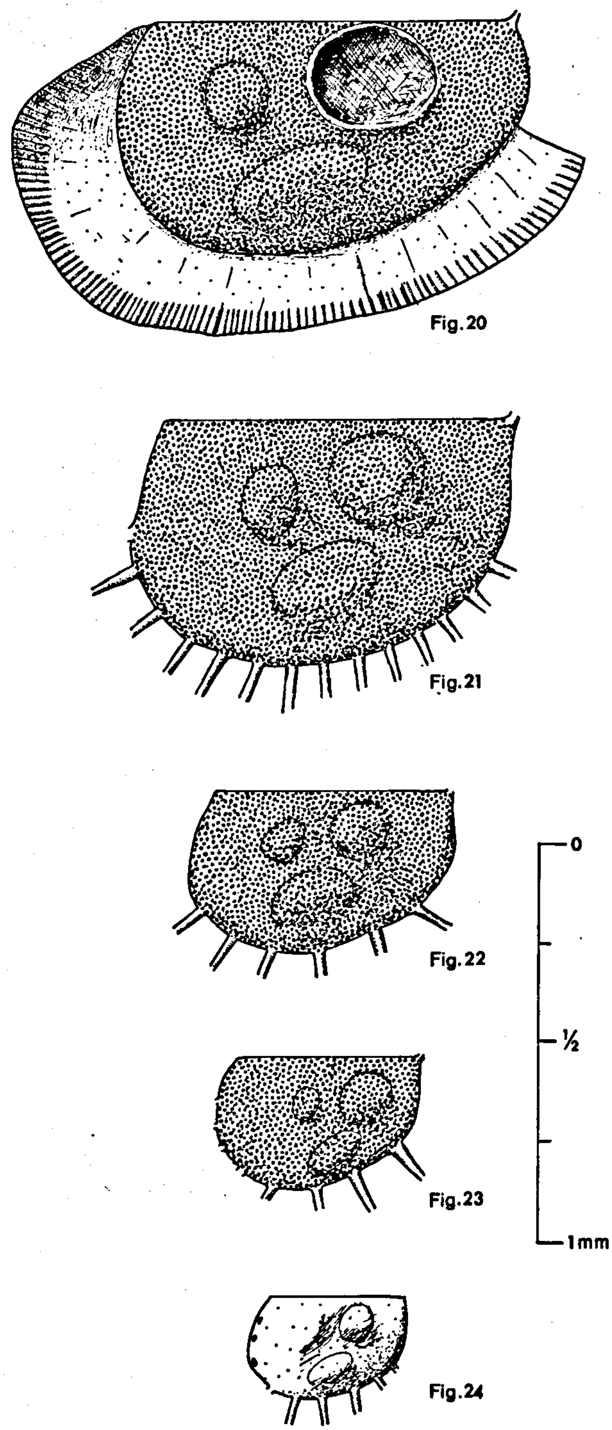



Fig. 20—24: *Hollinella cristinae* Bless, 1965

Fig. 20. LV of adult specimen. Fr4-25.
Fig. 21. LV of specimen of eighth instar. Holotype. Fr4-19.
Fig. 22. LV of specimen of seventh instar. Fr4-37.
Fig. 23. LV of specimen of sixth instar. Fr105-13.
Fig. 24. LV of specimen of fifth instar. Fr116-1.

Table IIA. Mean dimensions of *Hollinella cristinae* Bless, 1965.

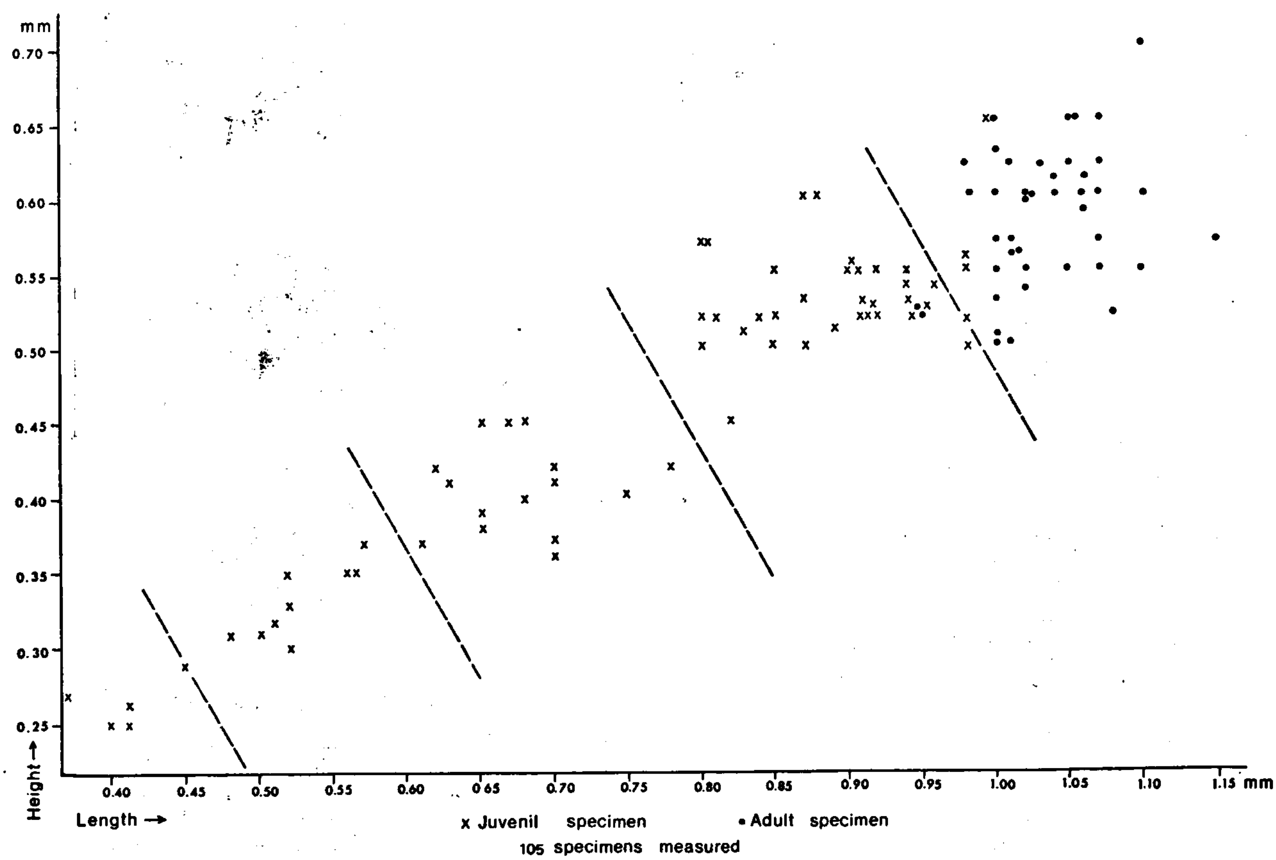
| INSTARS | Number of specimens | Height (domicilium) in mm | Mean height (domicilium) in mm | Length (domicilium) in mm | Mean length domicilium) in mm | Width of velum in mm | Mean width of velum in mm | Linear growth-factor of height | Linear growth-factor of length | H/L ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| ADULTS | 41 | 0.50-0.65 | 0.582 | 0.95-1.15 | 1.030 | 0.13-0.35 | 0.207 | 1.093 | 1.132 | 0.565 |
| EIGHTH INSTAR | 34 | 0.45-0.60 | 0.532 | 0.80-0.98 | 0.910 | x | x | 1.310 | 1.342 | 0.585 |
| SEVENTH INSTAR | 23 | 0.36-0.45 | 0.406 | 0.62-0.78 | 0.681 | x | x | 1.241 | 1.304 | 0.593 |
| SIXTH INSTAR | 8 | 0.30-0.35 | 0.327 | 0.48-0.56 | 0.522 | x | x | 1.311 | 1.317 | 0.626 |
| FIFTH INSTAR | 4 | 0.25-0.27 | 0.257 | 0.37-0.41 | 0.397 | x | x | | | 0.647 |

x Tubules of tubulous layer in velum broken or width of velum not measured

(table IIB). They are distinguished from adults by the absence of an external layer in the velum and by a proportionately smaller L3. The tubulous layer has relatively more tubules in older instars. The linear growth factor is nearly constant for the moultings of the juveniles, but relatively low for the last moulting. In the last moulting, however, the lobes and especially the L3 increase considerably in size. The H/L-ratio decreases in older instars.

*Occurrence in Spain:* Localities Fr1 — Fr104 (type-locality), Fr105 — Fr116, Fe130, La422, Fe494(?).

Table IIB. Height vs. length diagram for *Hollinella cristinae* Bless, 1965.



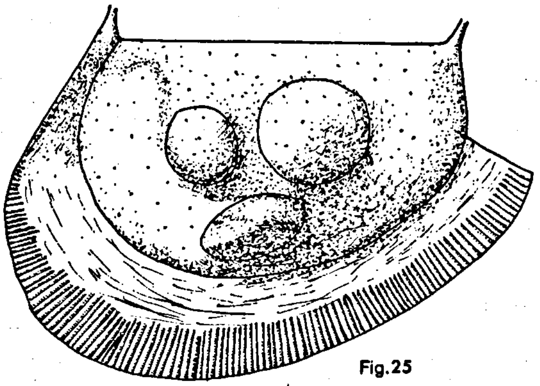


Fig.25

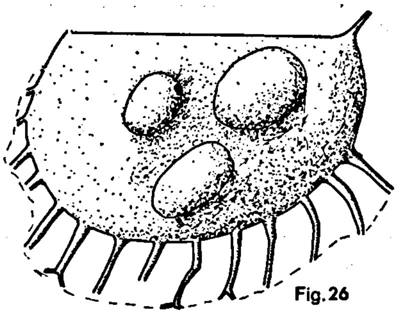


Fig.26

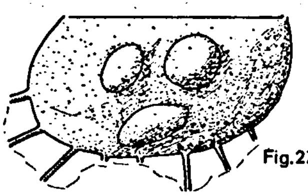
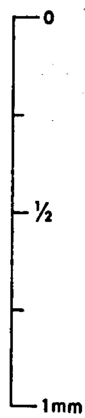


Fig.27



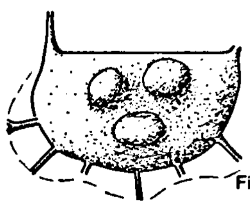



Fig.28

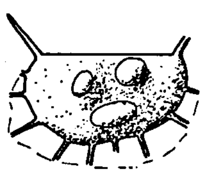


Fig.29

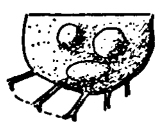


Fig.30

Fig. 25—30: *Hollinella hispanica* nov. spec.
Fig. 25. LV of adult specimen. Holotype. ml004a-1.
Fig. 26. LV of specimen of eighth instar. Paratype. ml004a-2.
Fig. 27. LV of specimen of seventh instar. Paratype. ml004a-3.
Fig. 28. LV of specimen of sixth instar. Paratype. ml004a-4.
Fig. 29. LV of specimen of fifth instar. Paratype. ml004a-5.
Fig. 30. LV of specimen of fourth instar. Paratype.

### *Hollinella hispanica* nov. spec.

Figs. 25—30; pl. 5—6, figs. 64—71.

non *Hollinella fraderae* Bless, 1965. Leidse Geol. Med., Deel 33, pp. 179—180, fig. II.
*Hollinella fraderae* Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, fig. 13 (not fig. 12).

*Holotype:* ml004a-1
*Paratypes:* ml004a-2
ml004a-3
ml004a-4
ml004a-5
ml004a-6
*Locus typicus:* Coal Mine "Llascaras" (La Felguera, Asturias, Spain), tercera planta, locality ml004a.
*Stratum typicum:* Westphalian D, Sama-Fm., first coal bed above the Dos Vetas coal, Soton coal member.
*Material:* About 125 valves, partly damaged.

*Description*

*Adults:* Hollinellid ostracodes with strongly developed lobation and wide, out-flaring velum.

L1 weakly developed, vertically elongated. L2 node. L3 bulb. L4 inconspicuous. Ventral lobe very prominent, high, pointed below S2 and thorn-shaped. All lobes below dorsal border. S1 shallow, faintly visible. S2 deep, slightly geniculate. S3 inconspicuous. Anterior cardinal angle obtuse, posterior cardinal angle obtuse to rectangular. Postero-dorsal spine present in left valve. Antero-dorsally a spinelike projection of the velum has been recognized. Surface with extremely small granules.

Juncture of domicilium with velum well-marked. Velum curved outward in the anterior part. External layer becomes extremely thin in the peripheral part of velum, where tubulous layer is visible. External layer with distinct, concentric striae in its proximal part. Sexual dimorphism not observed.

Dimensions: see table IIIA.

*Eighth instar:* Domicilium with same lobation, sulcation and ornamentation as adults, but lobes proportionately smaller.

Antero-dorsal spine present on left valve. Velum lacks external layer, but faint impression in shale between the tubules of tubulous layer does suggest that an external chitinous layer originally covered the tubulous layer. Tubules of tubulous layer long and thin, bi-furcated in their distal part. Tubules seem to communicate with interior of domicilium. They are placed with rather wide interspacing in one row.

Dimensions: see table IIIA.

*Seventh instar:* Valves with general shape and form as those in eighth instar. Tubules in velum placed with relatively wider interspacing.

Dimensions: see table IIIA.

*Sixth instar:* Valves with general shape and form as those in seventh instar, but valves nearly amplete. Tubules in velum placed with relatively wider interspacing. Dimensions: see table IIIA.

*Fifth instar:* Valves with general shape and form as those of sixth instar. Tubules in velum placed with relatively wider interspacing.

Dimensions: see table IIIA.

Table IIIA. Mean dimensions of *Hollinella hispanica* nov. spec.

| INSTARS | Number of specimens | Height (domicilium) in mm | Mean height (domicilium) in mm | Length (domicilium) in mm | Mean length (domicilium) in mm | Width of velum in mm | Mean width of velum in mm | Linear growth-factor of height | Linear growth-factor of length | H/L-ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| ADULTS | 21 | 0.40-0.57 | 0.518 | 0.90-1.07 | 0.970 | 0.12-0.30 | 0.219 | 1.079 | 1.156 | 0.534 |
| EIGHTH INSTAR | 18 | 0.40-0.56 | 0.480 | 0.77-0.95 | 0.841 | x | x | 1.256 | 1.291 | 0.570 |
| SEVENTH INSTAR | 9 | 0.33-0.42 | 0.382 | 0.60-0.70 | 0.651 | x | x | 1.312 | 1.309 | 0.586 |
| SIXTH INSTAR | 20 | 0.27-0.33 | 0.291 | 0.45-0.55 | 0.497 | x | x | 1.287 | 1.300 | 0.585 |
| FIFTH INSTAR | 14 | 0.20-0.25 | 0.226 | 0.35-0.40 | 0.390 | x | x | 1.177 | 1.231 | 0.579 |
| FOURTH INSTAR | 4 | 0.17-0.21 | 0.192 | 0.30-0.33 | 0.312 | x | x | | | 0.615 |

x Tubules of tubulous layer in velum broken or width of velum not measured

*Fourth instar:* Valves with general shape and form as those of fifth instar. Tubules in tubulous layer of velum placed with relatively wider interspacing.
Dimensions: see table IIIA.

*Type-description*

Holotype is cast of adult left valve with well-preserved velum and remnants of domicilial wall.

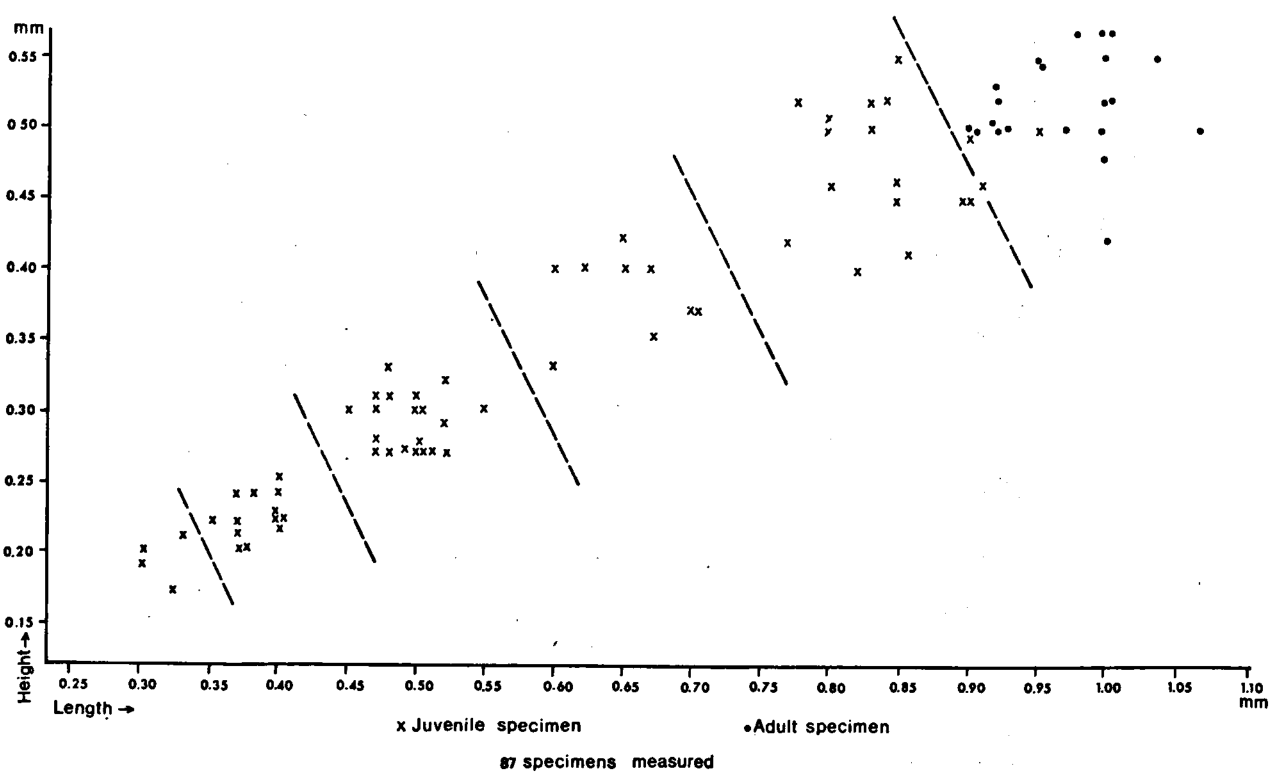
Height: 0.57 mm
Length: 1.00 mm
Width of velum: 0.28 mm

Paratypes are left valves of juvenile specimens with tubules of tubulous layer partly broken.

*Remarks:* Five juvenile instars have been recognized (table IIIB), which can be distinguished from adults by the absence of the external layer in the velum and by the presence of an antero-dorsal spine in their left valve. The linear growth factor is more or less constant for the moultings of these juvenile forms. The linear growth factor is distinctly lower for the last moulting, but the lobes increase relatively more in size than in the earlier moultings. The H/L-ratio decreases for older instars. *H. hispanica* resembles *H. cristinae* in general shape. The latter, however, has slightly larger dimensions, higher H/L-ratio and different ornamentation. Moreover, the velum is relatively smaller and the ventral lobe less prominent in *H. cristinae*.

*Occurrence in Spain:* Localities m1004a (type-locality), m1004, Fe455.

Table IIIB. Height vs. length diagram for *Hollinella hispanica* nov. spec.



*Hollinella micheli* nov. spec.
Pl. 7, fig. 72.

*Holotype:* Fe 361—86
*Locus typicus:* Coal Mine "Mosquitera 1" (Mosquitera, Asturias, Spain), tercera planta, locality Fe361.
*Stratum typicum:* Westphalian D, Sama-Fm., coal bed Adolfa, Modesta coal member.
*Material:* One single left valve of adult specimen.

*Description:* Hollinellid ostracode with developed lobation and sulcation and coarsely reticulate surface. L1 elongated, conspicuous, reaching slightly above dorsal border. L2 node, somewhat elongated vertically. L3 bulbous, reaching above dorsal border, prominent. L4 low, elongated. Ventral lobe continuous with L1, prominent. S1 shallow, but clearly visible. Velum smooth with some radial markings. Lateral surface coarsely reticulate with exception of S1 and S2 where reticulation becomes indistinct. A few, scattered low tubercles are present in the posterior part of the domicilium.
Dimensions:
Height: 0.65 mm
Length: 1.10 mm
Width of velum: 0.11 mm
*Remarks:* The only specimen recognized of this species is so different from other species of Hollinella that it seems justified to erect a new species. The coarse reticulation and the well-developed L1 are indicative for this species.
*Occurrence in Spain:* Locality Fe361 (type-locality).

*Hollinella philomenae* Bless, 1967
Figs. 31—32; pl. 7, figs. 73—74.

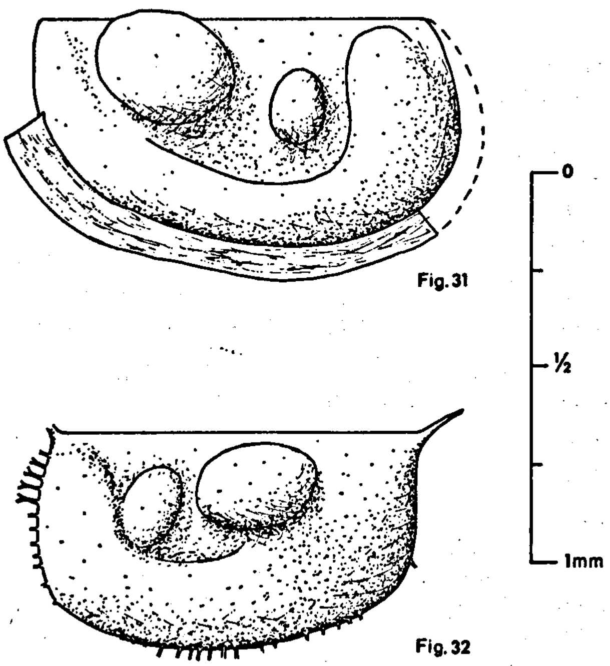



Fig. 31—32: *Hollinella philomenae* Bless, 1967.
Fig. 31. RV of adult specimen. Holotype. La393a-29.
Fig. 32. LV of specimen of eighth instar. La393b-14.

*Hollinella philomenae* Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, fig. 14.
*Material:* 8 single valves, partly damaged.

*Description*
*Adults:* Elongate hollinellid ostracodes with well developed lobation. L1 elongated, weakly developed. L2 node. L3 large bulb, reaching above dorsal border. L4 indistinct. Ventral lobe prominent. S1 small. S2 deep and broad, confluent with S1 below L2. Surface finely granulose. Velum with fine, concentric striae and some radial markings. Junction of velum and domicilium well marked.
Dimensions of specimen shown:
Height: 0.56 mm
Length: 1.10 mm
Width of velum: 0.11 mm
*Eighth instar:* Shape of domicilium as in adults. Postero-dorsal spine is present. Velum lacks external layer. Tubulous layer consists of row of thin, furcated tubules.
Dimensions:
Height: 0.56 mm
Length: 1.01 mm
*Remarks:* Only one juvenile specimen has been recognized, which is assigned to this species. According to its rather large dimensions it is thought to be a specimen of the eighth instar. The linear growth factor is very low for the last moulting when we compare the dimensions of this specimen and those of adults. The increase in volume of the L3 is considerable.
*Occurrence in Spain:* Locality La 393 (type-locality).

*Hollinella* spp.
Figs. 33—35; pl. 7, figs. 75—77.

*Remarks:* Several juvenile specimens of *Hollinella* have been collected which cannot be assigned to any of the species described in this paper. Some of them are shown here to illustrate the presence of the tubulous layer of the velum in juvenile instars of *Hollinella*. The L3 is only slightly larger than the L2 in these ostracodes. No adult specimens have been recognized which could be related to these juvenile forms.
*Occurrence in Spain:* Localities La412, m1023, m1050, m1070, m1081, m1091.

Genus JORDANITES Bless, 1967
*Type species:* By original designation *Jordanites rawihinggili* Bless, 1967.

*Diagnosis*
*Adults:* Small, nearly equivalved, straight-backed, preplete, lobate, sulcate and velate ostracodes.
L1 and L2 fused. L2 developed as small node at posterior part, just before S2. L3 large, inflated. L4 inconspicuous. Ventral lobe completely confluent with L1/L2 and L3. Ventral lobe not prominent. S2 is the only sulcus recognized. S2 may be well-developed, deep and broad or indistinct. Greatest height before the S2. Greatest width may be at ventral lobe or at L3. Velum sub-parallel to anterior and ventral parts of

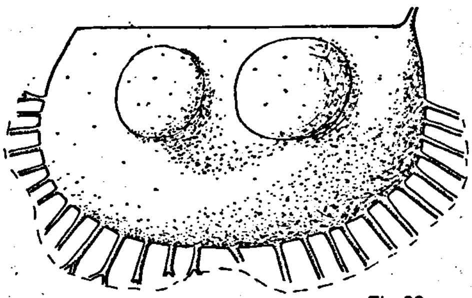
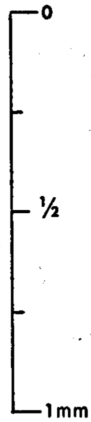


Fig. 33



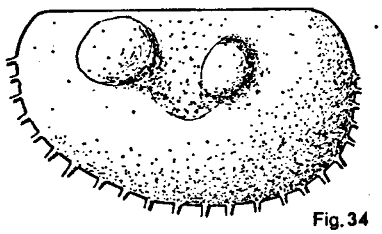



Fig. 34

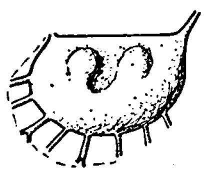


Fig. 35

Fig. 33—35: *Hollinella* spp.
Fig. 33. LV of juvenile specimen. m1091-2.
Fig. 34. RV of juvenile specimen. La412-4.
Fig. 35. LV of juvenile specimen. m1091-1.

free margin. In antero-dorsal part of free margin, the velum may be small or absent. The junction of the velum with the domicilium is indistinct. The velum seems to be a downward extension of the ventral lobe. On sub-velar surface low tubercles may be present. A small, low, postero-dorsal spine may be recognized on the left valve. The surface of the domicilium may be smooth, papillose or punctate. Other kinds of ornamentation may be noted also. The velum is less ornamented than the domicilium. Radial markings, caused by the tubulous layer, may be present.
The hingement has been observed in only a few poorly preserved specimens. Apparently the hingement consists of a simple bar and groove hingement. The contact margins are rabbeted in these specimens. Dimorphism may be present. The H/L-ratio of presumable females seems higher than that of presumable males. The place of greatest width is at the ventral lobe for presumable females. For presumable males the greatest width is at L3. If this is true for all species recognized could not be ascertained.
*Juveniles:* General shape of domicilium as that in adults. The postero-dorsal spine on the left valve is relatively longer than for adults. The presence of an antero-dorsal spine in the left valve could not be detected, but it is supposed that one may have been present. The velum lacks the external layer. The external chitin layer seems to have been present. The tubulous layer is well-developed. The domicilial wall is relatively thin in comparison to that of adults.
*Remarks:* The holotype of the type species is a juvenile specimen of the eighth instar. Because of the fact that it has a well-developed velum it was assumed to be an adult specimen. Later the close relationship with *Adelphobolbina? martinezi*, which was also originally described in 1967 by Bless, has been recognized (Bless, 1967b). The genus was originally characterized by the furcated tubules of the tubulous layer in the velum. This characteristic was later also noted for species of *Hollinella*. A detailed examination of juvenile and adult forms revealed that this genus shows a close relationship with *Adelphobolbina* from the Middle Devonian and with *Hollinella*. The genus differs from *Adelphobolbina* in its variable ornamentation in adults. Moreover the velum is thicker than in *Adelphobolbina*. The junction of the domicilium and the velum also seems different for these genera. The velum of *Adelphobolbina* commonly terminates in a spur as stated by Stover (1956), in contrast with the velum of *Jordanites*. The S3 is still feebly developed in *Adelphobolbina* but completely absent in *Jordanites*. Juvenile specimens of *Jordanites* show a striking resemblance to those of *Hollinella*. The L3 is, however, less bulbous in *Jordanites*.
The general shape of *Adelphobolbina*, *Hollinella* and *Jordanites* suggest a close familiar affinity. As stated above, it is presumed that they belong to a different group within the Hollininae in the sense of Jaanusson (1957, p. 409).
*Ecology:* The three species described so far are distinctly marine. They are assumed to have been near-bottom swimmers (see p. 173).
*Geographic distribution:* The genus is known so far only in Spain.
*Stratigraphic range:* Upper Westphalian.

*Jordanites rawihinggili* Bless, 1967
Figs. 38—44; pl. 8—9, figs. 78—85.

*Jordanites rawihinggili* Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, figs. 16—20.
*Adelphobolbina? martinezi* Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, figs. 4—7.

*Material:* About 350 valves and carapaces, partly damaged.

*Description*
*Adults:* Small, velate, preplete, hollinellid ostracodes with smooth surface. L1 partly fused with L2. L2 posteriorly developed as small, node-like elevation in some specimens. L3 large, inflated, extending to or slightly above dorsal border. L4 very small, inconspicuous. L2 and L3 fused by ventral lobe below S2. Ventral lobe not prominent. S2 deep, pit-like in the center of the carapace. Cardinal angles well-defined,

*) Figs. 36 & 37 have been omitted!

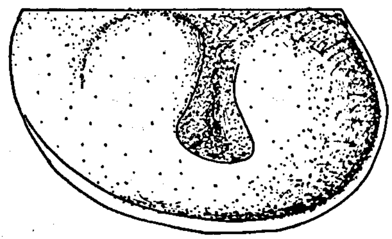


Fig. 38

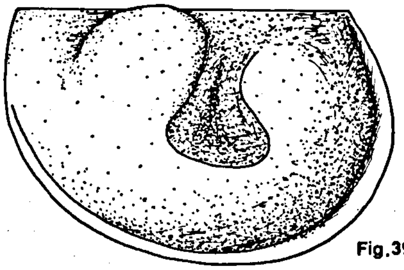


Fig. 39

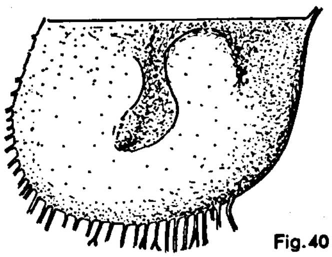
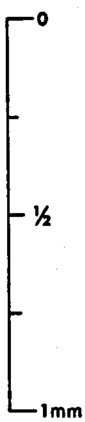


Fig. 40



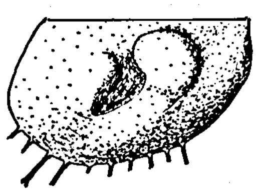



Fig. 41

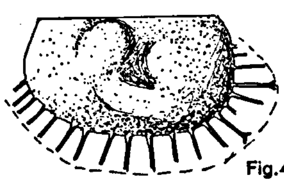


Fig. 42

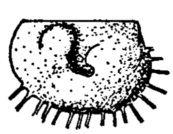


Fig. 43

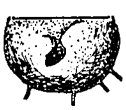


Fig. 44

Fig. 38—44: *Jordanites rawihinggili* Bless, 1967

obtuse. Carapace thick-shelled, especially in the ventral part and in S2. Surface usually smooth, with a few radial markings or some small papillae. Junction of velum with domicilium indistinct. Velum seems downward extension of ventral lobe. In a few specimens a very short, stout postero-dorsal spine has been recognized on the left valve. Small marginal tubercles may occur in sub-velar surface of carapace. Sexual dimorphism indistinct. Presumable males have lower H/L ratio than presumable females (0.58 and 0.67 respectively). The greatest width in females (?) is ventrally at ventral lobe, in males (?) located at L3. Velum in both males and females small. A number of specimens have been recognized with H/L ratio intermediate between that of males (?) and females (?).
Dimensions: see table IVA.

*Eighth instar:* Carapace of domicilium with same shape as that of adults, but S2 narrower and geniculate. Carapace thin-shelled. L3 proportionately as large as in adults. Postero-dorsal spine long. Antero-dorsal spine present. Velum lacks external layer. Tubules of tubulous layer irregularly placed in one row. Tubules long and thin, furcated in their distal section. They may be two-, three-, or multi-furcated.
Dimensions: see table IVA.

*Seventh instar:* General shape and form as in eighth instar.
Ventral lobe more prominent than in eighth instar. Tubules relatively longer than those in eighth instar and placed with wider interspacing. S2 distinctly geniculate.
Dimensions: see table IVA.

*Sixth instar:* Valves with general shape and form as those in seventh instar. Tubules of tubulous layer relatively longer than of seventh instar.
Dimensions: see table IVA.

*Fifth instar:* General shape and form as in sixth instar. Ventral lobe more prominent than L3.
Dimensions: see table IVA.

*Fourth instar:* Valves nearly amplete. L2 and L3 poorly developed. Ventral lobe prominent.
Dimensions: see table IVA.

*Remarks:* Juveniles are distinguished from adults by the absence of an external layer in their velum and by the presence of an antero-dorsal spine on their left valve. The S2 is proportionately narrower, the carapace wall thinner than in adults. The linear growth factor is more or less constant for all moultings (tables IVA-B). The H/L-ratio decreases slightly for older instars. An external chitinous layer seems to have covered the tubulous layer in the velum of juveniles. A faint impression in the shale between the tubules is

Fig. 38. RV of adult specimen. Fe361-91.
Fig. 39. RV of adult specimen. Fe361-92.
Fig. 40. LV of specimen of eighth instar. Holotype. Fe361-1.
Fig. 41. LV of specimen of seventh instar. Fe361-107.
Fig. 42. RV of specimen of sixth instar. Fe361-121.
Fig. 43. RV of specimen of fifth instar. Fe361-122.
Fig. 44. LV of specimen of fourth instar. Fe361-123.

Table IVA. Mean dimensions of *Jordanites rawihinggili* Bless, 1967.

| INSTARS | Number of specimens | Height (domicilium) in mm | Mean height (domicilium) in mm | Length (domicilium) in mm | Mean length (domicilium) in mm | Width of velum in mm | Mean width of velum in mm | Linear growth-factor of height | Linear growth-factor of length | H/L - ratio |
|---|---|---|---|---|---|---|---|---|---|---|
| ADULTS (Males and Females) | 59 | 0.48-0.70 | 0.598 | 0.80-1.06 | 0.948 | 0.02-0.07 | 0.032 | 1.317 | 1.257 | 0.609 |
| EIGHTH INSTAR | 20 | 0.40-0.52 | 0.455 | 0.70-0.77 | 0.738 | x | x | 1.185 | 1.204 | 0.615 |
| SEVENTH INSTAR | 23 | 0.35-0.47 | 0.383 | 0.55-0.68 | 0.613 | x | x | 1.268 | 1.277 | 0.624 |
| SIXTH INSTAR | 13 | 0.27-0.35 | 0.302 | 0.44-0.53 | 0.480 | x | x | 1.263 | 1.243 | 0.629 |
| FIFTH INSTAR | 11 | 0.20-0.32 | 0.239 | 0.35-0.42 | 0.386 | x | x | 1.257 | 1.317 | 0.614 |
| FOURTH INSTAR | 6 | 0.16-0.22 | 0.190 | 0.27-0.32 | 0.293 | x | x | | | 0.647 |

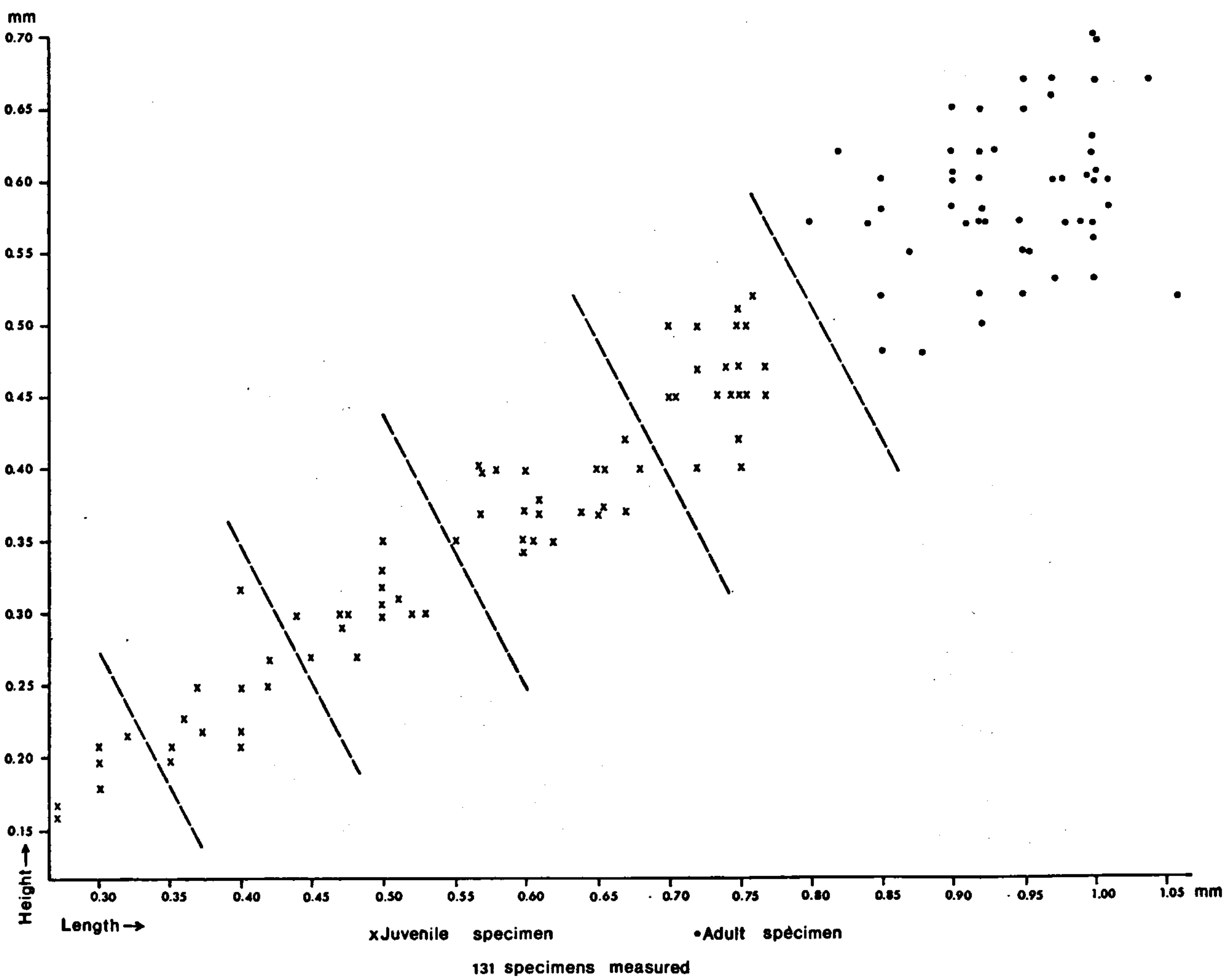
x Tubules of tubulous layer in velum broken or width of velum not measured

assumed here to be caused by this external chitinous layer.

Adults of *J. rawihinggili* are distinguished from *J. cristinae* by their smooth surface, relatively larger S2 and larger dimensions.

*Occurrence in Spain:* Localities Fe361 (type-locality), Fe249, As473, As475, Nu484, m1013, m1030, m1044, m1053, m1055, m1070, m1075, m 1090, m 1091, m1100.

Table IVB. Height vs. length diagram for *Jordanites rawihinggili* Bless, 1967.



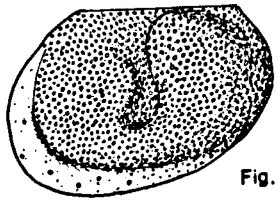


Fig.45

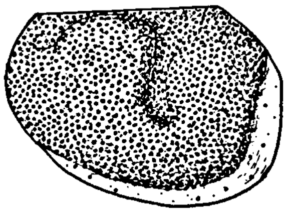


Fig.46

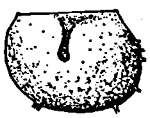


Fig.47

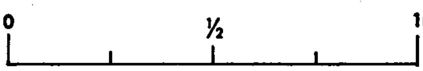



Fig. 45—47: *Jordanites cristinae* (Bless, 1967)
Fig. 45. LV of adult specimen. La412-8.
Fig. 46. RV of adult specimen. Paratype. Fr100-13b.
Fig. 47. RV of specimen of seventh (?) instar. m1091-5.

*Jordanites cristinae* (Bless, 1967)
Figs. 45—47; pl. 10. figs. 86—89.

*Adelphobolbina? cristinae* Bless, 1967. Notas y Comuns. Inst. Geol. Min. España, No. 99, figs. 1—3.

*Material:* About 60 carapaces and single valves, partly damaged.

*Description*
*Adults:* Small, sub-quadrate domicilium. L2 developed as little notch, fused with L1. L3 large, inflated, extending to dorsal border. L4 inconspicuous. Ventral lobe fusing L1 and L3. S2 narrow, geniculate.
Junction of velum with domicilium inconspicuous. Velum seems downward extension of ventral lobe. Velum widest antero-ventrally. Surface of domicilium papillose or punctate. In type-specimens papillose. Velum practically smooth, with a few low papillae.
Dimensions:
Height: 0.37—0.49 mm
Length: 0.55—0.65 mm
Width of velum: 0.02—0.05 mm
*Seventh instar?:* One single juvenile valve has been recognized, which is considered to be a specimen of the seventh instar of *J. cristinae*. The domicilium is smooth. L1—2 and L3 are equally large. S2 is very small. Velum lacks external layer. Fragments of a tubulous layer are present.
Dimensions:
Height: 0.25 mm
Length: 0.36 mm
*Remarks:* Ornamentation seems rather variable. The type-specimens are distinctly papillose. Specimens of the type-locality may also be scarcely papillose. In other localities punctate to papillose specimens have been recognized. Their shape and dimensions are the same. This variation may be due to ecological influences.
*Occurrence in Spain:* Localities Fr100 (type-locality), Fr6, Fr115, La412, m1030, m1031, m1091, m1093.

*Jordanites* sp. A
Figs. 48—49; pl. 10, figs. 90—93.

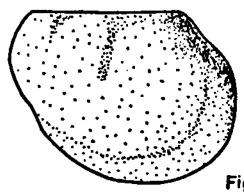


Fig.48

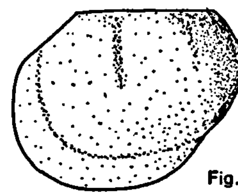


Fig.49

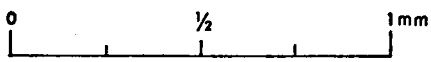



Fig. 48—49: *Jordanites* sp. A. Fe455-35.
Fig. 48. Right view.
Fig. 49. Left view.

*Type:* Fe455—35.
*Locus typicus:* Coal Mine "Fondon", septima planta (Sama de Langreo, Asturias, Spain), locality Fe455.
*Stratum typicum:* Westphalian D, Sama-Fm., first coal bed above the Primero San Luis coal, Entrerregueras coal member.
*Material:* One well-preserved adult carapace.

*Description:* Carapace swollen, L3 inconspicuous. Instead of S2, a distinct thickening of carapace wall; S2 externally quite weakly developed. Domicilium continuous with velar extension. Velum restricted to antero-ventral and ventral part of carapace, rather wide. When immersed in a liquid some tubules are visible in the velum. Carapace and velum smooth.
Dimensions:
Height (domicilium): 0.400 mm
Length (domicilium): 0.575 mm
Width of velum: 0.050 mm
*Remarks:* This specimen resembles *J. cristinae*, but is distinguished by its smooth surface and weakly developed S2.
*Occurrence in Spain:* Locality Fe455.

## SUMMARY

The carapace of *Hollinella* and *Jordanites* is three-layered. In this respect it resembles that of recent Podocopida and Myodocopida.
An inner and outer lamella cannot be distinguished in these genera in contrast to recent Podocopida. This is also the case in almost all other Palaeocopida.
The velum is distinctly three-layered and formed by a differentiation of the epidermal cells. The velum is continuous with the domicilial wall. The internal structure of the velum resembles that of the Eurychilinidae as described by Jaanusson (1957).
The velum is already present in early juvenile stages and developes gradually during ontogeny. This is also noted in other Beyrichicopina (cf. Spjeldnaes, 1951; Martinsson, 1957).
The only characteristics which are restricted to adult stages and which have been formed during the last moulting are apparently dimorphic characteristics.
The calcification of the carapace is better in the last moulting than in the moultings before. This can be noted in the relative thickness of the calcareous layer in the domicilial wall and in the development of the external layer in the velum in the last moulting.
The antero-dorsal and postero-dorsal spines are especially well-developed in juvenile instars. Although they may be present in some species in adults they are considered here to be a juvenile characteristic. This feature is also known in *Beyrichia*.
Przibram's Law that ostracodes double their size during each moulting is confirmed in the present investigation. Brook's Law that ostracodes increase their linear dimensions during each moulting by a fixed percentage is only valid for moultings between two juvenile stages. In the last moulting, when the animal reaches maturity this percentage may be distinctly lower.
*Hollinella* and *Jordanites* are placed here in the subfamily Hollininae Swartz, 1936. Together with *Adelphobolbina* they may be placed in a separate group in the future when more data become available.
The phylogeny of the Hollininae is poorly understood. No attempt has been made to reconstruct the phylogenetic relationships between the genera recognized so far.
At least six instars have been noted in species of *Hollinella* and *Jordanites*. Also six instars were recognized by Kesling (1952a) in *Ctenoloculina*. The possibility of three more instars as suggested by Kesling is not excluded here.
Several species of *Hollinella* and *Jordanites* are described in the present paper in order to illustrate the presence of the velum in juvenile instars and the presence of the tubulous layer in the velum of adults. The ontogeny of four species is described in detail.

## SAMENVATTING

De schaal van *Hollinella* en *Jordanites* bestaat uit drie lagen. In dit opzicht vertonen deze genera overeenkomsten met recente Podocopida en Myodocopida.
De binnenste en buitenste lamel kunnen in deze genera niet onderscheiden worden in tegenstelling tot Podocopida. Dit is ook het geval met bijna alle andere Palaeocopida.
Het velum bestaat uit drie lagen. Het is gevormd door een differentiatie van de huidcellen. Het velum vormt één geheel met de schaal. De opbouw van het velum is gelijk aan die van het velum der Eurichilinidae.
Het velum is al aanwezig in de jongste juveniele stadia en ontwikkelt zich langzamerhand gedurende de ontogenie van de ostracode. Dit is ook het geval in andere Beyrichicopina.
Alleen de dimorfe kenmerken schijnen beperkt te zijn tot het volwassen stadium. Alle andere kenmerken van de schaal zijn reeds aangelegd in juveniele stadia.
De verkalking van de schaal is sterker tijdens de laatste vervelling dan tijdens de vervellingen ervóór. Dit blijkt uit de relatieve dikte van de kalklaag in volwassen individuen en uit de ontwikkeling van de buitenste laag in het velum tijdens deze laatstevervelling.
De dorsale stekels zijn voornamelijk in juveniele vormen goed ontwikkeld. Zij worden hier beschouwd als een kenmerk voor juveniele stadia.
De wet van Przibram dat ostracoden tijdens elke vervelling hun volume verdubbelen is bevestigd in dit onderzoek. De wet van Brooks dat de lineaire afmetingen van de schaal met een vast percentage toenemen tijdens elke vervelling gaat alleen op voor vervellingen tussen twee juveniele stadia. Tijdens de laatste vervelling kunnen duidelijke afwijkingen optreden.
*Hollinella* en *Jordanites* zijn geplaatst in de subfamilie Hollininae Swartz, 1936. Samen met *Adelphobolbina* moeten ze misschien in een aparte groep worden geplaatst in de toekomst wanneer meer gegevens beschikbaar zijn.
De fylogenie van de Hollininae is nog slecht bekend. Er is hier geen poging gedaan om de fylogenetische verwantschap tussen de genera van deze subfamilie te reconstrueren.
Tenminste zes groeistadia zijn bekend in *Hollinella* en *Jordanites*. Kesling (1952a) vond eveneens zes groeistadia in *Ctenoloculina*. De mogelijkheid van nog drie groeistadia, zoals Kesling suggereerde is hier niet uitgesloten.
Een aantal soorten van *Hollinella* en *Jordanites* zijn hier beschreven om de aanwezigheid van het velum in juveniele stadia te illustreren en eveneens de aanwezigheid van de binnenste laag in het velum van volwassen individuen.
De ontogenie van vier soorten is in detail beschreven.

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