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FIFTH EUROPEAN OSTRACODOLOGISTS MEETING

«Building Bridges with Ostracods»

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EOM-V
Cuenca (Spain)
July, 2003

PREFACIO

Este número contiene los trabajos seleccionados entre los temas presentados al «Fifth European Ostracodologists Meeting (EOM-V)», celebrado en Cuenca (España) durante los días 20 al 28 de julio de 2003. Un total de noventa especialistas, procedentes de 22 países, presentaron contribuciones científicas a este congreso. La actividad congresual se completó con excursiones realizadas en materiales tan diversos como el Reciente kárstico de Cuenca, la Albufera de Valencia y las Salinas de Santa Pola (Alicante), o el Mioceno de la Cuenca del Ebro y el Devónico de la Cadena Ibérica (Rodríguez-Lázaro y Baltanás, Eds., *Serv. Editorial UPV, 2003).*

Los encuentros de ostracodólogos europeos comenzaron en 1989 (EOM-1, Frankfurt am Main, Alemania) y se celebran cada tres años, alternando con los congresos de ámbito mundial - International Symposium on Ostracoda (ISO), que se llevan celebrando desde hace más de 40 años. Ambos simposios constituyen la más alta representación de la investigación basada en los ostrácodos. Además de otras múltiples aplicaciones, estos microcrustáceos constituyen una herramienta de especial valor en las reconstrucciones paleoambientales, debido a su amplísima distribución tanto areal como temporal. El estudio de estos organismos congrega a grupos de investigación muy heterogéneos, que incluyen desde paleontólogos hasta neontólogos, con especialistas de campos tan diversos como la biogeoquímica, la genética o el Cambio Global, además de los más clásicos de la bioestratigrafía, (paleo)biogeografía, (paleo)oceanografía y (paleo)limnología. El interés del grupo salta al ámbito del gran público en algunas ocasiones, como la inusitada proyección mediática que hubo al conocerse el primer macho del reino animal, materializado por un ostrácodo del Silúrico de Gran Bretaña (Siveter *et al.,* 2003, *Science* y periódicos internacionales).

La particular riqueza taxonómica de la Clase Ostracoda le concede además un valor añadido en la evaluación de la biodiversidad de una gran variedad de ambientes ecológicos, desde el Cámbrico hasta la actualidad. Es precisamente en los numerosos representantes actuales de este grupo donde podemos encontrar los modelos que nos permitan interpretar el pasado, mediante la aplicación rigurosa de las claves actualísticas. A esta rigurosidad colabora de forma especial la utilización de la estadística multivariante con los resultados basados en datos actuales, así como las técnicas geoquímicas con las valvas de estos organismos. Ambos procedimientos representan alguno de los campos más novedosos de la investigación con los ostrácodos.

Quiero mostrar mi agradecimiento a los colegas que presentaron contribuciones al EOM-V, a los del Comité Científico y, en especial, al Dr. Ángel Baltanás, por la incondicional ayuda prestada a lo largo de la preparación y organización de este congreso. Hago extensivo este reconocimiento a los organismos que patrocinaron este evento: Ministerio de Ciencia y Tecnología, Universidad del País Vasco, Universidad Autónoma de Madrid, Universidad de Valencia, Asociación Española de Limnología y Junta de Castilla-La Mancha. Al director del Museo de la Ciencia de Cuenca (Dr. Jesús Madero), por la cesión del Museo como sede del congreso, así como por todas las facilidades concedidas para el eficaz desarrollo del mismo. Finalmente, quisiera mostrar mi especial reconocimiento a la Dra. Isabel Rábano, editora de la REM, por la cesión de un número de esta prestigiosa revista para la publicación de estos trabajos.

Julio Rodríguez-Lázaro
Presidente, Fifth European Ostracodologists Meeting

EOM-V
Cuenca (Spain)
July, 2003

FOREWORD

This issue contains selected papers from the themes presented at the Fifth European Ostracodologists' Meeting (EOM-V) at Cuenca (Spain), during July 20th to 28th 2003. Ninety Ostracoda specialists from 22 countries presented scientific contributions to this meeting. As a complement to the scientific activities, four different field-trips dealt with subjects as diverse as the recent karstic features in Cuenca, the Albufera Lake of Valencia, the Santa Pola salt marsh, the Miocene of the Ebro Basin and the Devonian of the Iberian Chains (Rodríguez-Lázaro & Baltanás, Eds., *Serv. Editorial UPV, 2003*).

The encounters among the European «ostracodologists» began in 1989 (EOM-1, Frankfurt am Main, Germany) and they are organised every 3 or 4 years, alternating with the International Symposium on Ostracoda (ISO), which started more than 40 years ago. Both meetings represent the highest standard of ostracod-based research. Among other diverse applications, these microcrustaceans are very useful in palaeoenvironmental reconstruction, due to their particularly wide geographical and temporal distributions. The study of these organisms brings together very heterogeneous research groups that include both palaeontologists and neontologists, as well as specialists from such diverse fields as biogeochemistry, genetics and Global Change, in addition to the classic fields of biostratigraphy, (palaeo)biogeography, (palaeo)oceanography and (palaeo)limnology. Ostracods are sometimes of direct public interest, as seen in the recent attention paid by the mass media to the oldest known male of the animal kingdom, a Silurian ostracod with its soft parts preserved in the Silurian of Great Britain (Siveter *et al.*, 2003, Science, and international newspapers).

The great diversity of the Class Ostracoda confers on it a further utility in the evaluation of the biodiversity of a variety of ecological contexts from the Cambrian to the Recent. Modern representatives of this group are very valuable models in the interpretation of the past environments, based on the appropriate application of uniformitarian clues. Multivariate statistical treatment of results based on modern ostracod data and geochemical analyses of their valves constitute important examples of the most up-to-date investigations carried out on these organisms.

I am indebted to all the colleagues who contributed to the EOM-V, to the Organising Committee and particularly Dr. Ángel Baltanás, for the help they provided during the organisation of this meeting. I am also indebted to the patrons of this event: Ministerio de Ciencia y Tecnología, Universidad del País Vasco, Universidad Autónoma de Madrid, Universidad de Valencia, Asociación Española de Limnología and Junta de Castilla-La Mancha. Our special thank to the Director of the Science Museum of Cuenca (Dr. Jesús Madero) who kindly provided the museum and facilities to make a success of this EOM-V. Finally the editor wants to thank Dr. Isabel Rábano as Chief Editor of the REM, for the publication of these papers in this international journal.

Julio Rodríguez-Lázaro
Chairman, Fifth European Ostracodologists Meeting

FIFTH EUROPEAN OSTRACODOLOGISTS MEETING

«BUILDING BRIDGES WITH OSTRACODS»
CUENCA, SPAIN, JULY 2003

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CALCIFICATION IN OSTRACODES

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Abstract

Ostracodes are often heavily calcified and their shell is mainly built of calcite. Investigations of the carapace reveal a crystalline structure which differs from the structure of chemically precipitated calcite. The calcium in the epidermal layer is concentrated in small globules which appear concentric when sectioned. Analyses show that the main component of these globules is calcium phosphate. When released from the globules, the calcium penetrates the epidermal membrane to form tiny granules of amorphous calcite outside the membrane. These gradually give rise to calcite crystals which are the main constituent of the shell of an ostracode. In some weakly calcified ostracodes such as *Cypria ophtalmica* the amorphous calcite is rarely transformed into calcite crystallites. Amorphous calcite, which dissolves easily, is usually not substantial enough to fossilise. Therefore, shells of these animals are rare in fossil samples.

Key words: Biomineralisation, Ostracode, amorphous calcite, carapace ultrastructure, SEM.

Resumen

Los ostrácodos están en general fuertemente calcificados y su concha está básicamente compuesta por calcita. Investigaciones realizadas sobre el caparazón revelan una estructura cristalina que difiere de la estructura de la calcita químicamente precipitada. El calcio de la capa epidérmica presenta una concentración de pequeños glóbulos que exhiben una estructura interna concéntrica. Los análisis realizados muestran que el componente mayoritario de dichos glóbulos es el fosfato cálcico. Al liberarse de los glóbulos, el calcio penetra en la membrana epidérmica para formar minúsculos gránulos de calcita amorfa en el exterior de la membrana. Esto da lugar al crecimiento gradual de cristales de calcita, que son los constituyentes mayoritarios de la concha de un ostrácodo. En algunos ostrácodos débilmente calcificados como *Cypria ophtalmica*, la calcita amorfa es raramente transformada en cristales de calcita. Esta calcita amorfa, al disolverse fácilmente, fosiliza raramente. Como consecuencia, las conchas de estos animales son raros en muestras fósiles.

Palabras clave: Biomineralización, Ostrácodo, calcita amorfa, ultraestructura del caparazón, MEB.

INTRODUCTION

Ostracodes are small crustaceans encased in a calcified shell. They can be found in a variety of different habitats from terrestrial such as wet moss and bromeliads to freshwater and marine environments including the deep sea. But in all cases they are characterised by the possession of a calcified carapace. Even the nauplius, the first instar with its three pairs of appendages, possesses a slightly calcified duplicature of the dorsal cuticle which encases the whole body. The ostracode carapace is shed by moulting up to eight times during development to the adult animal. As in other crustaceans, the cuticle of the carapace is mineralised with low magnesium calcium carbonate in the form of calcite (Kesling, 1951; Sohn, 1958). This differs from the molluscan shell which contains aragonite. In addition, the calcite is not recycled during moulting as happens in many malacostracean crustaceans, but is discarded with the old carapace and thus has to be formed again during calcification of the new shell (Turpen and Angel, 1971).

The calcified shell consists of small crystallites embedded in a chitinous and protein matrix (Bate and East, 1972, 1975; Langer, 1973; Keyser, 1982; Rosenfeld, 1979). Depending on the systematic relationship, the microstructure of the adult carapace is expressed in a variety of forms. The shell can be almost completely built of calcite crystals as in the Cytheroidea, or composed of parallel chitinous lamellae together with a layer of crystallites as in the Bairdioidea and Cyprioidea. However, these different calcification strategies can also be observed in larval animals during the individual valve formation process, depending on the length of time elapsed since the last moult. For example, if the animal did not have enough time to construct a fully calcified carapace, then the shell may consist of mainly chitinous fibres. This is also the case if animals live in an environment with low calcium content, for instance in brackish water.

Here we present results from a detailed micro-anatomical study of the calcification process, which demonstrates that calcium is concentrated first in the epidermal cell layer in the form of granules containing calcium phosphate and chitin, which are expulsed into the cuticular layer. Here the calcium phosphate is formed into amorphous calcium carbonate which, in a final step, is transformed into crystalline calcite. Our findings are essential not only for the understanding of the physiological and histological processes leading to the construction of the shell, but are also fundamental for the interpretation of the different internal structures and the external appearance (ornamentation, spines, etc.). It will also contribute to models describing the transfer of trace metals and stable isotopes from the ambient water into the ostracode carapace.

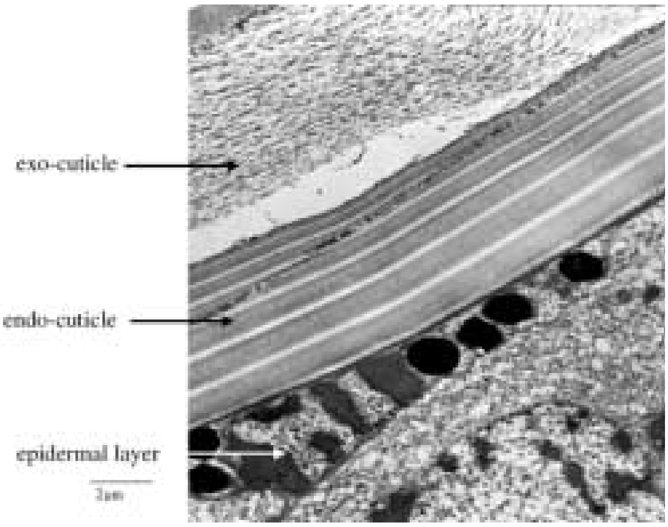

FIGURE 2–TEM-section of the calcified cuticle of *Hirschmannia viridis.*

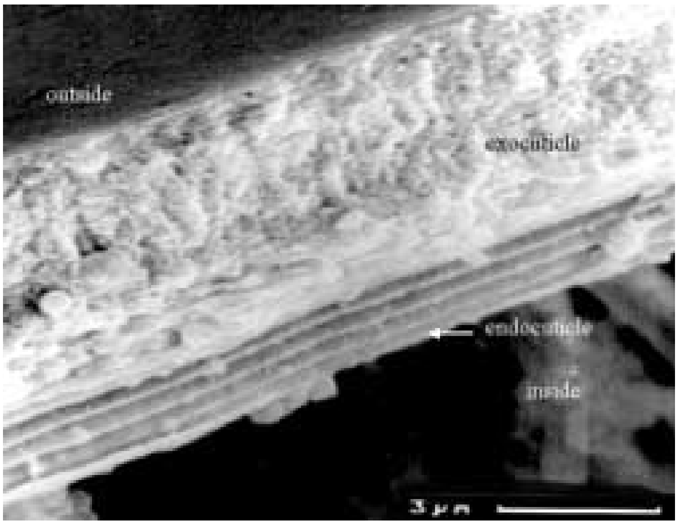

FIGURE 1–SEM picture of fracture across the calcified cuticular layer of *Bairdia* sp.

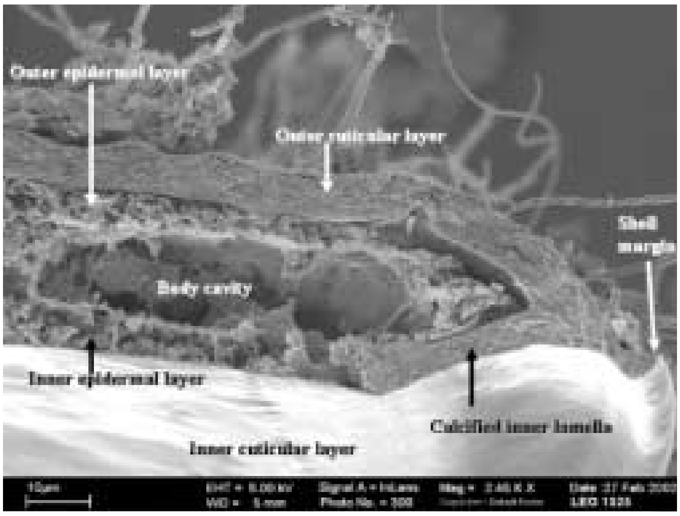

FIGURE 3–SEM picture of fracture of the shell margin of *Candona neglecta.*

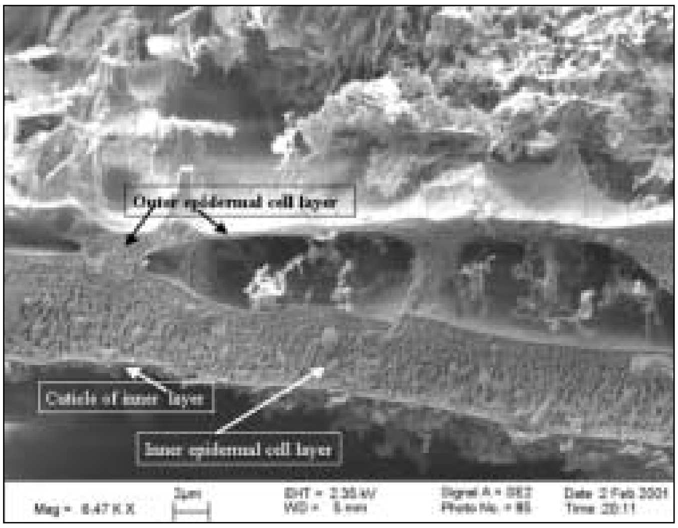

FIGURE 4–SEM picture of fracture through the shell of *Cyprideis torosa*, showing the cells of the outer and inner epidermal layer. The outer calcified layer is removed, remnants of the chitin sheets are still visible.

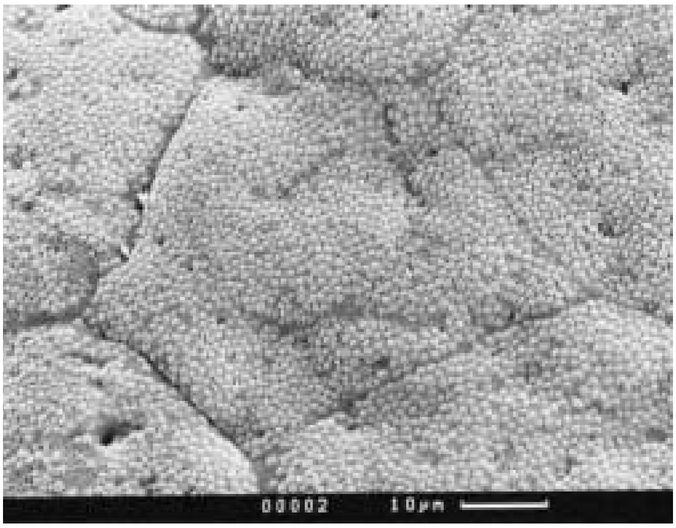

FIGURE 5–*Cyprideis torosa:* SEM picture of the top of outer epidermal cells just after moulting. (Calcified layer removed.)

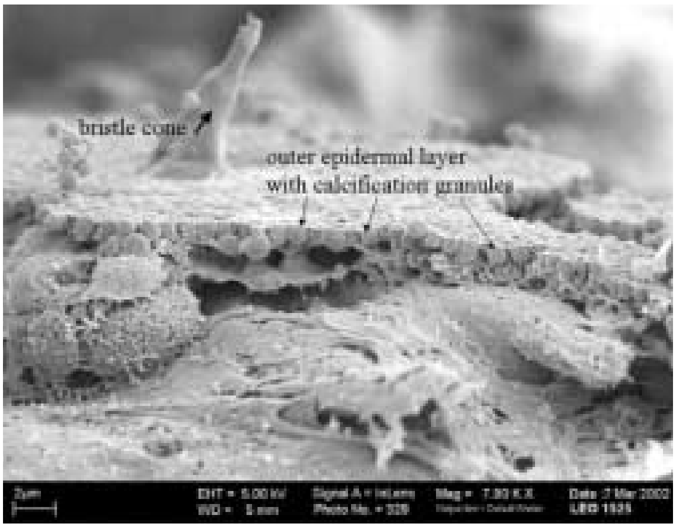

FIGURE 6–SEM picture of fracture of a shell of a moulting *Heterocypris salina* with calcified layer removed.

MATERIAL AND METHODS

Ostracodes of the species: *Bairdia* sp., *Boreostoma variabile* (Baird, 1835), *Hirschmannia viridis* (Müller, 1785), *Cyprideis torosa* (Jones, 1950), *Candona neglecta* (Sars, 1887), *Cypria ophtalmica* (Jurine, 1820) and *Heterocypris salina* (Brady, 1868) have been investigated. They were chosen on the basis of their preferred biotope, representing marine, brackish, saline and fresh water environments.

The animals were either taken directly from their biotope or were kept in aquaria with original water prior to study.

For SEM and TEM investigations the animals were fixed in 3% glutardialdehyde in 0.05% phosphate buffer for one to two hours, followed by three 15-minute washings in buffer alone. In addition, fixation with 2% osmium-tetraoxide in the same buffer was performed. Animals were then dehydrated in a graded series of ethanol from 30% to 100% in 10% steps.

At this point the animals for SEM were critical point dried in a Balzers CPT Dryer with CO_2. The animals were broken in the dried stage with needles or with razor blades. After a shading procedure with carbon in an evaporation unit PD170AZ from Leybold-Heraeus the shells were observed and photographed in a LEO 1525 SEM equipped with an EDAX energy spectrometer.

TEM samples were decalcified in a drop of Acetylchloride in 100% acetone (10 ml), embedded in Spurr’s resin and cured for two days at 60ºC. Sections were cut on a Reichert-Jung Ultracut E. After staining in uranyl-acetate and lead-citrate the sections were viewed in a Zeiss TEM 902 with an electron-filtering-system.

In some cases ostracodes were frozen alive in cold propane at -150ºC. The frozen animals were cut in the Ultracut E equipped with a freeze sectioning unit FC 4E manufactured by Reichert-Jung. After that they were kept in 100% acetone at -80ºC for four days and then slowly warmed to room temperature with an extra change of 100% acetone. They were dried in the CPT dryer, carbon coated and viewed in the Leo 1525.

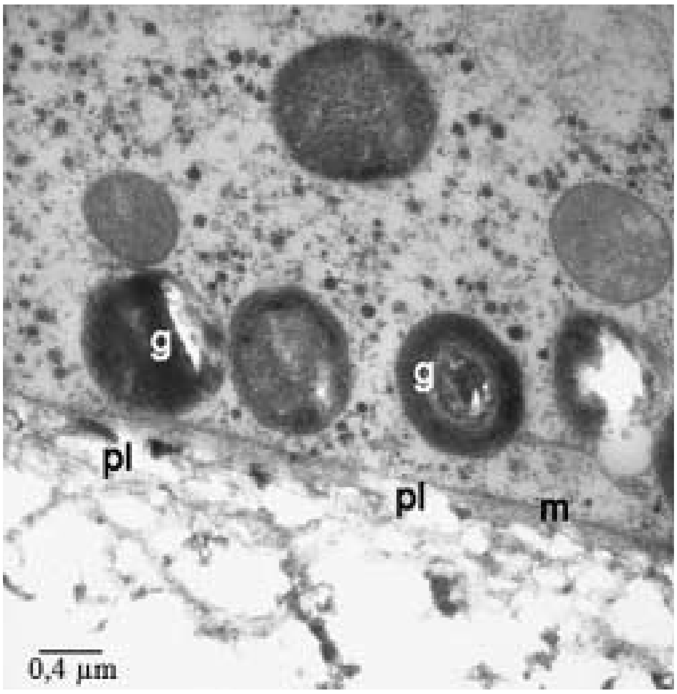

FIGURE 7–TEM Section of *Heterocypris salina*, showing the outer border of the outer epidermis layer with electron dense granules (g), the outer membrane of the epidermal cell (m) and in the decalcified cuticle unstained areas assumed to be the space of platelets (pl).

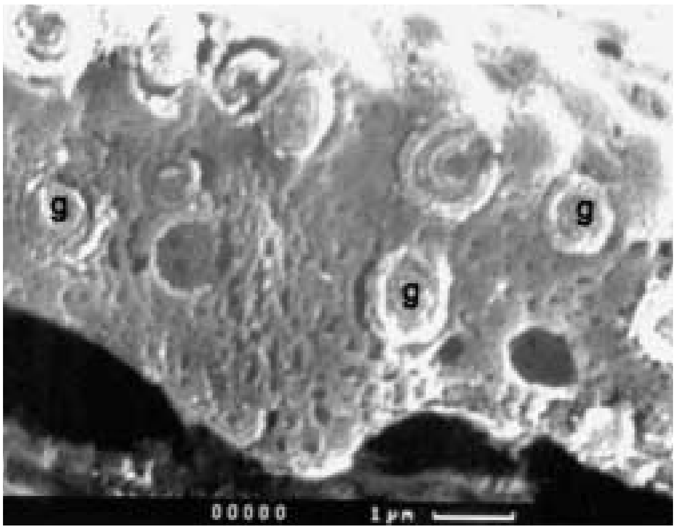

Figure 8–*Hirschmannia viridis*: SEM picture of a fracture of an outer epidermal cell during moulting, with several broken concentric granules (g).

Chemical analyses were performed on the bulk animals in the SEM with the help of the energy dispersive micro analysing system EDAX with the software Falcon. Electron spectroscopic imaging (ESI) was performed on sections in the TEM.

RESULTS

Sections and fractures through shells of some ostracodes (*Hirschmannia, Bairdia* sp.) show a calcified crystalline outer layer and a mainly lamellate inner layer without crystals (Figs. 1, 2). A fracture of the shell of *Candona neglecta* shows only crystalline structures underlain by living cells of the epidermis (Fig. 3). The difference in structure of the outer epidermal cells producing the calcified shell and the inner epidermal cells with their thin cuticle and osmoregulation capacities (Keyser, 1990) is well defined in the fractured shell of *Cyprideis torosa* (Fig. 4). During moulting the outer epidermal layer seen from the side shows the arrangement of cells beneath the calcified cuticle as well as large amounts of granules present within these epidermal cells (Figs. 5, 6). The granules are about one micron in size. Sections as well as fractures show that these granules are concentric in their inner structure (Figs. 7, 8, 14). At high magnification fractured dried specimens show granules with smaller grains within, some of which have dried to a crystalline shape (Figs. 10, 11, 12). EDX and ESI analyses show that these granules contain compounds of phosphorous and calcium with only small amounts of carbon (Fig. 14). Chloride and sulphur are also detectable in these small bodies (Fig. 13).

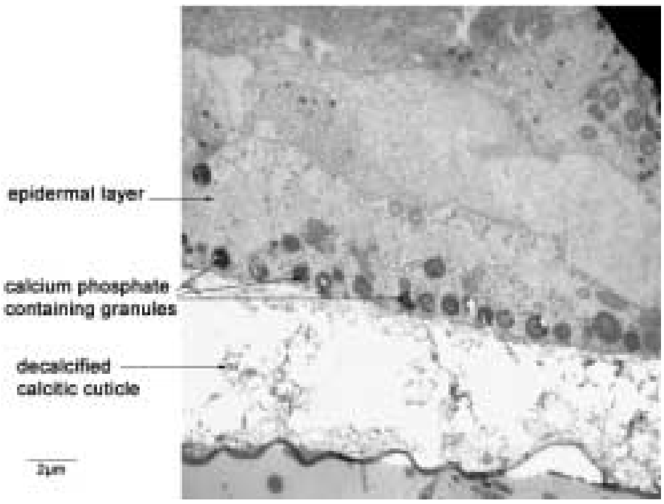

FIGURE 9–*Heterocypris salina:* TEM section of the shell.

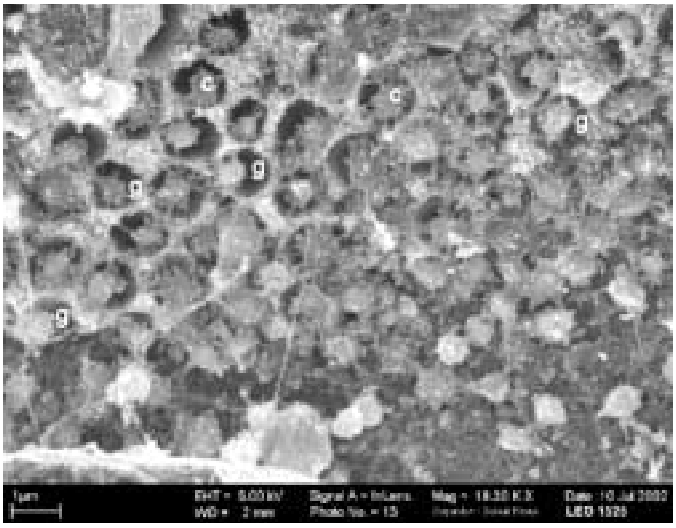

FIGURE 10–SEM picture of broken epidermal layer of a moulting *Heterocypris salina* showing the open granules (g) and some crystals within (c).

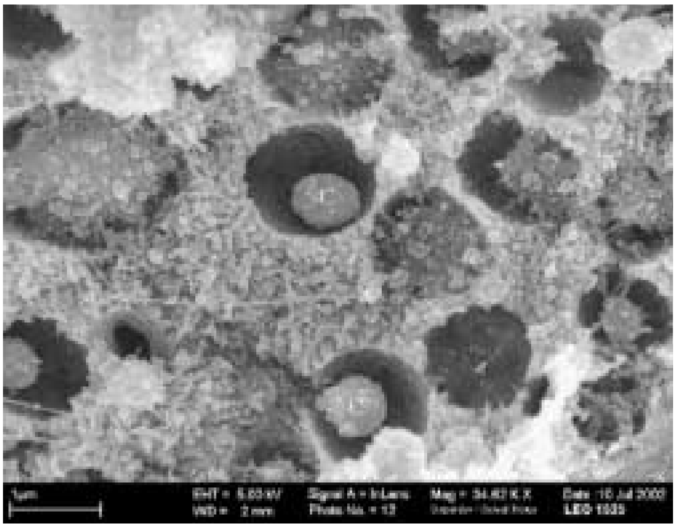

FIGURE 11–SEM picture of broken epidermal granules of a moulting *Heterocypris salina* with rounded crystals (c).

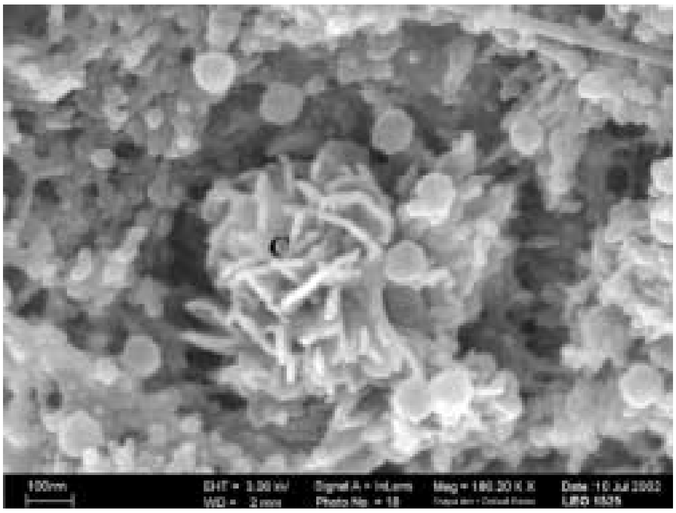

FIGURE 12–SEM picture of dried crystal (c) in the epidermal granule in *Heterocypris salina* resembling a macroscopic octo-calcium-phosphate crystal

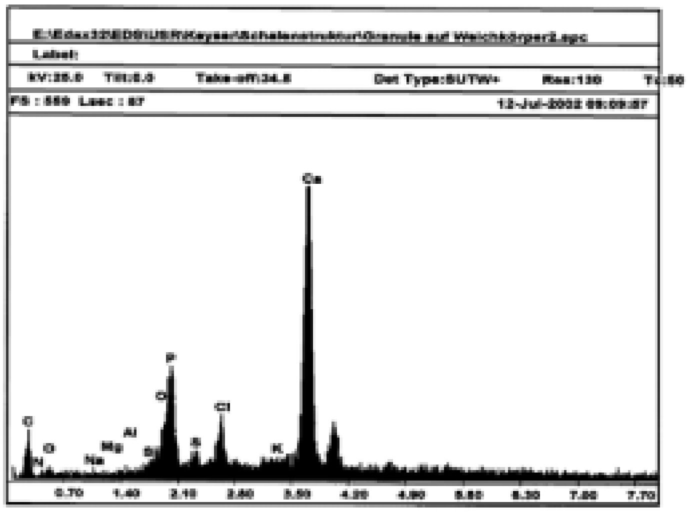

FIGURE 13–*Heterocypris salina*: EDX-Analysis of a granule in the outer epidermal cell.

Fig. 15 shows what might be the transition of the contents of two granules across the cell membrane into the calcified shell. Between the sectioned granule and the outer membrane is an electron dense area which is also visible outside the membrane and which appears similar to parts of the decalcified areas in the same region.

At high magnification fractures of epidermal cells show the outer structure of intact granules covered with short fibres (Figs. 16, 17). In some cases these granules seem to release a homogenous substance (Fig. 17). Outside the external cell membrane platelets are detectable, which, from their size and fine surface structure, appear to be derived directly from the material in the granules of the epidermal cells (Figs. 18, 19). A similar fine structure is also present on the surface of each crystal in the calcified shell (Fig. 20). Chemical analyses reveal that these crystals have a calciting origin

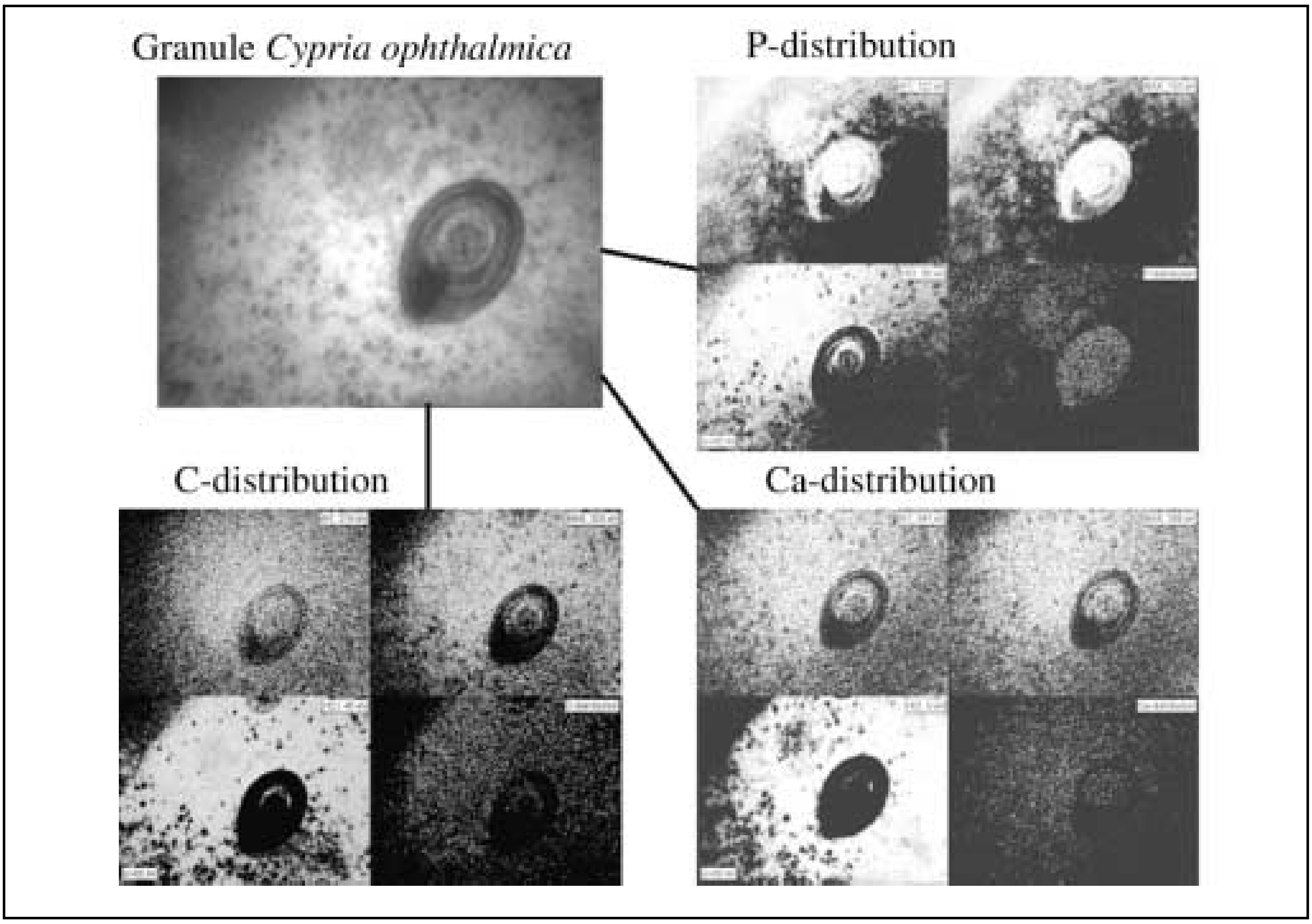

FIGURE 14–ESI-Analysis of a granule in *Cypria ophtalmica.*

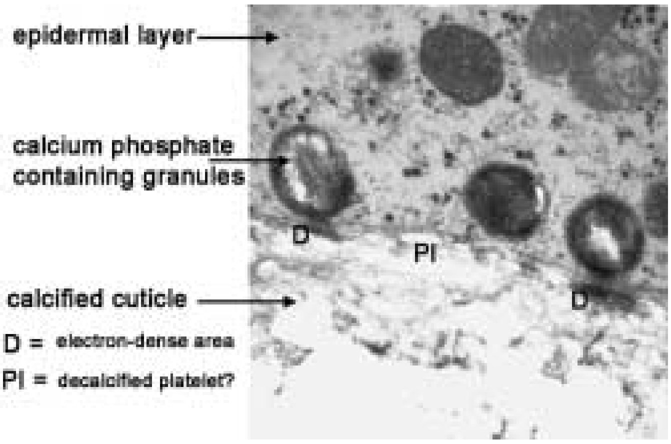

Figure 15–*Heterocypris salina:* TEM section through the border of the outer epidermal cells with the calcified layer showing granules and part of the platelets (pl). *(Please note the electron dense area (D) between the calcified cuticle and the granule, bridging the cell membrane area).*

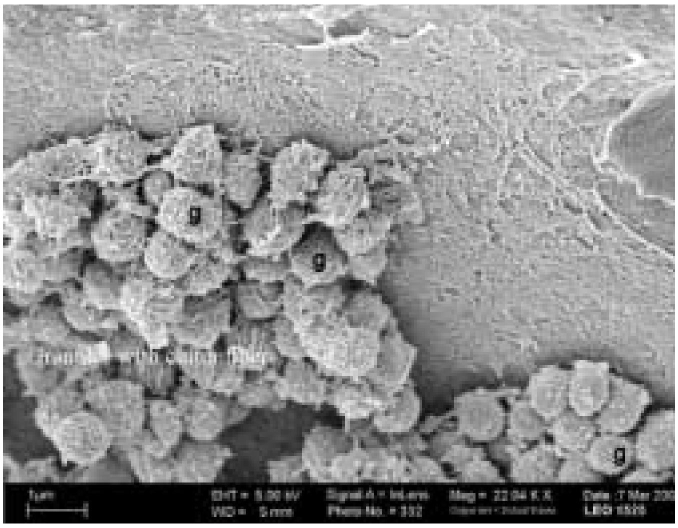

FIGURE 16–SEM picture of granules (g) of the cells in the outer epidermal layer of *Heterocypris salina.*

(Fig. 21). However, their appearance differs from that of mineral calcite which has a smooth surface without fine structures (Fig. 23). The transition from the platelets just outside the epidermal cell membrane to the final crystalline arrangement is achieved by a temporary formation of very small (<30 nm) calcitic granules (Figs. 19, 22).

In *Boreostoma variabile* the crystals adjacent to the epidermal cells are very small and show fine granular features on the side facing the epidermal cells (Fig. 24). In the hinge region in *Boreostoma* this fine granular substance is present between the chitinous fibres which are the main component in this region (Fig. 25). The size of these granules is about 20 to 30 nm. Small granular substances are also present just above the cell membrane of the outer epidermal layer in *Candona* (Fig. 26), *Cyprideis* and *Cypria*.

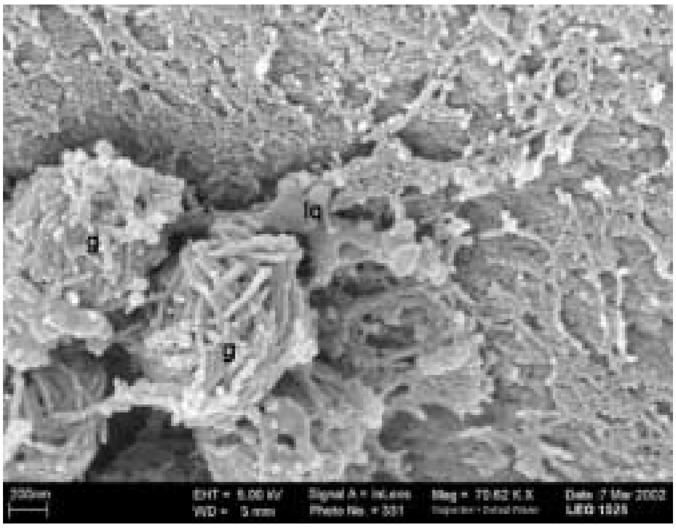

FIGURE 17–SEM picture of calcification granules (g) of the outer epidermal layer of *Heterocypris salina* with chitin fibres and the presumably liquid substance (lq) emerging from the granule.

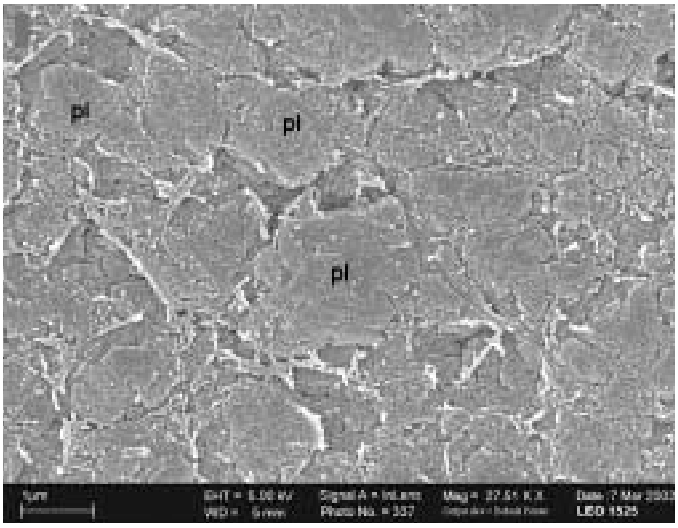

FIGURE 18–SEM picture of inside view of outer calcified cuticle with platelets (pl) of granule material in *Heterocypris salina*

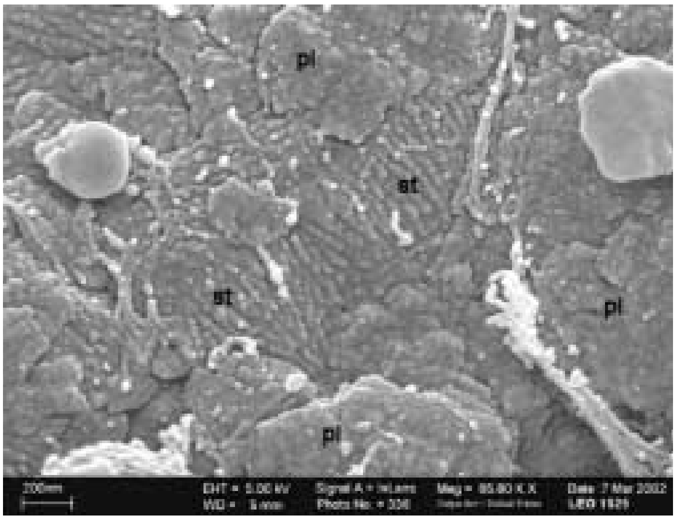

FIGURE 19–SEM picture of surface of the inside of the calcified outer cuticle, showing platelets (pl) and parallel chitin fibres (st) in *Heterocypris salina.*

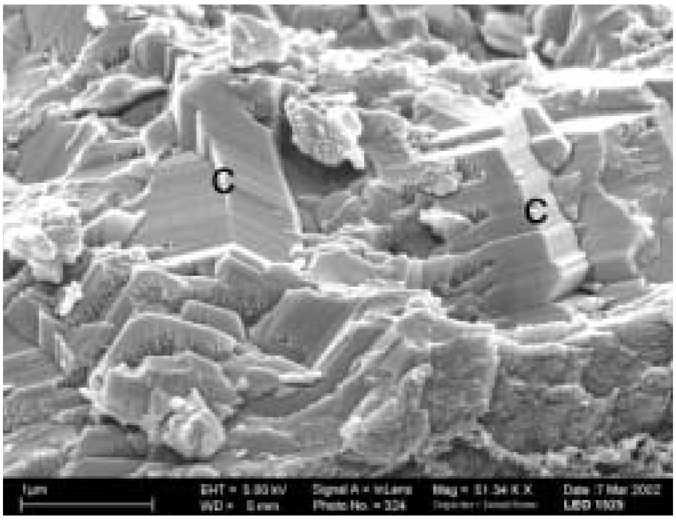

FIGURE 20–SEM picture of calcite crystals (c) in the calcified cuticle of the shell of *Heterocypris salina.*

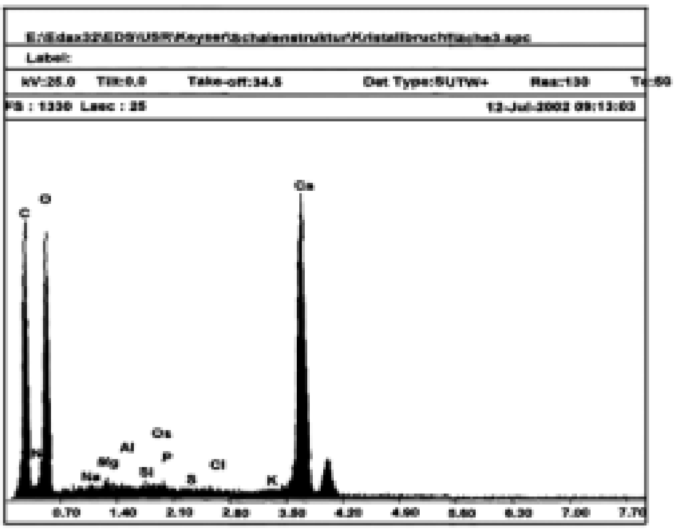

FIGURE 21–*Heterocypris salina*: EDX-Analysis of the fracture face of crystal.

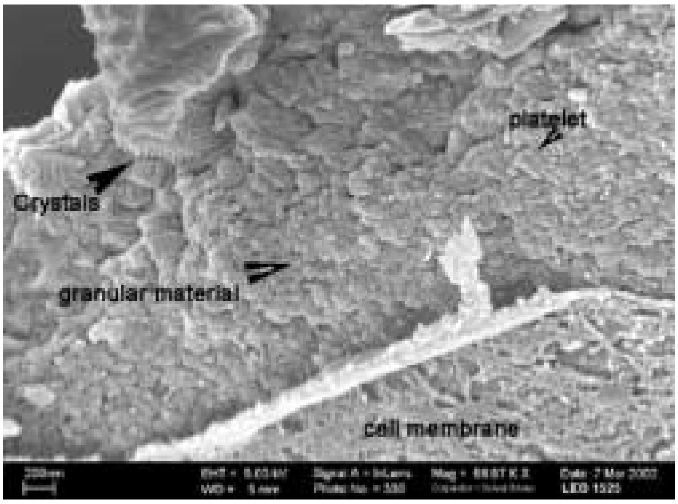

FIGURE 22–SEM picture of transition of platelet material to the calcitic shell cuticle in *Heterocypris salina.*

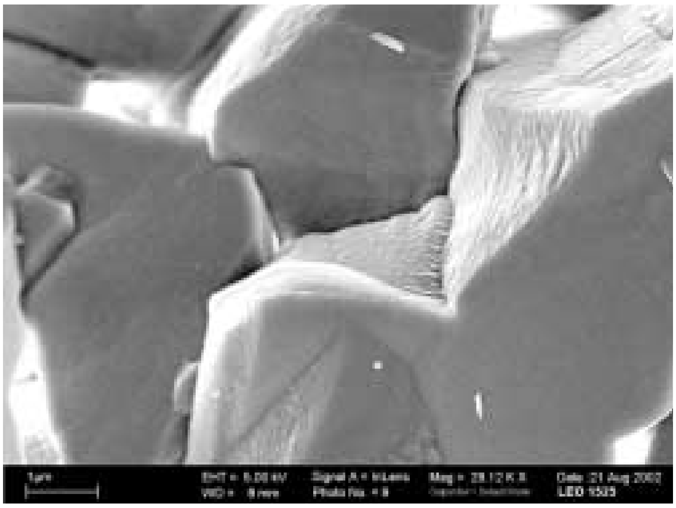

FIGURE 23–SEM picture of calcite crystals from the European Alps.

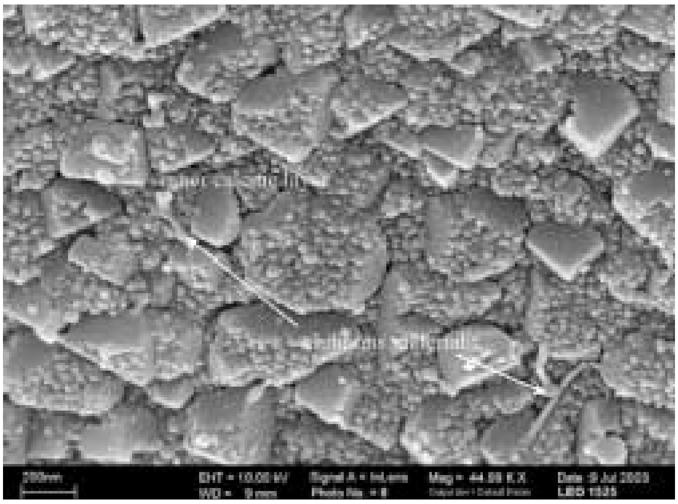

FIGURE 24–*Boreostoma variabile:* SEM inside view of the calcitic layer with the epidermal cells removed. *(Please note the extremely fine globules on the crystals).*

DISCUSSION

The calcified shell of ostracodes has been studied by many authors. G.W.Müller (1894) separated the chitinous layer from the outer calcified layer and found several lamellar striated chitinous shells in myodocopids. Schreiber (1922) mentioned an inner chitinous layer and an outer calcified layer. Kesling (1951) determined the crystalline structure in the shell as calcite. Sohn (1958) reported the different chemical constituents within the shell. He cited Kinser who found 12,8 % protein, 2,2% chitin, 82,7% calcium carbonate and 1,9% trace elements in *Chlamydotheca*. Sohn (1958) found 80-90% calcium carbonate and 2-15% organic material together with many trace elements such as K, Mg, Si, Al, Sr and Ba. Hartmann (1966) cited Dudich (1931), Zalanyi (1944) and Kesling (1951) who showed that the main mineral in ostracode shells is calcite and not aragonite as in molluscs.

Hartmann's (1966) explanation regarding the organic support of the calcified carapace was based mainly on work done by Fassbinder (1912) and is incorrect, as

FIGURE 25–*Boreostoma variabile:* SEM picture of hinge area with chitin fibres (ch) and fine calcitic granules (gr).

FIGURE 26–SEM picture of fracture of shell of *Candona neglecta,* showing the transition of calcitic material from cell to crystals.

shown in studies by Joergensen (1970), Bate and East (1972), Langer (1973), Bate and Sheppard (1982) and Rosenfeld (1979).

All these authors confirm what Müller (1894) had already illustrated, that there are three different mechanisms of chitinous support in the calcified carapace: a layered chitinous lamella, a penetration of chitin perpendicular to the surface, and a form of network. Rosenfeld (1979) and Dépêche (1982) were the first to illustrate granules in the living epidermal layer and tried to explain the secretion process of the carapace. Our results are in agreement with these findings.

The carapace is built from chitinous and crystalline layers (Figs. 1, 2). The epidermal layer secretes both of these substances. Particularly during moulting large amounts of granules are present in the outer epidermal layer (Figs. 5, 6; Rosenfeld, 1979). These granules contain calcium phosphate in addition to sodium, potassium, chloride and sulphur (Fig. 13). It is interesting to note, given these latter elements, that neither magnesium nor strontium (known to be present in the fully calcified valves) are present in these small intracellular bodies. In some instances the crystalline grains in these granules show a structure similar to that of large artificially produced crystals of octo-calcium-phosphate (Fig. 12). This also proves that the material in the granules is apatite. During the ongoing process the apatite is secreted through the outer epidermal cell membrane in the area beneath the shell. This can be achieved by several mechanisms. 1) It can be transported actively by an energy consuming process through the membrane. This is not very likely, since mitochondria, which would be necessary to fuel this process, are not sufficiently present in the area. 2) There could be an eccrine secretion of the contents of these granules, but we did not observe a stage in any of our sections which could provide evidence for such a secretion. Instead we found an electron dense stained area directly at the border of the membrane and the granule (Fig. 15). Whether this could be an osmotic or membrane driven process is not yet clear. But it is interesting that the material released from the cells gives rise to platelets on the inner surface of the new shell. The volume area of a single platelet corresponds well with the contents of one of the granules. The platelets are also distinctly separated from each other, probably by an organic substance (proteins?) (Figs. 18, 19). The platelets then lose their distinct form and build groups of very tiny granules of not more than 20 nm in diameter (Figs. 22, 26). However, at this stage, the material is already calcium carbonate and not phosphate (Fig. 21). Compared with the carbonate deposits in *Porcellio scaber* in a recent paper by Becker *et al.* (2003), these tiny little granules are also thought to represent an amorphous calcium-carbonate. Due to its higher solubility, this amorphous material can probably be mobilised by the animal. If the amorphous calcium-carbonate remains in the region for a longer period, it will eventually crystallise and produce the typical crystals in the shell of an ostracode (Figs. 20, 26). In some ostracodes, for instance in the genus *Cypria,* the main constituent of the shell remains the amorphous material (as in Fig. 25), so that these animals only rarely become fossilised. In shells of adult specimens of other genera all the amorphous material has already crystallised and so no amorphous material is left. In the larval stages on the other hand crystallisation is not complete and the animals have weaker shells.

Summing up, prior to moulting the ostracodes begin producing shells by storing a huge amount of calcium phosphate granules together with chitin precursors in the outer epidermal cells. These granules release their contents into the extra-cellular space directly outside the epidermal cells. This material is transformed into small platelets, each about the size of one granule. The platelets are no longer made of calcium phosphate but of calcium carbonate. These platelets disintegrate into small granular structures, which appear to be amorphous calcite. This granular substance then forms the crystals, which, in connection with chitin and proteins, build the shell of the ostracode. These statements are true for all investigated animals whether they are freshwater or marine organisms.

Several questions regarding the secretion of the calcified cuticle in ostracodes remain:

1. How are the contents of the intracellular granules released to the outside?
2. Where and when are the environmentally induced trace elements such as Mg, Sr, etc., incorporated in the shell crystals? Can the higher abundance of nano-granular amorphous calcium carbonate explain the usually higher Mg-concentration in juvenile shell material?
3. Is there an acidic micro milieu area present in the crystallisation process as suggested by Keatings (2002) and von Grafenstein (EOM V, abstract) to explain the positive O^{18}-offset of most ostracode valve carbonate compared to a theoretical calcite in isotopic equilibrium?

These points must be discussed and investigated bearing in mind the observation of Turpen and Angel (1971) that all the calcium secreted by the animal originates from the surrounding water and not from a storage within the animal. Therefore, another important step involved in the ostracode calcification process, the transport of those large amounts of calcium into the epidermal cells – has to be investigated.

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PATTERNS OF MORPHOSPACE OCCUPATION IN RECENT CYPRIDOIDEA (CRUSTACEA, OSTRACODA)

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Abstract

Patterns of morphological disparity are explored at different taxonomic levels within the ostracod superfamily Cypridoidea Baird, 1845. Valve outlines for 171 species in four families, fifteen subfamilies and forty genera have been extracted from existing literature and analysed using elliptic Fourier analysis. Once ostracod shapes are characterized numerically, the cypridoidean (empirical) morphospace is described accordingly. The position of the ostracod species within the morphospace allows the computation and comparison of the morphological disparity in different groups, as well as their relative contribution (partial disparity) to overall morphological variation. The family Candonidae is the group with the highest diversity in valve shape and accounts for more than 50% of total disparity in the superfamily. *Mixtacandona* and *Cypria*, with their extreme shapes, are mainly responsible for that pattern. However, as compared to the Cyprididae, taxonomic diversity of candonids is low suggesting that morphological diversity might better reflect ecological processes (*e.g.* adaptation to extreme environments) than branching phylogenetic patterns.

Key words: Morphometrics, disparity, non-marine ostracods, taxonomic diversity.

Resumen

Se exploran los patrones de disparidad morfológica en diferentes niveles taxonómicos dentro de la superfamilia de ostrácodos Cypridoidea Baird, 1845. Se han obtenido de la literatura los contornos de las valvas de 171 especies pertenecientes a cuatro familias, quince subfamilias y cuarenta géneros, y su forma ha sido analizada mediante el uso del análisis elíptico de Fourier. Una vez que los contornos han sido caracterizados numéricamente, se procede a construir el morfoespacio empírico de la superfamilia. La posición de las especies en dicho morfoespacio permite el cálculo y la comparación de la disparidad morfológica entre diferentes grupos, así como de su contribución relativa (disparidad parcial) a la variación morfológica total. Los Candonidae son el grupo con la mayor diversidad morfológica, que supone más del 50% de la disparidad total en la superfamilia. Los géneros *Mixtacandona* y *Cypria*, con sus formas extremas, son los principales responsables de esta circunstancia. Sin embargo, por comparación con los Cyprididae, la diversidad taxonómica de los candónidos es baja y sugiere que la disparidad morfológica es más el reflejo de procesos ecológicos (p. ej., adaptación a ambientes extremos) que de bifurcación filogenética.

Palabras clave: Morfometría, disparidad, ostrácodos no-marinos, diversidad taxonómica.

INTRODUCTION

Disparity, the amount of morphological diversity within a taxon, has become a major topic in evolutionary and systematic biology (Briggs *et al.*, 1992a; Foote, 1992a; Foote, 1996a; Foote, 1997a). Researchers have largely approached studies on morphological disparity within a grand-scale evolutionary framework (Knoll *et al.*, 1984; Foote, 1992a; Foote, 1993bb; Foote, 1997a; Wagner, 1997), but enquiries with a heavy ecological bias are common as well (Hertel, 1994; Ricklefs & Miles, 1994; Van Valkenburgh, 1994). Indeed, evolutionary and ecological arguments must necessarily concur on most hypotheses willing to explain the origin and pattern of morphological diversity (Foote, 1997a; Ciampaglio, 2002). Many taxonomic groups (blastozoans, blastoids, crinoids, trilobites, foraminiferans, brachiopods, ammonoids, gastropods, mammals) have been the subject of studies on disparity (see Foote, 1997a for references), and ostracods (Crustacea, Ostracoda) are no exception to that rule (Benson, 1975; Benson, 1976; Oertli, 1976; Whatley & Stephens, 1976; Benson, 1981; Benson, 1982; Benson *et al.*, 1982; Reyment, 1982; Reyment, 1985a; Reyment, 1985b).

Taking advantage of the recent progress experienced by both the quantitative measure of morphological disparity (Briggs *et al.*, 1992b; Foote, 1992a, 1992b, 1993a, 1993b, 1997a, 1997b; Wills *et al.*, 1994; Ciampaglio *et al.*, 2001) and morphometric analysis (Rohlf, 1990, 1998; Bookstein, 1991, 1996; Rohlf & Marcus, 1993; Zelditch *et al.*, 1998) we here address the exploration of morphospace occupation patterns in a major group of recent non-marine ostracods, the superfamily Cypridoidea Baird, 1845.

The Cypridoidea belong to the Podocopida Sars, 1866, which is the most diverse and widely distributed order among recent ostracods and the only one with non-marine representatives (Martens *et al.*, 1998; Smith & Horne, 2002). The oldest representatives of Cypridoidea were identified in Devonian sediments (c 400 Myr) (Maddocks, 1982), although diversity in the group burst much later, during the Upper Jurassic (c 165 Myr) (Whatley, 1992; Martens *et al.*, 1998). In addition to the Cypridoidea two other podocopid superfamilies have invaded continental habitats too: Cytheroidea Baird, 1850 and Darwinuloidea Brady & Norman, 1889. However, the Cypridoidea are dominant in continental habitats standing for nearly two thirds of the described Recent non-marine ostracod faunas, e.g. in Europe (Löffler & Danielopol, 1978), Africa and/or South America (Martens, 1998).

The superfamily Cypridoidea includes four Recent families: Cyprididae, Candonidae, Ilyocyprididae and Notodromadidae (see Appendix for comprehensive taxonomic information). The Cyprididae are the more diverse of them all with a number of described extant species approaching 1,000 and some estimates on expected actual diversity which double that figure (Martens *et al.*, 1998). Morphological diversity in the group runs in parallel to its taxonomic diversity with size ranging from the exceedingly small (less than 0.5 mm) to 'giant' species (more than 6 mm) and shape varying enormously as well (elongated, triangular, globose, subquadrangular, etc.). Candonidae follow cypridids in taxonomic diversity but beat them in morphological and ecological plasticity. Candonids –nearly 500 species have been described in Europe and Asia (Löffler & Danielopol, 1978; Martens *et al.*, 1998)– occur in both epigean habitats and groundwater systems. And the only marine lineage within the Cypridoidea, the Paracypridinae, belongs to the Candonidae too. Ilyocyprididae and Notodromadidae, the remaining two families, are species-poor lineages (less than hundred species each), the former with an almost invariant carapace morphology.

Within this framework we here address the search for patterns of morphological disparity at different taxonomic levels (families and subfamilies) within the Cypridoidea. Our aim is descriptive rather than evolutionary because the temporal dimension is not considered here but only recent species from a limited geographical range (Europe) will be included and, in doing so, our capabilities for making evolutionary inferences are severely limited. However, given the enormous amount of extant and fossil species involved and the uneven information available for different geographic areas, an attempt at a more modest scale sounds much more realistic as a first step.

Additionally the relationships between morphological and taxonomic diversity and the likely links between disparity and species environment will be explored as it has been suggested that selective pressures imposed by the physical structure of the habitat might have been of paramount importance in carapace shape evolution in these crustaceans (Danielopol, 1977, 1978, 1980a).

MATERIAL AND METHODS

Valve outlines from representatives of 171 recent species of non-marine ostracods in the superfamily Cypridoidea were digitized using scanned images from the literature (see Appendix). All sources refer to European (Russia not included) localities. This sample represents approximately 50% to 60% of the cypridoidean species recorded in the area (Martens *et al.*, 1998; Horne *et al.*, 1998). Representatives of all four families also have been included in numbers that parallel their proportional diversity at the continental scale: Cyprididae - 81 spp (47%); Candonidae - 81 spp. (47%); Ilyocyprididae - 6 spp. (3.5%) and Notodromadidae -3 spp.(1.7%).

Given that the focus of the study is on patterns of disparity at ranks above the genus level, sources of variation at levels below (like sexual dimorphism or asymmetries between left and right valves) must be kept to a minimum when not completely removed. Here females were selected over males because the latter have not been described for a significant number of cypridoid species which reproduces parthenogenetically (Horne *et al.*, 1998). Right valves were preferred over left valves because in many species this is the valve which contains more morphological details due to its functional role in the closing of the carapace (Baltanás & Geiger, 1998). Still, female left valves were used for three species (*Isocypris beauchampi*, *Psychrodromus betharrami* and *Ps. robertsoni*) for which we were not able to find any illustration of a right valve. Similarly, no proper illustration of a female of *Paracandona euplectella* was known to us. Accordingly we used the outline of the left valve of a male as redrawn by Meisch (2000) from Klie (1938) (see Appendix). Outlines, each one containing between 1,700 and 2,200 points, were digitized using tpsDig 1.311 software (Rohlf, 2001). These original outlines were smoothed by taking a weighted moving average over three successive coordinate points (Haines & Crompton, 2000),

$$\left[(x_i^*, y_i^*) = \frac{1}{4}(x_{i-1}, y_{i-1}) + \frac{1}{2}(x_i, y_i) + \frac{1}{4}(x_{i+1}, y_{i+1})\right]$$

and scaled to centroid size (Dryden and Mardia, 1998). Elliptic Fourier analysis (EFA)(Kuhl & Giardina, 1982), a Fourier technique for fitting functions to curves that has been extensively used with ostracods (Baltanás & Geiger, 1998; Baltanás *et al.*, 2000; Baltanás *et al.*, 2002; Danielopol *et al.*, 2002) and other groups of organisms (Rohlf & Archie, 1984; Ferson *et al.*, 1985; McLellan & Endler, 1998; Smith & Bunje, 1999), was applied to the ostracod outlines. The analysis results in a series of harmonic coefficients that were mathematically normalized to be invariant to rotation and digitizing starting point (Ferson *et al.*, 1985). These coefficients, which can be used to reconstruct the original outlines, were used as shape descriptors in subsequent analysis. Because ostracod valve outlines have rather simple shapes few harmonics are enough to describe them accurately. We have here used twenty harmonics (77 non-trivial coefficients), a number which assures goodness-of-fit above 97% between original and reconstructed outlines. Goodness-of-fit was measured as the mean distance between each point of the reconstructed image and the closest point in the original outline (McLellan & Endler, 1998).

We used principal component analysis (PCA) performed on the variance-covariance matrix of all 77 shape variables produced by EFA to construct an empirical morphospace for the superfamily Cypridoidea. It has been argued that performing PCA on the covariance matrix, as compared to correlation matrix, will diminish or even eliminate any influence of higher order harmonics because EFA effectively downweights all harmonics above the first (successive harmonics describe progressively finer details of the outline) (Haines & Crampton, 2000). Nevertheless, that is not necessarily a drawback of the method but depends on the aims of the study. In the present case our interest is on discriminating shapes by giving preference to general features over fine details. Sharing a tiny spine in the rear part of the valve, for instance, does not make two species as similar as if they were both equally triangular in overall shape.

Morphological disparity is defined as the amount of empirical morphospace which is occupied by a group of taxa. Such variable is here estimated from the locations of the species (*i.e.*, the species' scores) within the multidimensional space defined by PCA axes. Accordingly PCA eigenvectors were scaled to 1 (i.e., their length set to unity) to preserve Euclidean distances among objects (Marcus, 1993; Legendre & Legendre, 1998). Among the many possible ways of measuring morphological disparity (MD) we have selected the mean squared Euclidean distance $MD = \sum_i d_i^2/(N-1)$ where d_i^2 is the squared Euclidean distance between object i from the group centroid and N is the total number of observations (=species number) (Foote, 1993a; but see Ciampaglio *et al.*, 2001) for other indices of morphological disparity). MD is standardised to be independent of sample size (number of species in the group) so that the amount of morphospace occupied is not a function of the number of taxa included in the analysis (Foote, 1993a). There is no meaning in computing MD for the superfamily Cypridoidea as a whole (we have nothing else to compare to), hence morphological disparity is calculated only at the family and the subfamily levels using the corresponding centroids on each case.

The advantage in using MD as index of morphological disparity is that it can be partitioned among its several component subgroups. The contribution of each taxonomic subgroup *j* to the group MD is estimated as partial disparity $PD_j = \sum_i d_{ij}^2/(N-1)(MD = \sum_j PD_j)$ (Foote, 1993a).

Partial disparity is not dependent on subgroup size or variability within the subgroup but on the location of its members with respect to the overall centroid. Subgroups with a low number of members can contribute significantly to the group-MD if they have shapes which greatly differ from the group mean shape. Subgroups peripherally distributed in the morphospace have larger partial disparities than those placed close to the group centroid. It is like having hundreds of circles in a painting; a single square will add more morphological disparity to the whole group that any number of new circles we could add.

Here we have computed contributions to overall disparity in the superfamily Cypridoidea at the family, subfamily and genus levels. Given that the 171 species we are dealing with are just a sample of all the recent Cypridoidea it is helpful to attach a measure of variability to our estimates. However, data like these, with a taxonomic structure behind, are neither independent nor random so that standard parametric statistics cannot be applied (Harvey & Pagel, 1991). Instead we use the bootstrap to estimate both morphological and partial disparities and their variability, here expressed as the standard deviation of the bootstrap replicates, at all taxonomic levels selected by randomly drawing species within each genus with replacement (5,000 replicates) (Foote, 1992ab; 1993a). Variability in morphological disparity (VarMD) reflects the symmetry in the distribution of taxa around their group centroid in the morphospace; whereas variability in partial disparity (VarPD) measures shape redundancy within a group and its relative position to the overall centroid. The more similar the shapes for all the elements within a group (be it a genus, a subfamily or a family) the lower the expected variability in any statistic which is computed from samples randomly drawn (with replacement) from that group. PD estimates can be expressed either in their original units or as percentages of the overall disparity).

Morphological disparity is also related to diversity and to mean carapace size in the group. Diversity is measured both as species richness and as variation in taxonomic distinctness (VarTD or Λ+), an index which evaluates the unevenness of the taxonomic distribution of lower rank taxa within higher rank groups (Clarke & Warwick, 2001). Carapace size, which is a highly variable feature within a species, has been roughly approximated from records in the literature (see Appendix). For groups above the species level an average value was estimated.

RESULTS

Only 15 PCA axes (out of 77) were retained for further analysis as they explained 99.58% of the total variance in the original data set. Indeed, 88.26% of variance in the empirical morphospace is already explained by the first two PCA axes (Figure 1). First axis (77.79%) is mainly related to degree of elongation of outline shape with more rounded outlines (*Notodromas*, *Cypria*) located on the left side and those more lengthy (*Phreatocandona* and some *Mixtacandona*) on the right end side (Fig. 1). The second axis reflects changes in the triangularity of valves: those more quadrangular (e.g. *Ilyocypris spp.*, *Paracandona euplectella*) are displaced upwards and those triangular downwards (*e.g.: Mixtacandona tabacarui*, *Potamocypris fulva*).

Relative positions of members in each family within the two-dimensional morphospace are displayed in figure 2 whereas mean morphological disparity (+standard deviation) at the family and subfamily level are plotted in figure 3. Candonidae and Cyprididae differ markedly in disparity with the former occupying a larger portion of the morphospace than the latter (Fig. 2A-B & 3). Although both groups seem to coincide significantly within the 2D-morphospace plotted in figure 2

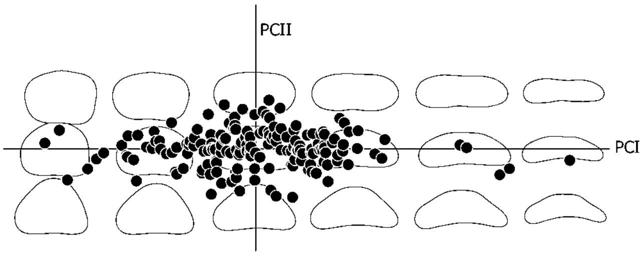

FIGURE 1–Distribution of Cypridoidean shapes (black dots) within the empirical morphospace as defined by the first two axes of a PCA (88.26% of total variance). Outlines are reconstructions of hypothetical shapes in different locations to better illustrate shape gradients within the two-dimensional morphospace.

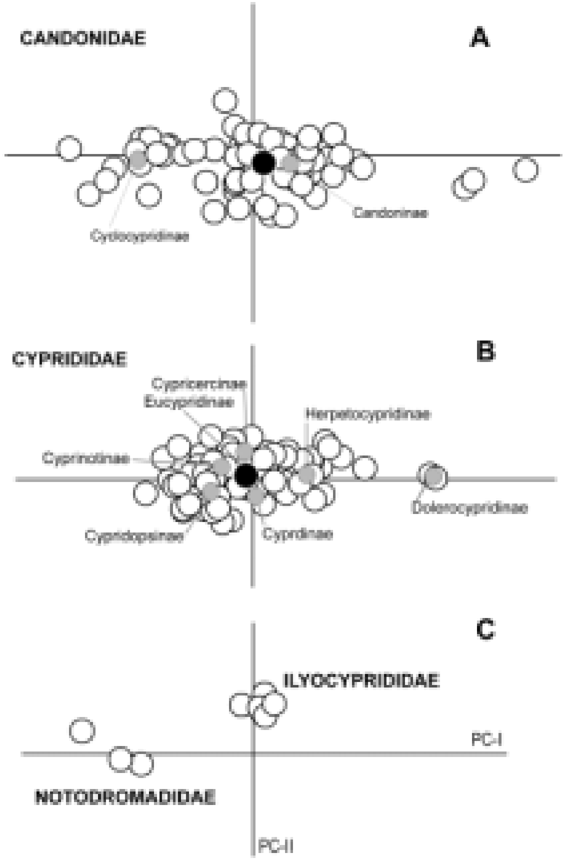

FIGURE 2–Morphospace occupation in Recent Cypridoidea. The empirical morphospace has been split into three plots to better show disparity within each family. Centroids for families (black dots) and subfamilies (grey dots) are included only for, Candonidae and Cyprididae, the species-rich groups.

(A-B) there is indeed a rather non-overlapping distribution as estimated from discriminant analysis performed on species positions within that morphospace (PCA scores for first fifteen axis) which produces 89.5% correct classifications in average. Taxonomic structure within each family, measured as variation in taxonomic distinctness, also differ for both families ($\Lambda^{+}_{\mathrm{CYPRIDIDAE}}$ =0.421; $\Lambda^{+}_{\mathrm{CANDONIDAE}}$ =0.387) reflecting a more even distribution of species among genera and of genera among subfamilies in the Candonidae as compared to the Cyprididae. Whereas half (7 out of 14) of the genera in the Candonidae includes only 1-2 species, five of the remaining seven genera include 8 species at least (10% of the total richness in the family). In the Cyprididae, however, there are few highly speciose genus (*Eucypris* – 21 spp.; *Heterocypris* – 9 spp.; *Potamocypris* – 9 spp.) and many (14 out of 23) genera with 1-2 species only. Taxonomic structure at the subfamily level is rather simple in the Candonidae with two subfamilies only: the Cyclocypridinae (17% of total species richness) and the Candoninae (83% of total species richness). In the Cyprididae there are many more subfamilies (10) but three of them (Eucypridinae, Herpetocypridinae and Cyprinotinae) include 60% of all the species in the group. Other families involved, Notodromadidae and Ilyocyprididae, are much less diverse morphologically (Figs. 2C, 3).

At the subfamily level the most morphologically diverse group and the one with highest species richness is the subfamily Candoninae (67 spp.), followed by the Eucypridinae (29 spp.), the Herpetocypridinae (12 spp.) and so on (Fig. 3). Some groups, like the Cyprinotinae (9 spp.), are highly redundant in shape as compared to less speciose groups like the Cypridinae (2 spp.) or the Cypricercinae (4 spp.) (Fig. 3). These latter groups, although including very few species, expand over a portion of the morphospace much larger than the Cyprinotinae.

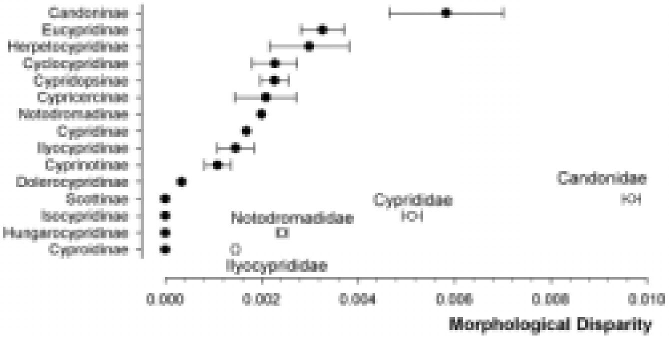

FIGURE 3–Estimates of morphological disparity (mean + SD) within families (white dots) and subfamilies (black dots) in the Cypridoidea (bootstrap estimates from 5,000 replicates).

At the genus level there is a decreasing gradient in morphological disparity from *Schellencandona* to *Dolerocypris* (Fig. 4), with *Mixtacandona* outstanding as the most morphologically diverse genus of them all (Fig. 4).

Partial disparities, the contributions to overall morphological disparity at different taxonomic ranks, are displayed in figures 5 and 6. Overall disparity in the superfamily Cypridoidea has been split into contributions by families, subfamilies and genera within (Fig. 5A-B). Candonidae explain more than half

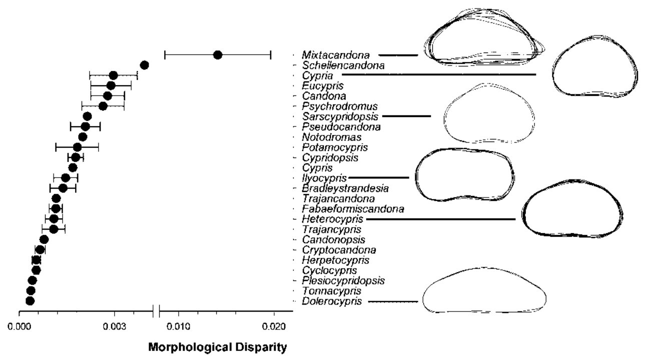

FIGURE 4–Estimates of morphological disparity within genera in the Cypridoidea. Genera with only one species are not included as they have null morphological disparity. Sets of outlines for some representative genera (*Mixtacandona*, *Cypria*, *Sarscypridopsis*, *Ilyocypris* and *Dolerocypris*) are displayed.

(59.5%) of the overall disparity in the Cypridoidea, followed by the Cyprididae (31.6%), Notodromadidae (6%) and Ilyocyprididae (2.9%) (Fig. 5A). At the subfamily level the Candoninae (39%) and the Cyclocypridinae (20%) are the major contributors to total cypridoidean disparity (Fig. 5). Indeed there is no main valve shape type left unexplored by those candonid groups which spread along the main axis of the morphospace (Fig. 2A). However, not all the genera in both subfamilies contribute equally but *Mixtacandona* and *Cypria*, which show extreme shapes, are largely responsible for the high PD of candonids (Fig. 5B). All subfamilies in the Cyprididae, Ilyocyprididae and Notodromadidae are of less quantitative importance to disparity in the superfamily (Fig. 5A). Still some cases are remarkable because of their disparate contribution as compared to their traxonomic diversity. For instance, the Dolerocypridinae, which include two species only, are 'outsiders' in the morphospace (see Fig. 2B) and hence have a striking contribution to overall shape diversity (PD=6.6%). Such a pattern is repeated, but less markedly, for the Notodromadinae (PD=4.8%) and the Ilyocypridinae (PD=2.6%). Notice that *Eucypris*, the genus with the highest taxonomic diversity (21 *spp.*), contributes less to total disparity in the Cypridoidea (PD=5.4%) than the species-poor genus *Dolerocypris* (2 *spp.*) (PD=6.6%) (Fig. 5B).

Contributions provided by subfamilies and genera to disparity at the family level are plotted in Figure 6. Disparity estimates have been computed for Cyprididae and Candonidae only given that Ilyocyprididae includes no more than one genus in a single subfamily and that Notodromadidae only has two genera and two subfamilies (Fig. 6A-D). As expected due to its higher species richness (67 *vs.* 14) and its wider range of valve shapes, Candoninae are more meaningful than Cyclocypridinae to overall candonid disparity (Fig. 6A). At the genus level, however, results are not so self-evident. Major contributors are not the most species-rich genera (*Candona*-18 *spp.*, *Fabaeformiscandona* – 14 *spp.* and *Pseudocandona* – 13 *spp.*) but *Mixtacandona* and *Cypria*, with 9 and 8 species respectively.

Within Cyprididae most of the morphological disparity is provided by Dolerocypridinae, Eucypridinae, Cypridopsinae and Herpetocypridinae at the subfamily level (Fig. 6C), and by *Dolerocypris*, *Eucypris*, *Herpetocypris* and *Potamocypris* at the genus level (Fig. 6D).

The contribution of the several genera to morphological disparity at the subfamily level does not differ greatly from patterns observed for the family or superfamily levels (Fig. 7). Still, some variations are worth to be stressed. For instance, *Trajancandona* and

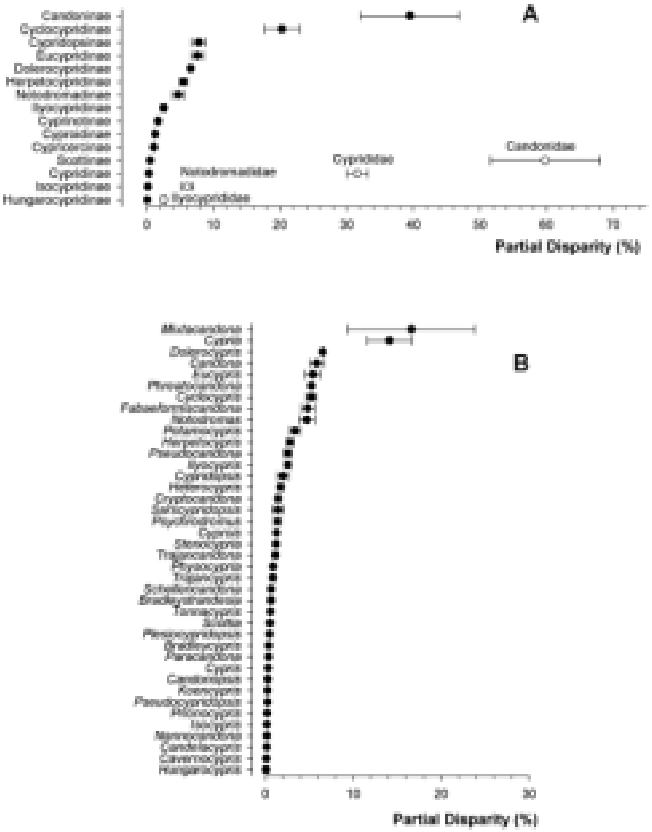

FIGURE 5–Partial disparities (mean contribution +SD) of families and subfamilies (A) and genera (B) to overall morphological disparity in Recent Cypridoidea (bootstrap estimates from 5,000 replicates).

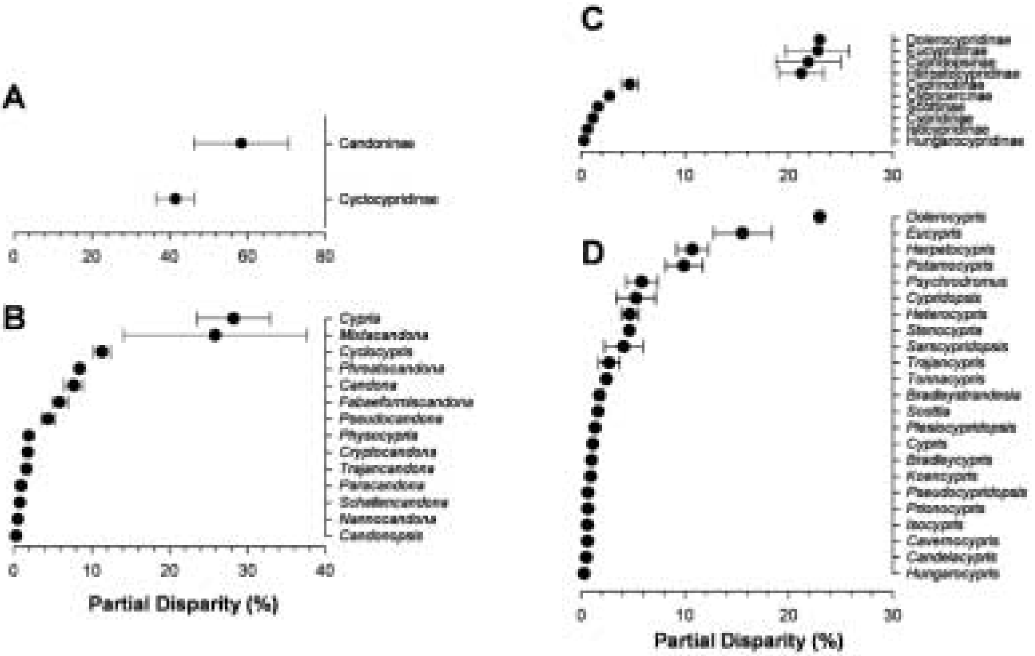

FIGURE 6–Partial disparities (mean contribution +SD) of subfamilies and genera to overall morphological disparity in Recent Candonidae (A, B) and Cyprididae (C,D) (bootstrap estimates from 5,000 replicates).

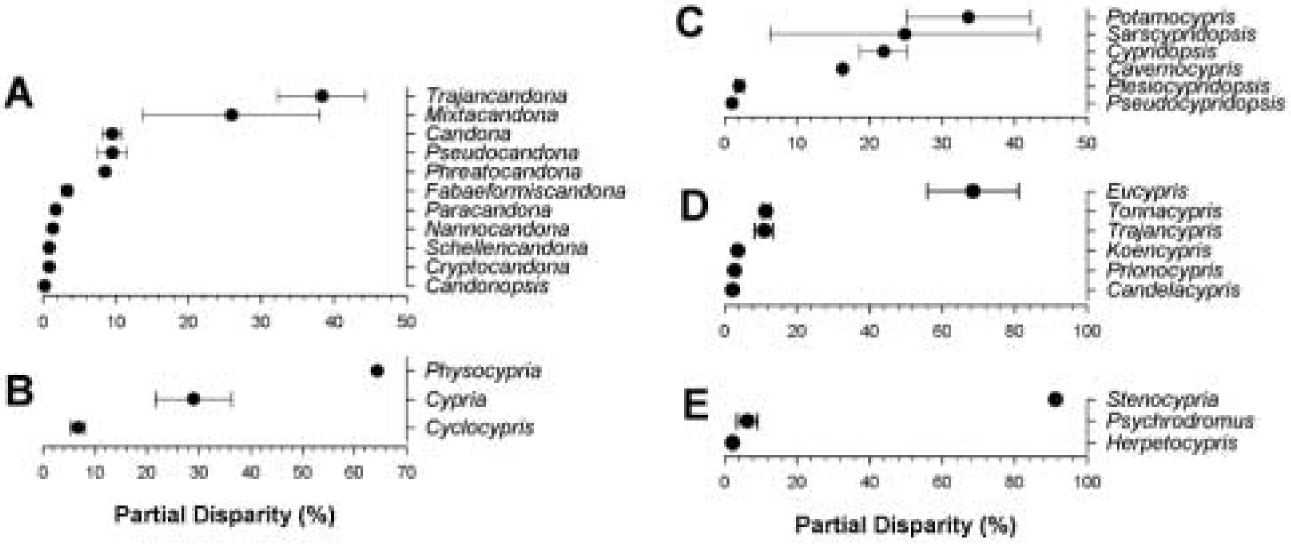

FIGURE 7–Partial disparities (mean contribution +SD) of genera to overall morphological disparity in the main subfamilies within Recent Candonidae (A-Candoninae; B-Cyclocypridinae) and Recent Cyprididae (C-Cypridopsinae; D-Eucypridinae; E-Herpetocypridinae) (bootstrap estimates from 5,000 replicates).

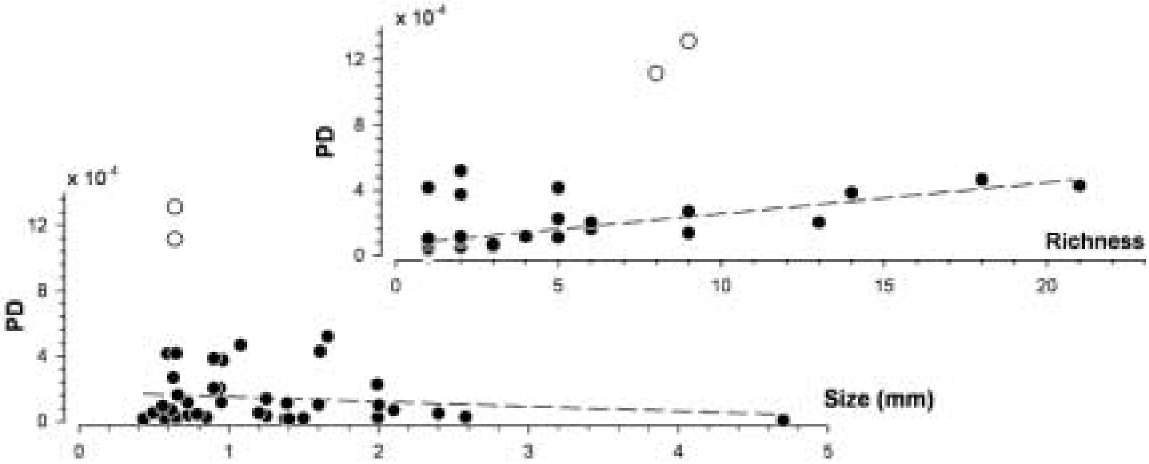

FIGURE 8–Relations of partial disparities at the genus level (contributions to overall disparity within the Cypridoidea) to valve size and species richness. Dashed lines correspond to the lineal regression model (*Mixtacandona* and *Cypria* excluded, see text).

Stenocypria do significantly contribute to disparity within the Candoninae (Fig. 7A) and the Herpetocypridinae (Fig. 7E), respectively, although both are of minor relevance to total disparity in their corresponding families, Candonidae (Fig. 6B) and Cyprididae (Fig. 6D).

Finally, the contributions (PDs) of all the genera in the analysis to overall disparity in the Cypridoidea are related to species richness and average size with *Cypria* and *Mixtacandona* as noteworthy outliers (Fig. 8).

After discarding both cases from the analysis partial disparity shows a slight but significant positive correlation with generic species-richness (Spearman R=0.7094; p<0.0001) and no significant correlation with carapace average size (Spearman R=-0.0554; p=0.741) (Fig. 8).

DISCUSSION

The Candonidae show higher morphological disparity than the Cyprididae; i.e. candonids occupy a larger portion of the cypridoidean morphospace and explore a wider range of carapace shape types than cypridids. At the subfamily level the Candoninae outrun in disparity all the others, including the candonid group Cyclocypridinae and all subfamilies in the Cyprididae. And a gradient exists at the genus level running from low variable highly redundant groups of species (*Dolerocypris, Plesiocypridopsis, Cyclocypris*) to those with a extreme disparity (*Mixtacandona* and *Cypria*). All these statements might be no surprise for most practitioners of ostracodology but this is the first time that they are demonstrated on a quantitative basis, and hence, fulfil one aim of this study –to test whether the methodological approach that we applied here can provide insights into morphological patterns of groups within a medium-rank taxonomic level, the Cypridoidea–.

Differences in disparity between Cyprididae and Candonidae seem not to be related to taxonomic diversity –estimated as species richness– because the same number of taxonomic units (N=81) was used for both families. However, taxonomic structure differs dramatically between them. Candonidae (81 species in 14 genera and 2 subfamilies) has a much simpler structure than the Cyprididae (81 species in 23 genera and 10 subfamilies). Taxonomic structure in the candonids is not only simpler but also more balanced, as shown by the slightly lower variation in taxonomic distinctness in that family. If taxonomic structure is to be used as a proxy for the geometry of branching, then one should conclude that evolutionary processes in the Candonidae promoted the appearance of low rank taxonomic units (species) within a limited array of higher rank levels (genera and, mainly, subfamilies). But, what is the role of carapace morphology in this context? Well, we should not expect a perfect match between morphological disparity and taxonomic diversity. Disparity at lower taxonomic ranks (*e.g.* genera and subfamilies) is likely to reflect patterns of species richness more than branching patterns (Foote, 1992, 1996b). So differences between lineages (*e.g.* Candonidae and Cyprididae) might result from the existence of different morphological constraints in each clade; although there are alternative processes –*e.g.* adaptive radiation or selective extinction– which could explain those patterns too (Simpson, 1953; Foote, 1993). One of those processes is ecological specialization; *i.e.* adaptation to narrow ecological niches. Specialization requires the acquisition of non-standard morphologies better equipped for a more efficient exploitation of a given microhabitat. If extreme forms are ecologically more specialized (Foote, 1993) then candonids must have, on average, narrower niches than the cypridids. Although that hypothesis has to be tested rigorously there are some preliminary observations to support it. For instance, those elongated forms in the genus *Phreatocandona* and *Mixtacandona* which occupy peripheral location in the morphospace belong to highly specialized, troglobitic organisms.

Still another argument can be invoked as a likely explanation for diverging patterns in morphological disparity between Candonidae and Cyprididae: how taxonomy is done on both groups. Whenever clades to be compared do not result from using similar taxonomic criteria for the recognition of subfamilies, genera and species, and as far as taxonomic work is idiosyncratic then any kind of analysis of the processes behind the observed patterns will be severely hampered. (Non-marine) ostracodology has been, and continues to be, a meeting point for a large number of paleontologists and neontologists, scientists with different training and aims, doing their work in places all around the world and experiencing the influence of a variety of scientific traditions. Working with fossils constrains the sort of features (mainly morphological characters in the carapace) which can be used for taxonomic purposes. Neontologists do use limbs in addition but the type and amount of characters considered have changed significantly through time posing some uncertainty in the taxonomic status of many taxa which were described previously. For instance, features of the hemipenis were not used in the taxonomy of the Candoninae until introduced by T. Petkovski and D.L. Danielopol in the late ‘60s (Petkovski, 1969; Danielopol, 1969), and those characters remain unused (they are inapplicable) in fossil species. ‘Splitters’ and ‘lumpers’ also exist among ostracodologists and despite valuable attempts to review and update existing information for some restricted taxonomic groups (*e.g.* Martens, 1990; González-Mozo *et al.*, 1996; Martens *et al.*, 1997; Namiotko & Danielopol, this volume) or geographic areas (Meisch, 2000) a lot of work is still to be done.

In the confidence that rigorous scientific knowledge must rest on sound and reliable observations the aim of this paper is not to provide explanations but to detect patterns concerning shape variability in ostracod carapaces. For doing that, methods for the analysis of shape variability have been applied to a set of valve outlines of a series of species belonging to the Cypridoidea. Undoubtedly, the time dimension, which has not been included here, is badly needed for a more comprehensive understanding of the whole picture (notice, for instance, that although some of the ‘hypothetical’ shapes depicted in figure 1 do not correspond to any recent species they are indeed realised in the fossil record). Concluding, it is our contention that the careful study of such patterns should lead to the formulation of testable hypotheses about the evolutionary and ecological processes involved.

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APPENDIX
TAXONOMIC INFORMATION

SUPERFAMILY CYPRIDOIDEA BAIRD, 1845

Family Candonidae Kaufmann, 1900

Subfamily Candoninae Kaufmann, 1900

Paracandona euplectella (Robertson, 1889)[37].

Nannocandona faba Ekman, 1914[37].

Candona acricauda Mikulic, 1961[38]; *C. alta* Klie, 1939[31]; *C. candida* (O. F. Müller, 1776)[37]; *C. cavicola* Klie, 1935[28]; *C. chappuisi* Klie, 1943[34]; *C. dedelica* Petkovski, 1969[44]; *C. depressa* Klie, 1939[32]; *C. expansa* Mikulic, 1961[38]; *C. marginata* Klie, 1941[33]; *C. media* Klie, 1939[32]; *C. meerfeldiana* Scharf, 1983[37]; *C. muelleri* Hartwig, 1899[46]; *C. neglecta* Sars, 1887[37]; *C. strumicae* Petkovski, 1959[40]; *C. trapeziformis* Klie, 1939[32]; *C. vidua* Klie, 1941[33]; *C. weltneri* Hartwig, 1899[46]; *C. angulata* G. W. Müller, 1900[17].

Fabaeformiscandona alexandri (Sywula, 1981)[37]; *F. angusta* (Ostermeyer, 1937)[37]; *F. breuili* (Paris, 1920)[37]; *F. brevicornis* (Klie, 1925)[37]; *F. caudata* (Kaufmann, 1900)[2]; *F. fabaeformis* (Fischer, 1851)[2]; *F. fabella* (Nüchterlein, 1969)[37]; *F. hyalina* (Brady & Robertson, 1870)[37]; *F. lapponica* (Ekman, 1908)[37]; *F. latens* (Klie, 1940)[37]; *F. siliquosa* (Brady, 1910)[37]; *F. tricicatricosa* (Diebel & Pietrzeniuk, 1969)[37]; *F. tyrolensis* (Löffler, 1963)[37]; *F. wegelini* (Petkovski, 1962)[37].

Schellencandona belgica (Klie, 1937)[37]; *S. triquetra* (Klie, 1936)[37].

Pseudocandona albicans (Brady, 1864)[37]; *P. compressa* (Koch, 1838)[2]; *P. eremita* (Vejdovsky, 1882)[2]; *P. insculpta* (G. W. Müller, 1900)[2]; *P. marchica* (Hartwig, 1899)[2]; *P. pratensis* (Hartwig, 1901)[2]; *P. regisnikolai* Karanovic & Petkovski, 1999[27]; *P. semicognita* (Schäfer, 1934)[37]; *P. serbani* Danielopol, 1982[12]; *P. simililampadis* Danielopol, 1978[9]; *P. sucki* (Hartwig, 1901)[2]; *P. szoecsi* (Farkas, 1958)[37]; *P. zschokkei* (Wolf, 1920)[30].

Cryptocandona kieferi (Klie, 1938)[37]; *C. matris* (Sywula, 1976)[8]; *C. reducta* (Alm, 1914)[37]; *C. vavrai* Kaufmann, 1900[37].

Mixtacandona botosaneanui Danielopol, 1978[13]; *M. italica* Karanovic, 2000[26]; *M. sp. gr. ljovuschkini* Danielopol, 1979[11]; *M. sp. gr. riongessa2* Danielopol, 1979[11]; *M. juberthieae* Danielopol, 1978[10]; *M. lattingerae* Rogulj & Danielopol, 1993[14]; *M. spandli* Rogulj & Danielopol, 1993[37]; *M. tabacarui* Danielopol, 1979[11]; *M. elegans* Danielopol & Cvetkov, 1979[16].

Candonopsis kingsleii Brady & Robertson, 1870[37]; *C. scourfieldi* Brady, 1910[21].

Phreatocandona motasi (Danielopol, 1978)[13].

Trajancandona natura Karanovic, 1999[25]; *T. particula* Karanovic, 1999[25].

Subfamily Cyclocypridinae Kaufmann, 1900

Cypria cavernae Wagenleitner, 1990[53]; *C. exsculpta* (Fischer, 1855)[52]; *C. karamani* Petkovski, 1976[42]; *C. ophtalmica* (Jurine, 1820)[52]; *C. reptans* Bronshtein, 1928[37]; *C. sketi* Petkovski, 1976[42]; *C. subsalsa* Redeke, 1936[37]; *C. sywulae* (Sywula, 1981)[37].

Physocypria kraepelini G. W. Müller, 1903[37].

Cyclocypris globosa Sars, 1863[52]; *C. helocrenica* Fuhrmann & Piertzeniuk, 1990[37]; *C. laevis* (O. F. Müller, 1776)[37]; *C. ovum* (Jurine, 1820)[52]; *C. serena* (Koch, 1838)[37].

Family Ilyocyprididae Kaufmann, 1900

Subfamily Ilyocypridinae Kaufmann, 1900

Ilyocypris bradyi Sars, 1890[37]; *I. decipiens* Masi, 1905[37]; *I. getica* Masi, 1906[37]; *I. gibba* (Ramdohr, 1808)[37]; *I. inermis* Kaufmann, 1900[37]; *I. monstrifica* (Norman, 1862)[37].

Family Notodromadidae Kaufmann, 1900

Subfamily Notodromadinae Kaufmann, 1900

Notodromas monacha (O. F. Müller, 1776)[37]*; N. persica* Gurney, 1921[18].

Subfamily Cyproidinae Hartmann, 1963

Cyprois marginata (Straus, 1821)[51].

Family Cyprididae Baird, 1845

Subfamily *Cypridinae* Baird, 1845

Cypris bispinosa Lucas, 1849[37]; *C. pubera* (O. F. Müller, 1776)[51].

Subfamily Eucypridinae Bronshtein, 1947

Candelacypris aragonica (Brehm & Margalef, 1948)[6].

Eucypris accipitrina Anichini-Pini, 1968[5]; *E. anglica* Fox, 1967[37]; *E. bronsteini* Petkovski, 1959[40]; *E. caralitana* Tagliasacchi-Masata, 1969[2]; *E. crassa* (O. F. Müller, 1785)[4]; *E. elliptica* (Baird, 1846)[19]; *E. heinrichi* Petkovski and Keyser, 1995[44]; *E. hieracina* Anichini-Pini, 1968[5]; *E. mareotica* (Fischer, 1855)[19]; *E. kerkyrensis* Stephanides, 1937[37]; *E. lilljeborgi* (G. W. Müller, 1900)[48]; *E. longisetosa* Anichini-Pini, 1968[5]; *E. molybdaena* Anichini-Pini, 1968[5]; *E. moravica* Jancarik, 1947[37]; *E. pigra* (Fischer, 1851)[52]; *E. stagnalis* Tagliasacchi-Masata, 1969[50]; *E. stephanidesi* Petkovski, 1959[40]; *E. sulcitana* Anichini-Pini, 1968[5]; *E. tarentina* Anichini-Pini, 1963[3]; *E. trajani* Sywula, 1967[48]; *E. virens* (Jurine, 1820)[52].

Koencypris ornata (O. F. Müller, 1776)[37].

Prionocypris zenkeri (Chyzer & Toth, 1858)[52].

Tonnacypris estonicus (Järvekülg, 1960)[23]; *T. lutaria* (Koch, 1838)[52].

Trajancypris clavata (Baird, 1838)[36]; *T. laevis* G. W. Müller, 1900[36]; *T. serrata* G. W. Müller, 1900[36].

Subfamily Cypricercinae McKenzie, 1971

Bradleycypris obliqua (Brady, 1868)[52].

Bradleystrandesia fuscata (Jurine, 1820)[37]; *B. hirsuta* (Fischer, 1851)[47]; *B. reticulata* (Zaddach, 1844)[52].

Subfamily Herpetocypridinae Kaufmann, 1900

Herpetocypris brevicaudata Kaufmann, 1900[20]; *H. chevreuxi* (Sars, 1896)[51]; *H. helenae* G. W. Müller, 1908[20]; *H. intermedia* Kaufmann, 1900[20]; *H. reptans* (Baird, 1835)[20].

Psychrodromus betharrami Danielopol & Baltanás 1993[7]; *P. peristericus* (Petkovski, 1959)[39]; *P. robertsoni* (Brady & Norman, 1889)[15]; *P. fontinalis* (Wolf, 1920)[37]; *P. olivaceus* (Brady & Norman, 1889)[15].

Stenocypria fischeri Lilljeborg, 1883[37].

Subfamily Cyprinotinae Bronshtein, 1947

Heterocypris barbara (Gauthier & Brehm, 1928)[19]; *H. bosniaca* Petkovski *et al.*, 2000[45]; *H. bulgarica* Sywula, 1967[48], *H. gevgelica* Petkovski, *et al.*, 2000[45]; *H. incongruens* (Ramdohr, 1808)[37]; *H. reptans* (Kaufmann, 1900)[37]; *H. rotundata* (Bronshtein, 1928)[37]; *H. vitrea* Sywula, 1967[45].

Subfamily Dolerocypridinae Kaufmann, 1900

Dolerocypris fasciata O. F. Müller, 1776[43]; *D. sinensis* Sars, 1903[37].

Subfamily Isocypridinae Rome, 1965

Isocypris beauchampi (Paris, 1920)[37].

Subfamily Scottinae Bronshtein, 1947

Scottia pseudobrowniana Kempf, 1971[37].

Subfamily Hungarocypridinae Bronshtein, 1947

Hungarocypris madaraszi Örley, 1886[37].

Subfamily Cypridopsinae Kaufmann, 1900

Cavernocypris subterranea Wolf, 1920[37].

Cypridopsis elongata (Kaufmann, 1900)[1]; *C. hartwigi* G. W. Müller, 1900[22]; *C. lusatica* Schäfer, 1943[37]; *C. pilosa* Anichini-Pini, 1967[4]; *C. sanctipetri* Anichini-Pini, 1968[5]; *C. vidua* (O. F. Müller, 1776)[37].

Plesiocypridopsis thermarum (Tagliasacchi-Masala, 1967)[49]; *P. newtoni* (Brady & Robertson, 1870)[37].

Potamocypris arcuata (Sars, 1903)[37]; *P. fallax* Fox, 1967[37]; *P. fulva* (Brady, 1868)[37]; *P. pallida* Alm, 1914[37]; *P. similis* G. W. Müller, 1912[37]; *P. steueri* Klie, 1935[29]; *P. tetrataeniata* Anichini-Pini, 1967[4]; *P. variegata* (Brady & Norman, 1889)[37]; *P. zschokkei* (Kaufmann, 1900)[22].

Pseudocypridopsis clathrata (Klie, 1936)[24].

Sarscypridopsis lanzarotensis (Mallwitz, 1984)[35]; *S. aculeata* (Costa, 1847)[37].

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CHECKLIST OF RECENT AND QUATERNARY OSTRACODS (CRUSTACEA) FROM FRESHWATER, BRACKISH AND MARINE ENVIRONMENTS IN MECKLENBURG-VORPOMMERN, NE GERMANY

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Abstract

We give an extensive list of Recent, Holocene and Pleistocene ostracods from Mecklenburg-Vorpommern based on a review of publications, unpublished reports and diploma theses as well as some new studies. The list contains additional data on the stratigraphic distribution and occurrence of the reported taxa within different types of waters from the study area. A total of 138 Quaternary ostracod species are known so far from Mecklenburg-Vorpommern, of which 115 live today in the study area. Twenty three of the 67 documented fossil and subfossil species are extinct here today. The Recent fauna contains 28 marine, 13 brackish and 74 freshwater species. A bibliography on Quaternary ostracods from Mecklenburg-Vorpommern is given as a reference for work on biogeography, ecology, stratigraphy and taxonomy of ostracodes from the Baltic Sea region.

Key words: Ostracoda, biogeography, stratigraphy, ecology, Holocene, Pleistocene, Baltic Sea.

Resumen

Se proporciona en este trabajo una lista extensiva de los ostrácodos del Reciente, Holoceno y Pleistoceno de Mecklenburg-Vorpommern (Alemania), basada en la revisión de las publicaciones, informes no publicados y tesis de diplomatura, así como algunos estudios nuevos. La lista contiene datos adicionales de la distribución estratigráfica y presencia de los taxones referidos en diferentes tipos de aguas del área de estudio. Un total de 138 especies de ostrácodos del Cuaternario son conocidos hasta ahora en Mecklenburg-Vorpommern, de las cuales 115 viven todavía en el área de estudio. Veintitrés de las 67 especies fósiles y subfósiles documentadas no aparecen actualmente en este área. La fauna del Reciente contiene 28 especies marinas, 13 de aguas salobres y 74 de aguas dulces. Se proporciona una bibliografía de los ostrácodos del Cuaternario de Mecklenburg-Vorpommern, como referencia para futuros trabajos acerca de la biogeografía, ecología, estratigrafía y taxonomía de los ostrácodos en la región del Mar Báltico.

Palabras clave: Ostracoda, biogeografía, estratigrafía, ecología, Holoceno, Pleistoceno, Mar Báltico.

INTRODUCTION

The exploration of the Recent ostracod fauna in Mecklenburg-Vorpommern has a long tradition and the beginning is closely related to some famous personalities of ostracodology as Gustav Wilhelm Müller and Walter Klie. The material of G. W. Müller's (1900) monograph „Süßwasser-Ostracoden Deutschlands“ is still stored at the Zoological Institute and Museum of the University of Greifswald, Germany. Today almost forgotten are the first mention of ostracods from our study area by Ehrenberg in 1842 and a first list of species from the Baltic Sea by G. W. Müller in 1884. The standard work written by Klie (1938) summarised the knowledge about the freshwater, brackish and marine species of Germany, supplying data on the distribution of ostracods in Mecklenburg-Vorpommern. Since this work, the information about Quaternary ostracods from our region has been scattered over a wide range of regional biological and geological journals. In the past decade an increasing amount of data about the distribution of ostracod species was gathered in the Pomeranian Bight, the shallow lagoons, the surroundings of Greifswald and from other distinct freshwater sites in Vorpommern (Western Pomerania). Also our knowledge about Holocene and Pleistocene ostracods increased remarkably. So, the present information about the distribution of Quaternary ostracods is relatively rich in comparison with adjacent regions. Our checklist gives an overview of the distribution of Recent ostracods in Mecklenburg-Vorpommern for the first time since Klie (1938) and for the first time a list of the Quaternary ostracods from our country. This is a contribution to the biogeography, stratigraphy and ecology of Quaternary ostracods in Northern Europe and the Baltic Sea region.

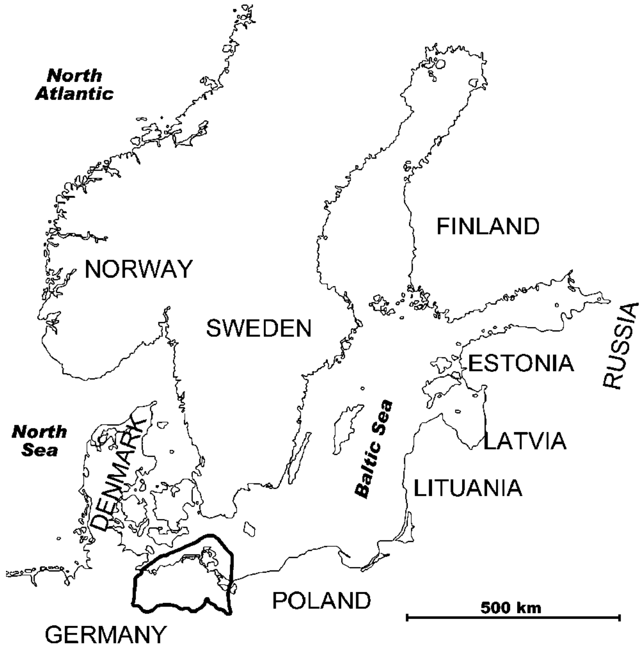

FIGURE 1–Mecklenburg-Vorpommern: the study area (outlined in black) within the southern Baltic Sea.

STUDY AREA

The Mecklenburg-Vorpommern state lies in the northeast of Germany at the southern coast of the Baltic Sea (Fig. 1) (and comprises Mecklenburg and the western part of Pomerania). Its climate is determined by the transition from the North Atlantic Sea climate of the temperate zone to a more continental climate. The Baltic Sea itself influences the climate of the mainland in an about 10-30 km wide strip along the coast (Duphorn *et al.* 1995). The land territory comprises 23170 km^2 and is covered almost exclusively by Weichselian tills and Holocene sediments. A large number of lakes, some with considerable depth, lie among the end moraines of the last glaciation. High carbonate concentrations in springs and surface waters are not rare because of the high $CaCO_3$ content of the moraines especially in the northeastern part of the country. Despite the relatively low density of human population (79 inhabitants per km^2), the streams, rivers and lakes show a high level of productivity caused by an intensive agriculture - oligotrophic waters are lacking. The largest rivers are the Elbe, touching the study area only for a short distance in the southwest, and the Oder in the east with discharge through the Oder estuary into the Pomeranian Bight. Most of the country belongs to the drainage area of the Baltic Sea. The coastline is extraordinarily long, 1712 km, but only 354 km of this belong to the outer coast, the higher proportion is built up by the shoreline of the inner coastal waters, as lagoons (Bodden), estuaries (partly called Haff) and straits between these (called Sund or Strom). The offshore area is part of the Mecklenburg Bay (Belt Sea) with a maximum depth of about 25 m and the Arkona Sea with down to 53 m depth in the study area. The salinity reaches highest values with up to about 18 psu in the deeper water of the basins below the intermediate water layer. The salinity of the surface water decreases from west to east from about 14 psu in the Mecklenburg Bay to about 7 psu in the Pomeranian Bay (Weber, 1998). The sediment is normally sand near to the coast and mud in basins of the innercoastal waters and the open sea. All coastal lagoons and the deeper basins of the open sea are strongly influenced by eutrophication.

During the Pleistocene Mecklenburg-Vorpommern was mostly covered by Scandinavian glaciers. Older Pleistocene sediments were eroded by Weichselian glaciers in large parts of the country. Elsterian sediments are known from the southwest of Mecklenburg. Also the Holsteinian complex is limited to the south and west of the study area (Rühberg *et al.*, 1995) but shows a marine transgression covering most of the country. In contrast the marine transgression of the Eemian formed only bights along the present day coastline around Herrnburg, Wismar, Rostock and the Isle of Usedom (Rühberg *et al.*, 1995). The Holocene evolution of our coast is influenced by changes in climate and sea level. Strong salinity variations in the water body of the Baltic Sea basin give important information usable for stratigraphic purposes in the Holocene of the southern Baltic Sea area. The rising sea level reached the present day coastline during the 2nd *Littorina* transgression about 5500 years B. P. This is also the initiation of the coastal lagoons development in Mecklenburg-Vorpommern.

MATERIAL AND METHODS

The present list (Table 1) is based on the evaluation of all known references from publications as well as unpublished notes, research theses and the authors' observations on Recent and Quaternary ostracods in Mecklenburg-Vorpommern, which are given in an annex. The entries were terminated in June 2003. We used our own results of systematical as well as occasional observations from Recent freshwater and brackish water localities of Vorpommern, vibrocores from the open Baltic Sea and the micropalaeontological collections of the Geological Service of Mecklenburg-Vorpommern.

The majority of unpublished theses were supervised by the Institute of Geology and the Institute of Zoology at the Universities of Greifswald and Rostock. All geological theses are now archived and accessible in Greifswald due to the closing of the University Institute of Geology in Rostock in the 1960s.

The mentioned specific palaeoenvironments were classified by means of the description by the cited author or by the known palaeogeographical situation respectively.

RESULTS AND DISCUSSION

137 ostracod species belonging to 61 genera are known from the Quaternary in Mecklenburg-Vorpommern. Twenty two species are recorded as fossil only and 71 extant species have no fossil record in the area. A total of 101 papers (70 publications and 31 unpublished papers) mention ostracods from Mecklenburg-Vorpommern (58 on Recent and 44 on fossil ostracods), 40 focus on ostracods.

The following list gives an overview on localities with ostracod occurences. The stratigraphical subdivision of the Holocene is based on the stages of the Baltic Sea evolution. Question marks indicate localities of uncertain stratigraphical position. The taxonomy follows Meisch (2000) and Athersuch *et al.* (1989). The order of taxa in Table 1 is alphabetical.

LOCALITIES IN STRATIGRAPHICAL ORDER

1. *Mya* stage (Recent, Fig. 2):

a: Open Baltic Sea: Baltic Sea in general (Gosselck *et al.*, 1996); Baltic Sea north off Kühlungsborn and north off Warnemünde (this paper); Mecklenburg Bight, Arkona Basin, Adlergrund (Klie, 1929, 1938; Rosenfeld, 1977; B. Müller, 1979; Arlt *et al.*, 1982); western Arkona Sea (Rosenfeld, 1977; Reich & Frenzel, 1996); Oderbank (Klie, 1938); Pomeranian Bight (Arlt, 1970; Arlt *et al.*, 1982; Stuck, 1995; Frenzel, 1996; Roßdeutscher, 1996; Trapp, 1998).

b: Lagoons and bights: in general (Arlt, 2000); Wismar Bight (Klie, 1938; Arlt, 1970; Jahn, 1996; Jahn *et al.*, 1996; Schubert, 2001); Boiensdorfer Werder at Salzhaff (Siccha, 2003); Kirr Bight and Rassower Strom (Arlt & Georgi, 1999); Darß-Zingst Bodden chain in general (Lange *et al.*, 1971); Saaler Bodden (Klie, 1938; Beschnidt *et al.*, 1970; Lange *et al.*, 1971; Beschnidt & Noack, 1976; Arlt, 1984; Köhler, 1990; Frenzel, 1990, 1991; Arndt, 2001; Henkel & Tschendel, 2003); Bodstedter Bodden (Beschnidt *et al.*, 1970; Arlt, 1984; Köhler, 1990; Frenzel, 1990, 1991); Barther Bodden (Beschnidt *et al.*, 1970; Groth & Zander, 1973, Holtfreter, 1973; Möller, 1974; Arlt & Holtfreter, 1975; Arlt, 1984; Grote, 1985; Köhler, 1990; Frenzel, 1990, 1991); Grabow (Beschnidt *et al.*, 1970; Lange *et al.*, 1971; Köhler, 1981, 1990; Arlt, 1984; Köhler & Arlt, 1984; Frenzel, 1990, 1991); lagoons in the north and west off the Isle of Rügen (Seifert, 1933; Schäfer, 1953; Arlt, 1970; Frenzel, 1990, 1991; Vopel & Arlt, 1995; Vopel, 1997); Großer Jasmunder Bodden (Trahms, 1939; Schäfer, 1953; Arlt, 1970; Frenzel, 1990, 1991); Strelasund (Frenzel, 1996, Frenzel & Oertel, 2002); Greifswalder Bodden (G. W. Müller, 1884, 1900; Hirschmann, 1912, 1916; Stammer, 1928; Klie, 1929, 1938; Seifert, 1938; Schäfer, 1953; Arlt, 1970, 1973, 1977; Frenzel, 1990, 1991, 1996); Ryck estuary in Greifswald (Stammer, 1928; this paper); Selliner See (Arlt, 1970); Achterwasser, Peenestrom (Arlt, 1970; Frenzel, 1990, 1991; Janz, 1994; this paper); Oderhaff (Arlt, 1970; Frenzel, 1990, 1991; Scharf *et al.*, in preparation; this paper).

taxa	Recent	Subatlantic	Atlantic and Subboreal	Boreal and late Preboreal	Early Preboreal	Late Glacial (Weichselian)	Weichselian (stadial)	Eemian	Early Saalian	Holsteininan	Late Elsterian	Lakes	Running water	Small periodic waters	Springs and ground water	Brackish water lagoons	Baltic Sea Proper	Marine	Continental salt water sites	references
Acanthocythereis dunelmensis (Norman, 1865)	X									X	X						X	X		29; 125; 156
Acanthocythereis horrida (Sars, 1866)										?								X		156
Bradleystrandesia fuscata (Jurine, 1820)	X											X			X					85; 141
Bradleystrandesia reticulata (Zaddach, 1844)	X											X								85; 118; 119
Candona angulata G. W. Müller, 1900	X											X	X			X				5; 25; 26; 45; 85; 96; 101; 103; 112
Candona candida (O. F. Müller, 1776)	X			X	X	X	X	X	X			X	X	X	X	X				2, 4; 9; 18a; 31; 45; 48; 49; 50; 55; 60; 69; 72; 85; 87; 90; 99; 106; 107; 111; 113; 114; 118; 119; 130; 131
Candona improvisa Ostermeyer, 1937	X															X				45
Candona lindneri Petkovski, 1969	X															X				66
Candona muelleri Hartwig, 1899	X													X						85
Candona neglecta Sars, 1887	X		X	X	X	X	X		X	X		X	X			X	X		X	2; 4; 13; 14; 15; 25; 26; 28; 32; 45; 46; 48; 50; 55; 64; 66; 70; 85; 90; 91; 97; 99; 103; 104; 106; 107; 108; 113; 131; 130; R
Candona weltneri (Hartwig, 1898)	X											X								50; 64; 85
Candona weltneri (Hartwig, 1898) var. *obtusa*								X	X			X								107
Candonopsis kingsleii (Brady & Robertson, 1870)	X											X								49; 85; 118; 119
Cryptocandona vavrai Kaufmann, 1900	X											X			X					49; 60; 64; 111
Cyclocypris globosa (Sars, 1863)	X	?										X	X						X	5; 85; 118; 119; 143
Cyclocypris laevis (O. F. Müller, 1776)	X							X				X	X		X					60; 85; 107; 111; 118; 119
Cyclocypris ovum (Jurine, 1820)	X	?		X	X	?	X	X	X			X	X		X	X			X	5; 13; 14; 18a; 39; 49; 50; 57; 60; 63; 85; 87; 88; 90; 99; 107; 111; 113; 118; 119; 131; 132; 133; 139; 143

TABLE 1–Stratigraphical occurence of Recent and subfossil/fossil ostracod taxa from the Quaternary of Mecklenburg-Vorpommern and their distribution in different types of waters. The number in the reference column indicates the number given in our literature list. R) indicates unpublished results by Rusbühlt on (sub)fossil associations, A) those of Ansorge.

taxa	Recent	Subatlantic	Atlantic and Subboreal	Boreal and late Preboreal	Early Preboreal	Late Glacial (Weichselian)	Weichselian (stadial)	Eemian	Early Saalian	Holsteininan	Late Elsterian	Lakes	Running water	Small periodic waters	Springs and ground water	Brackish water lagoons	Baltic Sea Proper	Marine	Continental salt water sites	references
Cyclocypris serena (Koch, 1837)				X	X	X	X	X	X			X								69; 90; 99; 106; 107; 133
Cypria exsculpta (Fischer, 1855)	X											X								85
Cypria ophtalmica (Jurine, 1820)	X				X	X	X					X	X	X	X	X				5; 8; 13; 14; 25; 26; 28; 49, 50; 51; 60; 65; 66; 67; 69; 70; 85; 97; 99; 101; 103; 106; 111; 118; 119; 129; 131; 132; 133; 134; 139
Cypria subsalsa Redeke, 1936	X															X				25; 26; 32; 45; 66; 120; 121
Cyprideis torosa (Jones, 1850)	X		X				X	X		X			X			X		X		8; 15; 23; 29; 32; 35; 36; 41; 46; 52; 53; 64, 66; 67; 79; 80; 85; 97; 98; 102; 114; 118; 119; 120; 121; 153; 154; 155; R
Cyprideis torosa (Jones, 1850) f. *litoralis*	X	?	X				X	X	X	X		X	X			X			X	2, 4, 5; 13; 14; 25; 26; 28; 31; 32; 39; 42; 45; 46; 51; 65; 66; 70; 94; 96; 101; 107; 130; 131; 138; 143; 150
Cyprideis torosa (Jones, 1850) f. *torosa*	X	?	X				X	X	X	X		X	X			X	X		X	13; 14; 25; 26; 28; 39; 45; 46; 51; 66; 70; 96; 103; 107; 108; 130; 131; 138; 143; 151
Cypridopsis vidua (Sars, 1864)	X			X	X	X		X				X	X			X				15; 25; 26; 49; 50; 69; 85; 87; 90; 99; 103; 105; 114; 113; 118; 119; 131; 134a
Cypris pubera O. F. Müller, 1776	X			X		X	X					X		X						56; 85; 87; 90; 105, 106; 113; 118; 119, 134
Cyprois marginata (Straus, 1821)	X											X								85; 132; 134a
Cythere lutea O. F. Müller, 1785	X															X				64
Cytherissa lacustris (Sars, 1863)	X			X	X	X	X	X		X		X				?				12; 15; 23; 31; 39; 55; 56; 59; 64; 72; 73; 79; 88; 90; 97; 104; 106; 113; 155
Cytherois arenicola Klie, 1929	X															X	X			2, 3, 4, 5; 28; 38; 62; 64; 65; 66; 67; 96; 101
Cytherois fischeri (Sars, 1865)	X															X	X			89; 96

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Cytheromorpha fuscata (Brady, 1869)	X	X		?								?				X	X			2, 4, 5; 8; 12; 13; 14; 25; 26; 28; 32; 45; 46; 51; 65; 66; 67; 70; 88; 96; 97; 101; 113; 130; 131
Cytheropteron cf. *inornatum* Brady & Robertson, 1872							X			X								X		27; R
Cytheropteron latissimum (Norman, 1865)	X	X															X			88; 89
Cytheropteron montrosiense (Brady, Crosskey & Robertson, 1874)							X			X	X							X		27; 106; R
Cytheropteron pseudomontrosiense Whatley & Masson, 1979							X											X		27, 30; 75; 106
Cytheropteron testudo Sars, 1870							X			?								X		27; R
Cytherura atra Sars, 1865	X																X			89
Cytherura fulva Brady & Robertson, 1874	X																X			89
Cytherura gibba (O. F. Müller, 1785)	X	X	?													X	X			2, 4, 5; 8; 21; 28; 32; 36?; 45; 46; 51; 62; 64; 65; 66; 67; 84; 85; 96; 97; 101; 102; 112; 113; 120; 121; 129
Darwinula stevensoni (Brady & Robertson, 1870)	X	?		X	X	X		X				X	X			X				13; 14; 15; 25; 26; 28; 45; 48; 49; 56; 64; 66; 70; 85; 88; 90; 97; 107; 108; 118; 119; 131; 134a; 142
Dolerocypris fasciata (O. F. Müller, 1776)	X											X								50; 85
Elofsonella concinna (Jones, 1857)							X	X		X	X							X		27; 29; 106; 156; 157
Elofsonia baltica (Hirschmann, 1909)	X															X				2, 4, 5; 65; 66; 67; 96; 112
Elofsonia pusilla (Brady & Robertson, 1870)	X															X				2; 66; 96; 101
Eucypris crassa (O. F. Müller, 1785)	X													X						85
Eucypris elliptica (Baird, 1846)	X											X		X	X					49; 60; 85, 111
Eucypris lilljeborgi (G. W. Müller, 1900)	X													X						85
Eucypris pigra (Fischer, 1851)	X											X			X					18a; 49; 60; 85; 111
Eucypris virens (Jurine, 1820)	X													X						85
Eucythere argus (Sars, 1865)	X	X	X														X	X		88; 89; 90;108; 113
Fabaeformiscandona acuminata (Fischer, 1851)	X											X								50; 85; 136; 140

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Fabaeformiscandona alexandri (Sywula, 1981)					?															33
Fabaeformiscandona balatonica (Daday, 1894)	X											X								85
Fabaeformiscandona brevicornis (Klie, 1925)	X											X			X					18a; 49; 61; 64; 111
Fabaeformiscandona fabaeformis (Fischer, 1851)	X											X				X				45; 85; 97; 118; 119
Fabaeformiscandona fragilis (Hartwig, 1898)	X											X			X					85; 111; 118; 119
Fabaeformiscandona holzkampfi (Hartwig, 1898)	X	?										X								85; 118; 119; 142
Fabaeformiscandona hyalina (Brady & Robertson, 1870)	X											X								85
Fabaeformiscandona levanderi (Hirschmann, 1912)	X	?		X						X		X	X			X				18; 25; 26; 39; 64; 88; 97; 108; 113; 130; 142
Fabaeformiscandona protzi (Hartwig, 1898)	X			X	X		X	?	?			X	X			X				25; 26; 85; 88; 97; 99; 106; 107; 113; 114; 118; 119; 130; 131
Fabaeformiscandona tricicatricosa (Diebel & Pietrzeniuk, 1969)						?			X			X								69; 107
Herpetocypris chevreuxi (Sars, 1896)	X											X				X				50; 96; 118; 119
Herpetocypris intermedia Kaufmann, 1900	X											X								118; 119
Herpetocypris reptans (Baird, 1835)	X			?	X	X		X	X			X								50; 85; 87; 99; 105; 107; 113; 118; 119
Heterocyprideis sorbyana (Jones, 1856)	X	X															X			88; 89; 127
Heterocypris incongruens (Ramdohr, 1808)	X											X		X						49; 64; 85; 118; 119; 135; 137
Heterocypris salina (Brady, 1868)	X						X					X		X		X			X	85; 91; 96; 106; 118; 119
Hirschmannia viridis (O. F. Müller, 1785)	X									X						X	X			5; 32; 28; 46; 64; 65; 67; 89; 102; 103; R
Ilyocypris bradyi Sars, 1890	X			X	X	X	X					X			X					15; 18a; 55; 72; 85; 88; 106; 113
Ilyocypris decipiens (Masi, 1905)	X	?		X					X			X	X			X			X	13(?); 18; 25; 26; 54; 64; 66; 85; 90; 97; 107; 108; 113; 118; 130; 131; 138; 143
Ilyocypris gibba Ramdohr, 1808	X				X	X	X			X		X		X		?				13?; 14; 15; 49; 72; 79; 87; 97; 105; 134; R
Ilyocypris inermis Kaufmann, 1900	X														X					18a

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Jonesia acuminata (Sars, 1866)	X																X			62; 64; 89
Koencypris ornata (O. F. Müller, 1776)	X											X		X						85
Leptocythere baltica Klie, 1929	X															X	X			2, 4; 28; 89; 96
Leptocythere castanea (Sars, 1865)	X		X					X								X	X			46; 70; 84; 96; 101; 108
Leptocythere lacertosa (Hirschmann, 1912)	X		X	?												X	X			2, 4, 5; 12; 28; 32; 46; 65; 66; 67; 89; 96; 101; 102; 108
Leptocythere pellucida (Baird, 1850)	X		X							?						X	X			62; 64; 89; 96; 108; R
Leptocythere porcellanea (Brady, 1869)	X															X				28; 32; 46; 96; 101
Leptocythere psammophila Guillaume, 1976	X	X	X					X								X	X			28; 32; 108; 113; 152
Leptocythere tenera (Brady, 1868)	X																X			89
Leucocythere baltica (Diebel, 1965a)				?	X	X	X	X		X		X								15, 16; 31; 39; 64; 75; 79; 88; 92; 104; 106; 114; A; R
Limnocythere blankenbergensis Diebel, 1968						X	X					?								17; 72
Limnocythere falcata Diebel, 1968				?								?								17; 88; 146
Limnocythere inopinata (Baird, 1843)	X			X	X	X			X			X	X			X				2; 13; 14; 15; 25; 26; 45; 48; 49; 50; 55; 64; 66; 70; 79; 85; 87; 88; 90; 96; 97; 101; 106; 107; 113; 118; 130; 131; 134a
Limnocythere stationis Vavra, 1891					X							X								15
Limnocytherina sanctipatricii (Brady & Robertson, 1869)				X	X	X	X	X				X								15; 25; 26; 48; 55; 104; 105; 106; 107; 108; 113
Loxoconcha elliptica Brady, 1868	X		X					X								X	X			2, 4, 5; 8; 28; 42; 51; 64; 65; 66; 67; 90; 96; 101; 102; 120; 121; 152
Loxoconcha rhomboidea (Fischer, 1855)	X															X				2, 4; 62; 84; 85; 101
Metacypris cordata (Brady & Robertson, 1870)	X	?		X				X				X								48; 49; 50; 63; 64; 90; 107; 114; 142
Neocytherideis crenulata (Klie, 1929)	X																X	X		62; 64; 89
Notodromas monacha (O. F. Müller, 1776)	X											X								50; 85; 118; 128; 134a

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Palmenella limicola (Norman, 1865)	X																X			89
Palmoconcha guttata (Norman, 1865)							X											X		27; 147
Palmoconcha laevata (Norman, 1865)	X	X															X			32; 62; 64; 89; 108
Paracandona euplectella (Robertson, 1889)	X											X								85
Paracyprideis fennica (Hirschmann, 1909)	X		X														X	X		62; 64; 88; 89
Paradoxostoma abbreviatum Sars, 1866	X															X				64
Paradoxostoma variabile (Baird, 1835)	X																X			64; 89
Paralimnocythere psammophila (Flössner, 1965)	X											X								24
Paralimnocythere relicta (Lilljeborg, 1863)	X											X								85
Physocypria kraepelini G. W. Müller, 1903	X												X			X				25; 26; 97; 118; 131
Plesiocypridopsis newtoni (Brady & Robertson, 1870)	X											X	X							49; 50; 85; 103
Pontocythere elongata (Brady, 1868)								X								X				31; 39
Potamocypris fulva (Brady, 1868)	X											X		X	X					49; 60; 64; 85; 111
Potamocypris unicaudata Schäfer, 1943	X											X								49; 50
Potamocypris variegata (Brady & Norman, 1889)	X											X								50; 64
Potamocypris zschokkei Kaufmann, 1900	X											X		X	X					18a; 49; 60; 61; 64; 111
Pseudocandona albicans (Brady, 1864)	X											X			X					18a; 49; 60; 64; 85; 111; 118
Pseudocandona compressa (Koch, 1838)	X					X	X	X				X			X	X				50; 60; 66; 69; 85; 101; 106; 107; 118; 129
Pseudocandona eremita (Vejdovsky, 1880)							X					X								106
Pseudocandona hartwigi (G. W. Müller, 1900)	X											X								49
Pseudocandona insculpta (G. W. Müller, 1900)	X											X				X				85; 118
Pseudocandona lobipes (Hartwig, 1900)	X											X	X							49; 85; 103
Pseudocandona marchica (Hartwig, 1899)	X											X	X			X				45; 85; 118
Pseudocandona pratensis (Hartwig, 1901)	X											X	X		X	?				49; 60; 85; 111; 103

TABLE 1–Stratigraphical occurence of Recent and subfossil/fossil ostracod taxa from the Quaternary of Mecklenburg-Vorpommern and their distribution in different types of waters. The number in the reference column indicates the number given in our literature list. R) indicates unpublished results by Rusbühlt on (sub)fossil associations, A) those of Ansorge. *(Continuation)*

taxa	Recent	Subatlantic	Atlantic and Subboreal	Boreal and late Preboreal	Early Preboreal	Late Glacial (Weichselian)	Weichselian (stadial)	Eemian	Early Saalian	Holsteininan	Late Elsterian	Lakes	Running water	Small periodic waters	Springs and ground water	Brackish water lagoons	Baltic Sea Proper	Marine	Continental salt water sites	references
Pseudocandona rostrata (Brady & Norman, 1889)	X											X			X					60, 85; 101; 111
Pseudocandona sarsi (Hartwig, 1899)	X											X			X					1; 64; 85
Pseudocandona stagnalis (Sars, 1890)	X											X								85
Psychrodromus olivaceus (Brady & Norman, 1889)	X						X					X			X					18a; 49; 60; 106; 111
Pterygocythereis jonesii (Baird, 1850)							X											X		27
Robertsonites tuberculatus (Sars, 1865)	X	X	X				X										X	X		27; 29; 64; 88; 89; 106; 123; 124; 125; 126; 146; 147
Roundstonia globulifera (Brady, 1868)							X											X		27; 29; 30; 149
Sarscypridopsis aculeata (Costa, 1847)	X											X	X	X		X	X			5; 13; 14; 70; 85; 96; 103; 66; 118
Sarsicytheridea bradii (Norman, 1865)	X		X				X										X	X		27; 62; 64; 88; 89; 106; 123; 125; 126; 147
Sarsicytheridea punctillata (Brady, 1865)	X	X	X				X			X						X	X	X		5; 27; 29; 64; 80; 88; 89; 106; 108; 148
Scottia browniana (Jones, 1856)								X		X				X						31; 39
Scottia huckei (Triebel, 1941)										X		?								23; R
Scottia pseudobrowniana Kempf, 1971	X											X			X					18a; 49; 58; 60; 61; 64; 111
Scottia tumida (Jones, 1850)										X		?				?				58; R
Semicytherura cf. *concentrica* (Brady, Crosskey & Robertson, 1874							X											X		27
Semicytherura nigrescens (Baird, 1838)	X		X							X						X	X			25; 26; 28; 32; 46; 62; 64; 89; 90; 96; 108; 120; 121; R
Semicytherura sella (Sars, 1865)	X							X									X			89; 152
Stenocypria fischeri (Lilljeborg, 1883)	X											X								85
Tonnacypris lutaria (Koch, 1838)	X													X						85
Trajancypris clavata (Baird, 1838)	X											X		X						85
Trajancypris laevis (G. W. Müller, 1900)	X											X								85
Trajancypris serrata (G. W. Müller, 1900)	X																			85

Table 1–Stratigraphical occurence of Recent and subfossil/fossil ostracod taxa from the Quaternary of Mecklenburg-Vorpommern and their distribution in different types of waters. The number in the reference column indicates the number given in our literature list. R) indicates unpublished results by Rusbühlt on (sub)fossil associations, A) those of Ansorge. *(Continuation)*

taxa	Recent	Subatlantic	Atlantic and Subboreal	Boreal and late Preboreal	Early Preboreal	Late Glacial (Weichselian)	Weichselian (stadial)	Eemian	Early Saalian	Holsteininan	Late Elsterian	Lakes	Running water	Small periodic waters	Springs and ground water	Brackish water lagoons	Baltic Sea Proper	Marine	Continental salt water sites	references
Xestoleberis aurantia (Baird, 1838)	X															X	X			2, 4, 5; 8; 13; 14; 28; 32; 42; 46; 51; 62; 64; 84?; 89; 96; 101; 103; 112; 120; 121
Xestoleberis nitida (Liljeborg, 1853)	X							X								X		X		65; 66; 67; 102; 152

TABLE 1–Stratigraphical occurence of Recent and subfossil/fossil ostracod taxa from the Quaternary of Mecklenburg-Vorpommern and their distribution in different types of waters. The number in the reference column indicates the number given in our literature list. R) indicates unpublished results by Rusbühlt on (sub)fossil associations, A) those of Ansorge. *(Continuation)*

c: Freshwater: Schwichtenberg near Friedland, Hermsdorf in Mecklenburg and Schaalsee near Ratzeburg (Klie, 1938); Neu Gaarz in Mecklenburg (this paper); Müritz (Hollwedel & Scharf, 1996); Pisede near Malchin (Diebel & Pietrzeniuk, 1975b); Tiefwarensee at Waren and Kummerower See near Malchin (Diebel & Pietrzeniuk, 1975a); Barthe at Divitz (this paper); Hiddensee (Schäfer, 1953; Hollwedel & Scharf, 1994); Rügen (Klie, 1925, 1927, 1937, 1938; Thienemann, 1926; Kempf, 1971; Diebel & Pietrzeniuk, 1984; Hollwedel & Scharf, 1994; this paper); Greifswald and surroundings (G. W. Müller, 1900; Klie, 1938; Janz, 1994; Viehberg, 2000, 2001; this paper); Petschsee, Großer Glietzensee and Thurower See in south eastern Mecklenburg (Flössner, 1965); Lendershagen, Letzin, Vietlipp, Löcknitz, Rotes Moor near Anklam and Peene swamps near Gützkow (this paper); Haussee near Feldberg (Klie, 1938).

d: Saline water: Salines of Greifswald (G. W. Müller, 1900; Rudat, 1993; Viehberg, 2000, 2001).

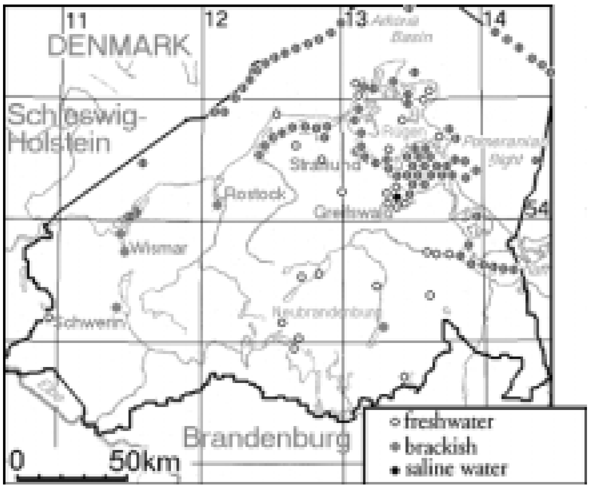

FIGURE 2–Documented occurence of Recent ostracods in Mecklenburg-Vorpommern.

2. Post *Littorina* stage (Subatlantic, Fig. 3):

a: Marine/brackish: Teterower See? (this paper); Vibrocores from the Arkonasea (Reich & Frenzel, 1996); vibrocores from the Pomeranian Bight and submarine Oder channel (Stuck, 1995; Roßdeutscher, 1996; Trapp, 1998).

b: Freshwater: Glambecker See? near Schwerin (this paper).

3. *Littorina* Sea (Atlantic and Subboreal, Fig. 3):

a: Marine: Rostock-Warnemünde (Geinitz, 1902); vibrocores from the Arkona Sea (Reich & Frenzel, 1996); vibrocores from the Greifswalder Bodden (Verse *et al.*, 1994, 1998; Samtleben & Niedermeyer, 1999); vibrocores from the Pomeranian Bight and the

Oder channel (Stuck, 1995; Roßdeutscher, 1996; Trapp, 1998); drill cores from Boock near Pasewalk and Karlshagen? on the Isle of Usedom (Rusbühlt unpublished).

4. *Ancylus* Sea (Boreal and Preboreal, Fig. 3):

a: Freshwater: Vibrocores from Mecklenburg Bight (Jensen *et al.*, 1999); vibrocores from the Tromper Wiek and Arkona Sea (Reich & Frenzel, 1996; Jensen *et al.*, 1999); Neu Pansow? near Greifswald, Mukran? on Jasmund peninsula / Isle of Rügen (this paper); vibrocores from the Pomeranian Bight (Stuck, 1995; Roßdeutscher, 1996; Trapp, 1998; Verse & Wunderlich, 2002); vibrocores from the Greifswalder Bodden (Verse *et al.*, 1994); drill core from Krumminer Wiek/Isle of Usedom (Hoffmann, 2000).

5. *Yoldia* Sea (Preboreal, Fig. 3):

a: Freshwater: Vibrocores from Mecklenburg Bight (Diebel, 1965a, 1965b, 1968); vibrocores from Tromper Wiek Bay (Bennike & Lemke, 2001); core from the Herthamoor on Jasmund peninsula/Isle of Rügen (Schumacher & Endtmann, 1998); Ferdinandshof(?) near Ückermünde (Fuhrmann & Pietrzeniuk, 1990).

b: Brackish?: Vibrocores from Tromper Wiek Bay (Bennike & Lemke, 2001).

6. Late Glacial (Weichselian, Fig. 3):

a: Freshwater: Vibrocores from Mecklenburg Bight (Diebel, 1965a, 1965b; Lemke *et al.*, 1998); Wolfshagen near Woldegk? (Diebel, 1965b); Stoltera (Diebel, 1965b); Rostocker Heide (Ludwig, 1964a); Tessin near Rostock (Krienke *et al.*, 1999); Fischland on Darß peninsula (Ludwig, 1963; Diebel, 1968; Pietsch, 1991; Steinich, 1992a); cores from Tromper Wiek at Rügen (Lemke *et al.*, 1998); cores from Arkona Basin (Jensen *et al.*, 1997).

7. Pleniglacial (Weichselian, Fig. 4):

a: Marine: Mecklenburg-Vorpommern in general (Frenzel, 2001); Isle of Hiddensee (Ludwig, 1964b; Frenzel, 1993; this paper); Arkona/Isle of Rügen (Ludwig, 1964b; Diebel, 1965b; Steinich, 1992b; Frenzel, 1993); Tützpatz near Altentreptow (glacial erratic lump; this paper); island Greifswalder Oie (Frenzel & Ansorge, 2001).

b: Brackish: Klein-Klütz-Höved (Ullerich, 1991; Strahl *et al.*, 1994).

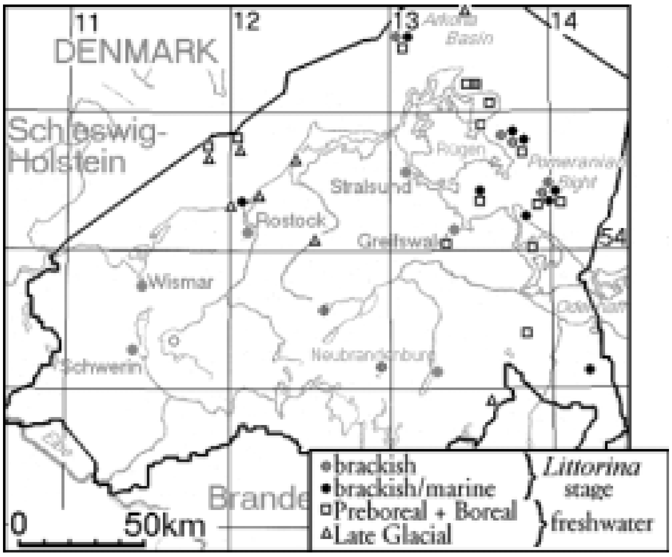

FIGURE 3–Documented occurence of ostracods from Late Glacial and Holocene sediments in Mecklenburg-Vorpommern.

c: Freshwater: Klein-Klütz-Höved (Ullerich, 1991); Groß-Klütz-Höved (Ludwig, 1964b); Gustävel, Thurow and Wipersdorf near Schwerin (Langer, 1964); Blankenberg near Warin (Ludwig, 1960; Kriebel, 1964; Langer, 1964; Diebel, 1968); Isle of Poel (Ludwig, 1964b; Rühberg, 1965); Kühlungsborn, Heiligendamm and Doberan (Ludwig, 1964b); Stoltera near Rostock (Ludwig, 1964b; Ansorge, pers. comm.); Tessin near Rostock (Krienke *et al.*, 1999); Arkona/Isle of Rügen (Ludwig, 1964b; Steinich, 1990, 1992b); Jasmund/Isle of Rügen (Ludwig, 1959, 1964b; Diebel, 1965b; Steinich, 1992a; Keding, 1993; Frenzel in Griffiths, 1995).

8. Eemian (Fig. 4):

a: Marine: Drill cores from Mecklenburg-Vorpommern in general (Frenzel, 2001); drill core at Herrnburg near Lübeck (Rusbühlt, unpublished; this paper); Groß- and Klein-Klütz-Höved, drill cores Rubow near Schwerin (glacial erratic lump), Schönberg near Lübeck, Schlemmin? north of Sternberg and Bergen? on the Isle of Rügen (Rusbühlt, unpublished); Schwaan near Rostock (Frenzel & Ansorge, in press).

b: Brackish: Drill cores from Mecklenburg-Vorpommern in general (Frenzel, 2001); drill core

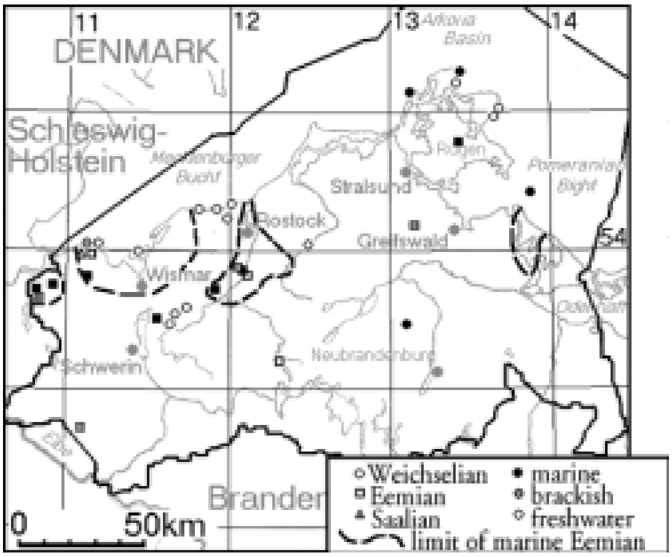

FIGURE 4–Documented occurence of ostracods in Saalian, Eemian and Weichselian (without Late Glacial) sediments in Mecklenburg-Vorpommern. Limit of the marine Eemian modified after Rühberg *et al.* (1995).

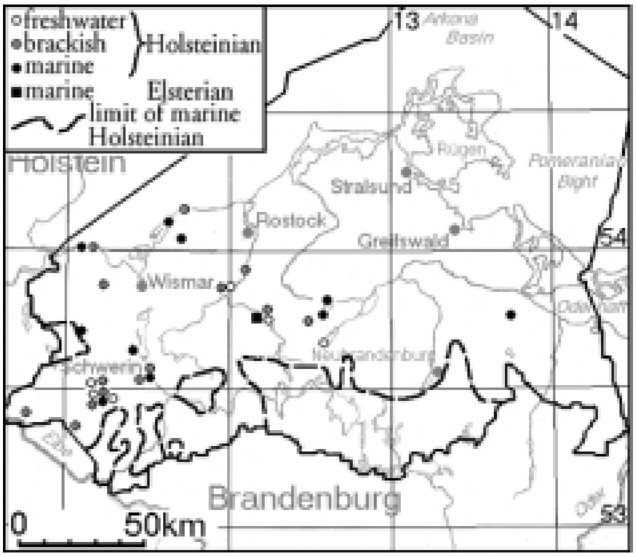

FIGURE 5–Documented occurence of ostracods from Elsterian and Holsteinian sediments in Mecklenburg-Vorpommern. Limit of the marine Holsteinian after Rühberg *et al.* (1995).

Herrnburg near Lübeck (this paper); Schwaan near Rostock (Frenzel & Ansorge, 2004); Grimmen quarry (this paper).

c: Freshwater: Klein-Klütz-Höved (Klengel, 1954; Ullerich, 1991; Strahl *et al.*, 1994); drill core Glave near Krakow am See (Rusbühlt, unpublished); Schwaan near Rostock (Frenzel & Ansorge, in press).

9. Saalian (Fig. 4):

a: Freshwater: Klein-Klütz-Höved (Strahl *et al.*, 1994).

10. Holsteinian (Fig. 5):

a: Marine: Drill cores from Mecklenburg-Vorpommern in general (Frenzel, 2001); drill core Thürkow near Teterow (this paper); drill cores Gadebusch, Rerik, Teterow, Kraak near Schwerin, Schwerin (glacial erratic lump), Granzin near Hagenow, Dargibell near Anklam (Rusbühlt, unpublished); drill core Neubukow? near Salzhaff lagoon (this paper).

b: Brackish: Drill cores from Mecklenburg-Vorpommern in general (Frenzel, 2001); Klein-Klütz-Höved (Gehl, 1961); Kühlungsborn? (Ludwig, 1964b); Boizenburg (Madsen, 1902; Rusbühlt, unpublished); drill core Güstrow (this paper); Pätow-Steegen near Hagenow, drill cores Granzin, Bolzin, Bengerstorf (glacial erratic lump) and Bobzin near Hagenow, Hagenow, Grevesmühlen, Rachow near Teterow, Kraak and Plate near Schwerin, glacial erratic lumps et Neuendorf near Güstrow and at Lübtheen (Rusbühlt, unpublished).

c: Freshwater: Granzin near Hagenow (Erd, 1969, Rusbühlt, unpublished); drill cores Bobzin and Moraas near Hagenow, Dahmen near Teterow and Güstrow (Rusbühlt, unpublished).

11. Late Elsterian (Fig. 5):

a: Marine: drill cores from Southwestern Mecklenburg (Frenzel, 2001); drill core Güstrow (Rusbühlt, unpublished).

RECENT OSTRACODS

Well examined locations are the surroundings of Greifswald, where G. W. Müller had done intensive field work, and the lagoons and estuaries (with the exception of those of the Isle of Rügen). Other reports on freshwater ostracods are isolated localities throughout Mecklenburg-Vorpommern concentrating on the Isle of Rügen and on West Pomerania (Fig. 2). The ostracod fauna from the open Baltic Sea is known so far from only one transect touching the periphery of the study area (Rosenfeld, 1977) and some isolated localities (Klie, 1938).

A total of 115 Recent ostracod species are known from Mecklenburg-Vorpommern today; comprising 28 marine, 13 brackish and 74 freshwater species. Twenty species published by G. W. Müller (1900) have not been reported in more recent works from the study area; these are particularly species of temporary water bodies. The apparent loss of these taxa from the study area may reflect the loss of small temporary water bodies due to human activity. However, it is also possible that they are gone unrecorded through lack of sampling, since recent research has concentrated on larger, permanent water bodies.

The coastal and drainage area of the Baltic Sea in Sweden, Denmark, Schleswig-Holstein, Mecklenburg-Vorpommern and Poland contains a total of 142 freshwater and 80 brackish/marine ostracod species. Table 2 shows a general decrease of the marine and brackish water species number from the Belt Sea (Schleswig-Holstein) with relatively high salinity to brackish water conditions at the Polish coast. With 74 species Mecklenburg-Vorpommern shows the second largest number of freshwater taxa behind Poland. The higher Polish number is explainable by the larger territory with supplementary habitats, e. g. waters of the mountains, but reflects a high level of ostracod research also. In contrary the number of taxa reported from Sweden and Denmark is surely too low. Meisch (2000) notes the poor knowledge on freshwater ostracods from Denmark.

Gerlach (2000) reports a total of 87 ostracod species from brackish water localities of the Kiel Bay area. This higher number than 61 species from brackish water localities in Mecklenburg-Vorpommern is not surprising because of the higher salinity in the Kiel Bay, reaching up to 22 psu. Taxa from the Kiel Bay missing in our study area are consequently marine species as *Cytherois pusilla* G. O. Sars, 1928, *Cytherois vitrea* (G. O. Sars, 1865), *Cytherura bidens* Klie, 1929, *Cytherura inconspicua* Klie, 1934, *Cytherura nasuta* Klie, 1934, *Eucythere declivis* (Norman, 1865), *Eucythere undulate* Klie, 1929, *Finmarchinella angulata* (G. O. Sars, 1865), *Hemicythere villosa* (G. O. Sars, 1865), *Hemicytherura cellulosa* (Norman, 1865), *Loxoconcha*? *fragilis* G. O. Sars, 1865, *Paracytherois arcuata* (Brady, 1868), *Polycope schulzi* Klie, 1950, *Sclerochilus contortus* (Norman, 1861), *Semicytherura acuticostata* (G. O. Sars, 1865), *Semicytherura angulata* (Brady, 1868), *Semicytherura similis* (G. O. Sars, 1865), *Semicytherura simplex* (Brady & Norman, 1889), *Semicytherura striata* (G. O. Sars, 1865), *Semicytherura undata* (G. O. Sars, 1865), *Xestoleberis depressa* G. O. Sars, 1865; as well as *Acanthocythereis dunelmensis*, *Elofsonella concinna* and *Palmoconcha guttata* known from Mecklenburg-Vorpommern only as fossils. Seven freshwater species reported from brackish water in the Kiel Bay area were found in Mecklenburg-Vorpommern in freshwater localities only. The freshwater species *Pseudocandona sucki* (Hartwig, 1901), reported from the Schlei, was not found so far in our study area. Ostracods from brackish water in Mecklenburg-Vorpommern and missing in the Kiel Bay area are *Candona lindneri*, *Cypria subsalsa*, *Ilyocypris decipiens* (misidentified as *I. bradyi*?), *Leptocythere porcellanea* and *L. psammophila* (misidentified as *L. confusa*?), *Physocypria kraepelini* and *Pseudocandona insculpta*.

	Sweden	Denmark	Schleswig-Holstein	Mecklenburg-Vorpommern	Poland
freshwater	36	11	52	74	122
brackish/marine	45	62	83	61	43
Total	81	73	112	115	158

TABLE 2–Number of Recent ostracod species in freshwater and brackish water from Mecklenburg-Vorpommern and adjacent areas at the Baltic Sea coast. The number of taxa for the adjacent areas is compiled from the works of Elofson 1941, Hagermann 1969, Muus 1967, Theisen 1966 (Denmark), Gerlach 2000, Günter 1983 (Schleswig-Holstein), Sywula & Namiotko 1997 (Poland), Ganning 1971, Sars 1922-28 (Sweden) and Klie 1938, Meisch 2000 as well as Rosenfeld 1977 in general.

The freshwater species *Candona muelleri, Herpetocypris intermedia, Paralimnocythere psammophila* and *Trajancypris laevis* from Mecklenburg-Vorpommern are not known from the adjacent areas. *C. muelleri* is a northeastern European and northern Asiatic species (Meisch, 2000) and reaches in the study area probably its westernmost distribution. Contrarily the western and southern European species *H. intermedia* seems to have its northeastern limit in our area. *Cypria subsalsa* is indicated by Meisch (2000) from brackish water localities in the Netherlands and Belgium only, but he supposes a larger distribution along the North Sea coast. It seems to be often misinterpreted as the report from Mecklenburg-Vorpommern coastal waters shows now.

Bradleystrandesia hirsuta (Fischer, 1851), which occurs in Poland, Sweden and other countries, lacks in Mecklenburg-Vorpommern. This species is very similar to *B. reticulata*. Probably it was not correctly identified in the study area so far. Also *Candonopsis scourfieldi* Brady, 1910, *Cryptocandona reducta* (Alm, 1914), *Isocypris beauchampi* (Paris, 1920) and *Potamocypris arcuata* (Sars, 1903) should occur in the study area, regarding their general distribution as indicated in Meisch (2000). *Fabaeformiscandona caudata* (Kaufmann, 1900) and *Leucocythere mirabilis* Kaufmann, 1892 are supposed too to occur in Mecklenburg-Vorpommern, but they are typical for the profundal and sublittoral zone of lakes, which was scarcely sampled in the study area and often seriously changed by eutrophication during the last 50 years.

SUBFOSSIL AND FOSSIL OSTRACODS

The results from published works referring to subfossil and fossil ostracods in the Quaternary of Mecklenburg-Vorpommern are based on isolated localities. There are several Pleistocene and Holocene coastal and some inland exposures. Another source of information are cores from mainly Pleistocene sediments on the mainland and prodcores from Holocene sediments of the Baltic Sea (Fig. 3-5).

Unpublished reports by Jutta Rusbühlt from the former Geological Service of Mecklenburg-Vorpommern mention Pleistocene ostracods from several localities in the mainland of our country. The oldest Quaternary ostracod fauna is known from some cores taken in the southwest of Mecklenburg and reflects a marine facies of Late Elsterian age (Fig. 5). Marine species like *Elofsonella concinna, Cytheropteron montrosiense* and *Acanthocythereis dunelmensis* belong to this fauna. Although the whole territory of Mecklenburg-Vorpommern is suspected to be covered by the Holsteinian sea, the published material is dominated by brackish water associations in this period. The few marine associations known are similar to those found in Late Elsterian deposits. There is only one evidence for a freshwater succession within the Saalian so far, which is located at Klein-Klütz-Höved in the northwest of the study area (Strahl *et al.*, 1994). A rich marine Eemian ostracod fauna was found at several localities along the present shoreline, besides a few brackish water associations (Fig. 4). The so called *Cyprina* clay, dated as Early Weichselian, is known from some coastal exposures and has been studied already (Frenzel, 1993). There are two associations to be distinguished: a rich boreal fauna with *Robertsonites tuberculatus, Elofsonella concinna, Sarsicytheridea punctillata, Cytheropteron montrosiense,* etc., and an arctic cold-water fauna consisting of only two species *Roundstonia globulifera* and *Cytheropteron pseudomontrosiense*. Pleistocene ostracod associations are not known from the open Baltic Sea except a few Late Glacial freshwater associations. In total 54 ostracod species are known today from the Pleistocene of Mecklenburg-Vorpommern (Table 3). This number is similar to that one of Poland (calculated from literature data). The documented fossil record for Sweden, Denmark and Schleswig-Holstein is poor compared with the study area. An exception is the marine/brackish Holsteinian from Schleswig-Holstein, where extensive faunal lists are given (e. g. Lange, 1962; Lord *et al.*, 1993).

Late Glacial and Holocene associations are reported from Baltic Sea prodcores and from mainland exposures (Fig. 3). The cores sampled from the coastal region contain freshwater ostracods, which are dated back to the Younger Dryas until Preboreal (Diebel, 1965a). The changing of ostracod associations reflects the Late Glacial to Holocene succession from a *Candona candida* fauna to a *Metacypris cordata* fauna (Absolon, 1973) as discussed by Griffiths & Evans (1995). Besides Prelitorine freshwater ostracod associations brackish-marine taxa have been reported from the *Littorina* stage (Atlantic) (unpublished works of Stuck, 1995; Reich & Frenzel, 1996; Rossdeutscher, 1996; Trapp, 1998), indicating partly higher salinities than today (Table 3). The succession of associations from these sections reflects the evolution of the Baltic Sea and redraws sea-level and salinity variations. Unfortunately the organic rich brackish water sediment samples do often not

	marine	brackish	freshwater	total
Littorina and postlittorine stages	0	21	4	25
Ancylus stage	0	2	18	20
Yoldia stage	0	0	17	17
total Holocene (without Recent)	**0**	**22**	**23**	**42**
Late Glacial	0	0	18	18
Weichselian	12	3	16	30
Eemian	4	5	14	23
early Saalian	0	1	10	11
Holsteinian	9	2	8	19
late Elsterian	3	0	0	3
total Pleistocene	**18**	**10**	**29**	**54**
total Quaternary (without Recent)	**21**	**24**	**33**	**67**

TABLE 3–Number of ostracod species documented from Quaternary environments in Mecklenburg-Vorpommern.

contain any calcareous fossils as these may be easily dissolved.

The given information on stratigraphic distribution of ostracods is not strong enough to declare certain species as stratigraphic guide fossils. But it seems to be possible to set up some ecostratigraphic forms or associations. For instance the monospecific or dominant occurrence of *Roundstonia globulifera* indicates a specific and easily recognizable facies within the Weichselian. The limnocytherid freshwater ostracods *Leucocythere baltica, Limnocythere blankenbergensis, Limnocythere falcata,* as well as *Limnocytherina sanctipatricii* in a lesser degree, are characteristic for late glacial or interstadial waters under arctic/subarctic climate. *Cyprideis torosa,* widely distributed in Holocene and Pleistocene, is an important bioindicator for brackish water sediments in shallow lagoons and estuaries.

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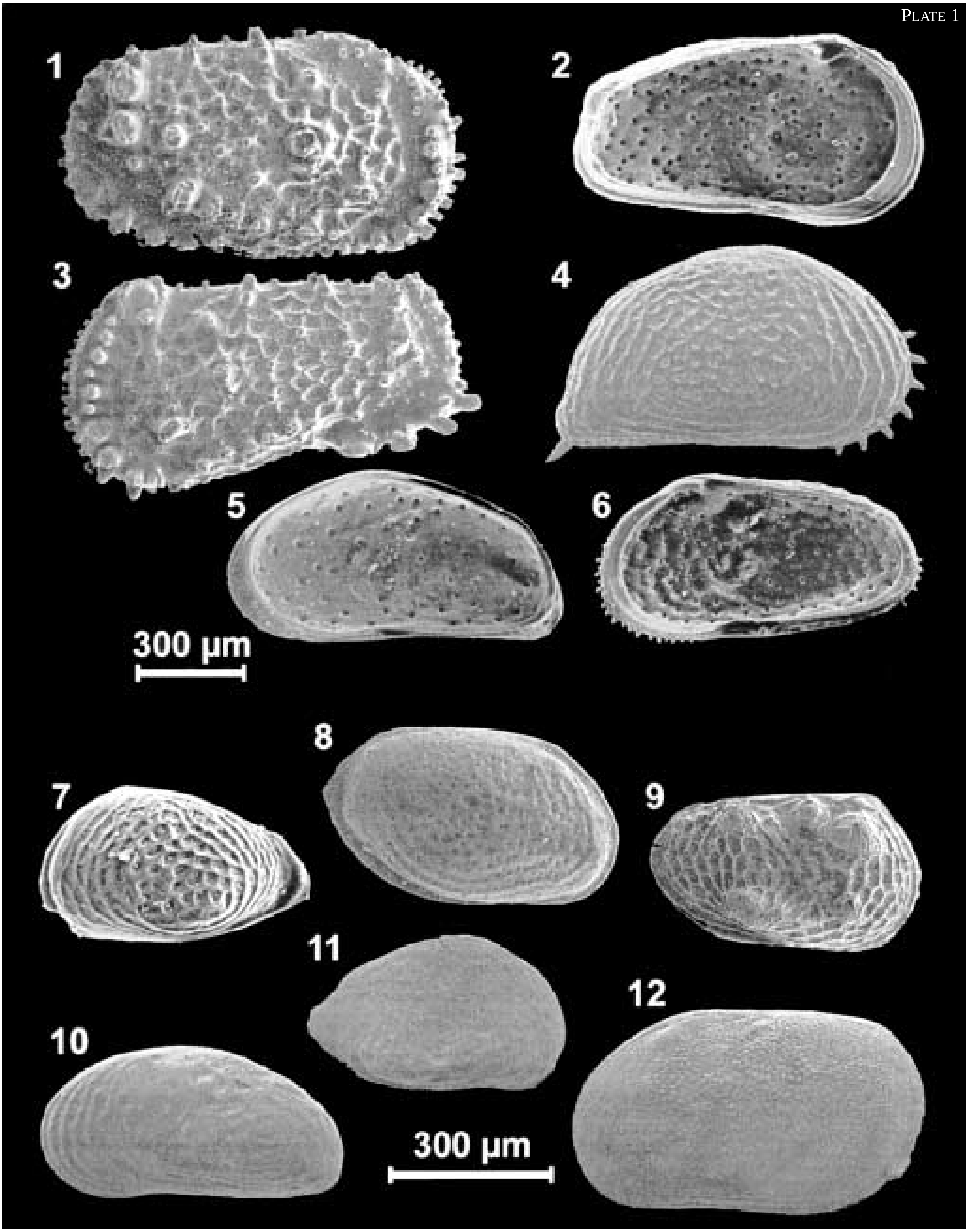
PLATE 1–Ostracods from brackish/marine environments. *1, Acanthocythereis horrida* (Sars, 1866), female right valve – well Hy Neubukow 1/92, 93-94 m, Holsteinian. *2, Elofsonella concinna* (Jones, 1857), female left valve, internal view – Klüsser Nische, Arkona, Rügen, sample H33, *Cyprina* clay, Weichselian. *3, Acanthocythereis dunelmensis* (Norman, 1865), male left valve – well Hy Neubukow, 1/92 93-94 m, Holsteinian. *4, Heterocyprideis sorbyana* (Jones, 1856), female right valve – Arkona Sea, *Mya*-Stage. *5, Sarsicytheridea bradii* (Norman, 1865), female right valve, internal view – Klüsser Nische, Arkona, Rügen, sample H5, *Cyprina* clay, Weichselian. *6, Robertsonites tuberculatus* (Sars, 1865), female right valve, internal view – Klüsser Nische, Arkona, Rügen, sample H5, *Cyprina* clay, Weichselian. *7, Cytheropteron pseudomontrosiense* Whatley & Masson, 1979, female? left valve – Klüsser Nische, Arkona, Rügen, sample H33, *Cyprina* clay, Weichselian. *8, Palmoconcha guttata* (Norman, 1865), female right valve – cliff NE Hucke, Hiddensee, *Cyprina* clay, Weichselian. *9, Roundstonia globulifera* (Brady, 1865), female? right valve – Klüsser Nische, Arkona, Rügen, sample H33, *Cyprina* clay, Weichselian. *10, Eucythere argus* (Sars, 1865), female left valve – Arkona Sea, *Mya*-Stage. *11, Cytheropteron latissimum* (Norman, 1865), right valve – Arkona Sea, Recent. *12, Loxoconcha elliptica* (Brady, 1868), male left valve – Strelasund, station SL3, Recent.

PLATE 1



CONCLUSIONS

The knowledge about the Recent ostracod fauna of Mecklenburg-Vorpommern is quite good compared to other regions. But existing data, especially on freshwater ostracods, were collected about 50 years ago and often represent only the distribution of species. So, a rather rough overview can be given on the ostracod fauna of the study area. Faunistical changes such as the extinction or the invasion of species, discussed in the context of anthropogenic influence, cannot be evaluated with this database only.

The occurence of Recent ostracod taxa in Mecklenburg-Vorpommern in comparison with adjacent regions shows a decreasing diversity from the west to the east caused by the higher salinity of the Baltic Sea in the western parts. No tendency is recognizable for the freshwater taxa.

The knowledge about the distribution of subfossil and fossil Quaternary ostracods from the study area is rather poor but comparable to this one of adjacent regions. The comparison of ostracod occurences from Quaternary sediments of different regions reflects more the state of knowledge on these ostracods than real diversity phenomena. No real stratigraphical index forms within the Quaternary ostracod associations of Mecklenburg-Vorpommern are recognizable. However, ecostratigraphic work with associations is possible.

In future work, special emphasis has to be put on getting data about whole ostracod associations and environmental parameters in context. This knowledge may be used in environmental monitoring programmes or palaeoenvironmental analysis of Quaternary sediments. Ostracods have still a great potential which just has to be utilised.

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PLATE 2–Ostracods from brackish/freshwater environments. *1, Bradleystrandesia fuscata* (Jurine, 1820), female left valve – south of Wampen near Greifswald, tempoary pond, Recent. *2, Cyprois maginata* (Straus, 1821), female left valve, internal view – Löcknitz near Pasewalk, Recent. *3, 4, Fabaeformiscandona holzkampfi* (Hartwig, 1898). 3. male right valve – Greifswald, Recent. 4. female right valve – Greifswald, Recent. *5, 6, Limnocytherina sanctipatricii* (Brady & Robertson, 1869). 5. male left valve – Pomerian Bight, *Ancylus*-stage. 6. female left valve – Pomerian Bight, *Ancylus*-stage. *7, Leucocythere baltica* (Diebel, 1965a), female right valve – Klüsser Nische, Arkona, Rügen, sample H6, *Cyprina* clay (redeposited?), Weichselian. *8, Physocypria kraepelini* (G. W. Müller, 1903), female left valve - river Ryck, Greifswald, Recent. *9, Cytherissa lacustris* (Sars, 1863), female left valve – Pomerian Bight, *Ancylus*-stage. *10, Sarsicytheridea punctillata* (Brady, 1865), female left valve – Klüsser Nische, Arkona, Rügen, sample P4, *Cyprina* clay, Weichselian. *11, Leptocythere lacertosa* (Hirschmann, 1912), female right valve – Greifswalder Bodden, sample GB47, Recent. *12, Leptocythere psammophila* (Guillaume, 1976), male left valve - well Herrnburg, 1/58 41,9-42,7 m, Eemian. *13, Loxoconcha elliptica* Brady, 1868, female right valve – well Herrnburg 1/58, 41,9-42,7 m, Eemian.

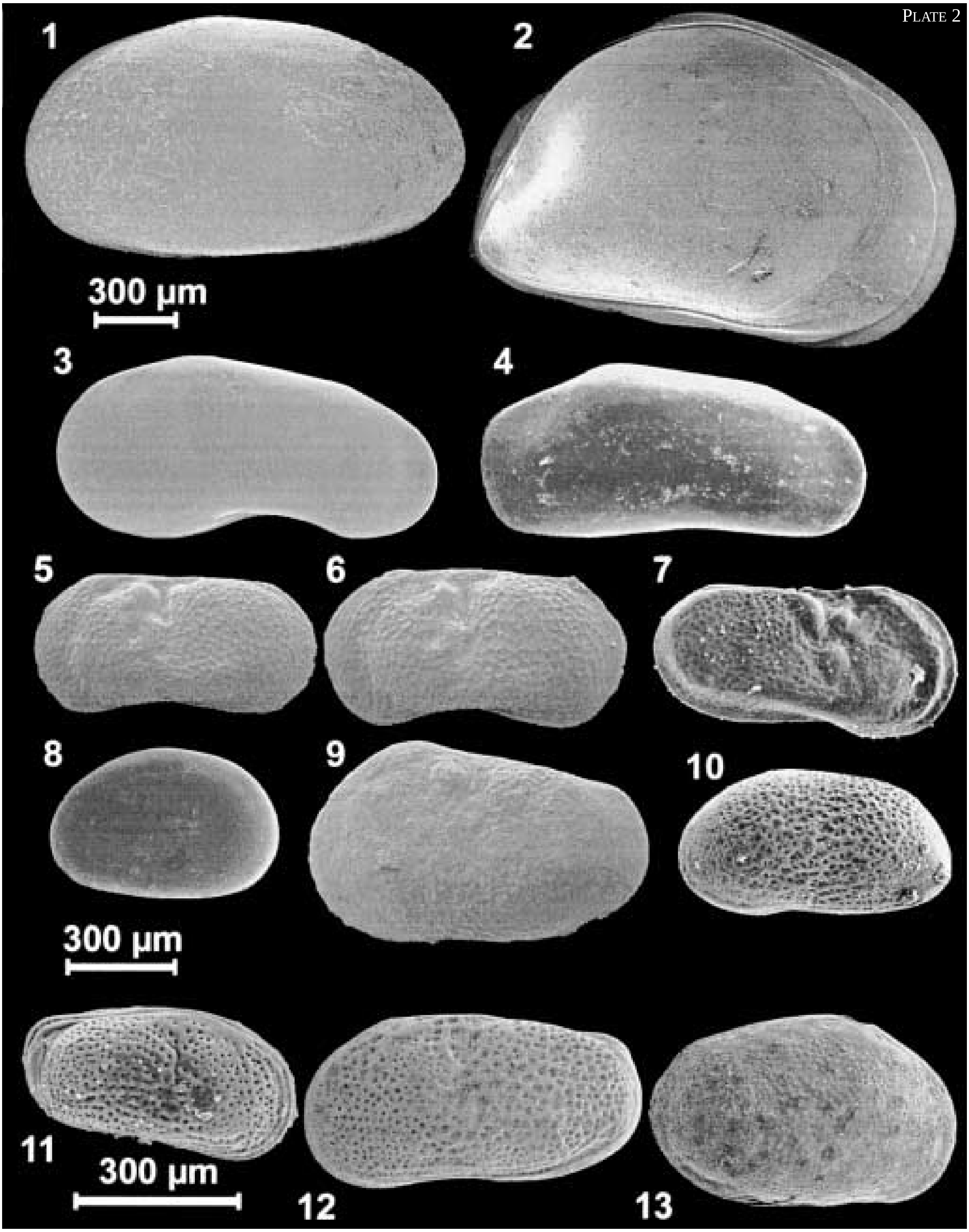
PLATE 2

No. and Locality	**Stratigraphy**	**Taxa**
[123] Baltic Sea north off Kühlungsborn (54°14.0’/11°42.8’)	Recent (October, November 2001)	*Robertsonites tuberculatus, Sarsicytheridea bradii*
[124] Baltic Sea north off Kühlungsborn (54°14.0’/11°42.8’)	Recent (February 2002)	*Robertsonites tuberculatus*
[125] Baltic Sea north off Kühlungsborn (54°14.0’/11°42.8’)	Recent (April 2002)	*Acanthocythereis dunelmensis, Robertsonites tuberculatus, Sarsicytheridea bradii*
[126] Baltic Sea north off Warnemünde (54°14.86’/11°58.01’)	Recent (November 2001 and April 2002)	*Robertsonites tuberculatus, Sarsicytheridea bradii*
[127] Arkona Basin (OS 226210)	Recent	*Heterocyprideis sorbyana*
[128] Barthe at Divitz (Brücke; 0.2 psu)	Rezent (December 2002)	*Notodromas monacha*
[129] Ryck in Greifswald	Recent (July 1992)	*Cypria ophtalmica, Cytherura gibba, Pseudocandona compressa*
[130] Achterwasser (Usedom; brackish water)	Recent (June 1992)	*Candona candida, Candona neglecta, Cyprideis torosa* f. *litoralis* + f. *torosa, Cytheromorpha fuscata, Fabaeformiscandona levanderi, Fabaeformiscandona protzi, Ilyocypris decipiens, Limnocythere inopinata*
[131] Oderhaff	Recent (August 2001)	*Candona candida, Candona neglecta, Cyclocypris ovum* f. *impressopunctata, Cypria ophtalmica, Cyprideis torosa* f. *torosa, Cyprideis torosa* f. *litoralis, Cypridopsis vidua, Cytheromorpha fuscata, Darwinula stevensoni, Fabaeformiscandona protzi, Ilyocypris decipiens, Limnocythere inopinata, Physocypria kraepelini, Pseudocandona* spp.
[132] Lendershagen near Velgast	Recent (May 2001)	*Cyprois marginata, Cypria ophtalmica, Cyclocypris ovum,* juv. *Pseudocandona*
[133] Letzin near Demmin	Recent (March 2002)	*Cypria ophtalmica, Cyclocypris ovum, Cyclocypris serena*
[134] Vietlipp near Grimmen	Recent (May 1998)	*Cypria ophtalmica, Cypris pubera, Ilyocypris gibba*
[134a] Löcknitz near Pasewalk	Recent (June 2003)	*Cypridopsis vidua, Cyprois marginata, Darwinula stevensoni, Limnocythere inopinata, Notodromas monacha*
[135] Neu Gaarz (Mecklenburg), small artificial water basin	Recent (August 2002)	*Heterocypris incongruens, Cypria ophtalmica*
[136] Rügen (Ossen near Bergen)	Recent (May 2002)	*Fabaeformiscandona acuminata*

APPENDIX

[137] Ladebow, Irrigation plant near Greifswald	Recent (July 1992)	*Heterocypris incongruens*
[138] Peenestrom near Rankwitz	Recent (June 1992)	*Cyprideis torosa* f. *litoralis* + f. *torosa*, *Ilyocypris decipiens*
[139] Peene swamps near Gützkow	Recent (July 1992)	*Cyclocypris ovum*, *Cypria ophtalmica*, *Ilyocypris* sp.
[140] Rotes Moor near Anklam	Recent (April 2000)	*Fabaeformiscandona acuminata*
[141] Wampen near Greifswald	Recent (March 1998)	*Bradleystrandesia fuscata*
[142] northern periphery of lake Glambecker See near Schwerin	Subfossil (Subatlantic?)	*Darwinula stevensoni*, *Fabaeformiscandona holzkampfi*, *Fabaeformiscandona levanderi*, *Metacypris cordata*
[143] Teterower See	Subfossil (Subatlantic?)	juv. *Candona* sp., *Cyclocypris globosa*,*Cyclocyprisovum impressopunctata*, *Cyprideis torosa* (f. *torosa* and f. *litoralis*), *Ilyocypris decipiens*, juv. *Pseudocandona* sp.
[144] Mukran on Jasmund peninsula / Isle of Rügen	Holocene	Rich freshwater fauna
[145] Neu Pansow near Greifswald	Holocene	Rich freshwater fauna
[146] Jasmund north of Witt, Isle of Rügen (erratic)	Weichselian (I_1 interstadial)	*Limnocythere falcata*
[147] Dornbusch NE from Hucke, Hiddensee	Weichselian (*Cyprina* clay)	*Palmoconcha guttata* f. *granulata*, *Robertsonites tuberculatus*, *Sarsicytheridea bradii*
[148] Dornbusch, Hiddensee	Weichselian (*Cyprina* clay)	*Robertsonites tuberculatus*, *Sarsicytheridea punctillata*
[149] Tützpatz near Altentreptow, well Tützpatz 1/62, 59.65 m	Weichselian (*Cyprina* clay)	*Roundstonia globulifera*
[150] Kühlungsborn near Rostock, cliff near Fulgenbach	Eemian?	*Cyprideis torosa* f. *litoralis*
[151] Grimmen, quarry	Eemian	*Cyprideis torosa* f. *torosa*
[152] Herrnburg near Lübeck, well Herrnburg 1/58, 40.0-42.7 m	Eemian	*Leptocythere psammophila*, *Loxoconcha elliptica*, *Semicytherura sella*, *Xestoleberis nitida*
[153] Herrnburg near Lübeck, well Herrnburg 2/74, 33-34 m	Eemian	*Cyprideis torosa*
[154] Güstrow, well Hy Güstrow 4/77, 75-76 m	Holsteinian	*Cyprideis torosa*
[155] Güstrow, well Hy Güstrow 7/77, 70-72 m (?)	Holsteinian	*Cyprideis torosa*, *Cytherissa lacustris*
[156] Neubukow near Salzhaff lagoon, well Hy Neubukow 1/92, 93-94 m	Holsteinian?	*Acanthocythereis dunelmensis*, *Acanthocythereis horrida*, *Elofsonella concinna*
[157] Thürkow near Teterow, well Thürkow 1/63, 88.55 m	Holsteinian	*Elofsonella concinna*

APPENDIX *(Continuation)*

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THE MORPHOLOGY AND CLASSIFICATION OF PARADOXOSTOMATINAE (OSTRACODA) FROM THE NEARSHORE ZONE OF MADEIRA AND THE CANARY ISLANDS

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Abstract

From a total of 50 ostracod species in the nearshore zone of Madeira and the Canary Islands, twelve belong the subfamily Paradoxostomatinae Brady & Norman, 1889 emend. Schornikov, 1993. For the first time a clear definition of the genus *Paradoxostoma* Fischer s. s. is given and the type species *P. dispar* redescribed and fully illustrated. Fifteen nov. comb. are proposed and two nov. syn.: *Paradoxostoma insigne* Hartmann, 1959 = *Paradoxostoma sarniense* Brady, 1868 and *Paradoxostoma lunatum* Okubo, 1977 = *Pontostoma honssuense* (Schornikov, 1975) are established. "*Paradoxostoma*" *planum* Müller, 1894 is provisionally placed in *Paradoxostoma* s. l. as details of the soft parts are unknown. Morphological details of five new genera and nine new species are provided: *Paradoxostoma wirtzi* sp. nov., *Lanceostoma* gen. nov. with *Lanceostoma tenerifense* sp. nov.; *Calcarostoma* gen. nov. with *Calcarostoma calcaratum* Schornikov & Wouters sp. nov.; *Bradystoma* gen. nov. with *Bradystoma bradyforme* sp. nov.; *Pontostoma* gen. nov. with *Pontostoma paraponticum* sp. nov., *Pontostoma atlanticum* sp. nov.; *Triangulostoma* gen. nov. with *Triangulostoma madeirense* sp. nov.; *Brunneostoma littorale* sp. nov. and *Brunneostoma cuneatum* sp. nov. The differences, on which the discrimination of genera in the Paradoxostomatinae is based, are of the same scale as those used to distinguish genera in other Cytherocopina families. Diagnostic characters include shape and expression of sexual dimorphism of the shell, structure of the fused zone, muscle scar patterns, hinge and penis. The appendages of different genera vary in the degree of reduction of various parts of the antenna, mandible, and maxillula.

Key words: Ostracoda, Paradoxostomatinae, morphology, taxonomy, Recent, marine, Madeira, Canary Islands.

Resumen

De un total de 50 especies de ostrácodos reconocidas en la zona marina costera de Madeira y las islas Canarias, 12 pertenecen a la subfamilia Paradoxostomatinae Brady & Norman, 1889 emend., Schornikov, 1993. Se propone por vez primera una definición clara del género *Paradoxostoma* Fischer s.s. y la especie tipo *P. dispar* es redescrita y convenientemente ilustrada. Se proponen 15 nuevas combinaciones y se establecen dos nuevos sinónimos: *Paradoxostoma insigne* Hartmann, 1959 = *Paradoxostoma sarniense* Brady, 1868, y *Paradoxostoma lunatum* Okubo, 1977 = *Paradoxostoma honssuense* (Schornikov, 1975). "*Paradoxostoma*" *planum* Müller, 1894, es incluido provisionalmente en *Paradoxostoma* s. l. debido al desconocimiento de detalles de sus partes blandas. Se describen detalles morfológicos de cinco géneros nuevos y de nueve especies nuevas: *Paradoxostoma wirtzi* sp. nov., *Lanceostoma* gen. nov., *Lanceostoma tenerifense* sp. nov., *Calcarostoma* gen. nov., con *Calcarostoma calcaratum* Schornikov & Wouters sp. nov.; *Bradystoma* gen. nov. con *Bradystoma bradyforme* sp. nov.; *Pontostoma* gen. nov. con *Pontostoma paraponticum* sp. nov., *Pontostoma atlan-*

ticum sp. nov*; Triangulostoma madeirense* sp. nov*; Brunneostoma littorale* sp. nov. y *Brunneostoma cuneatum* sp. nov. Las diferencias en las cuales se ha basado la discriminación de los géneros dentro de Paradoxostomatinae son de la misma escala que las empleadas en otras subfamilias de Cytherocopina. Los caracteres diagnósticos incluyen la forma y la expresión del dimorfismo sexual del caparazón, la estructura de la zona de fusión, la configuración del campo de huellas musculares, de la charnela y del pene. Los apéndices de los diferentes géneros varían en el grado de reducción de varias partes de la antena, mandíbula y maxílula.

Palabras clave: Ostracoda, Paradoxostomatinae, morfología, taxonomía, Reciente, marino, Madeira, islas Canarias.

INTRODUCTION

In a study on ostracods from Peter the Great Bay (Sea of Japan), Schornikov (1993a, b) revised the Paradoxostomatidae and divided the family into three subfamilies: Cytheroisinae Schornikov, 1993, Paradoxostomatinae Brady & Norman, 1889 and Paracytheroisinae Schornikov, 1993. Basically, the families can be separated using differences in the structure of the mouthparts. However, the transformations in the oral region do not represent three subsequent stages of reduction, but are instead the result of parallel evolution from an ancient stock.

At present the subfamily Paradoxostomatinae comprises 11 genera with approximately 62 species: *Acetabulastoma* Schornikov, 1970 (9 species); *Austroparadoxostoma* Hartmann, 1979 (type species only, *Austroparadoxostoma pliocenica* Whatley & Maybury, 1983 belongs to a different genus); *Echinophilus* Schornikov, 1973 (1 species); *Echinositus* Schornikov, 1973 (1 species); *Obesostoma* Schornikov, 1993 (4-7? species); *Paradoxostoma* Fischer, 1855 s. s. (9 species); *Xiphichilus* Brady, 1870 (10 species, 5 in open nomenclature). Schornikov (1993a, b) separated the most aberrant species into three genera: *Boreostoma* Schornikov, 1993 (11 species); *Brunneostoma* Schornikov, 1993 (11-13? species); *Obesostoma* Schornikov, 1993 (4-7? species).

In striking contrast, *Paradoxostoma* s. l. is home to an estimated 150 named species and a great number in open nomenclature. Its representatives are known throughout the World Ocean, and its fossil record dates back to the Lower Jurassic (Michelsen, 1975). It encompasses a large variety of species groups characterised by morphological similarities as well as peculiarities of distribution and ecology. Distinguishing features include the shape and sexual dimorphism of the shell, the structure of the fused zone, muscle scar patterns, hinge and penis. Peculiarities of the exo- and endopodite of antenna, the chaetotaxy of the mandibular palp and coxa, the structure of the maxillula and brush-shaped organ can also be used to discriminate between closely related groups. These differences are of the same magnitude as those used to distinguish genera in other Cytherocopina families.

Prior to our study a total of eight Paradoxostomatinae species were known from the nearshore region of Madeira and the Canary Islands. Fischer (1855) first recorded four marine podocopid species among algae on rocks in the littoral zone of Madeira; three of them, including *Paradoxostoma dispar,* were described as new. Brady (1911) reported 46 ostracod species from Madeira, five of which he assigned to *Paradoxostoma*: *P. hibernicum* Brady, 1868, and *P. arcuatum* Brady, 1868, from the littoral zone, and *P. gracile* Brady, 1911, *P. cylindricum* Müller, 1894, and *P. flexuosum* (Brady, 1867) from deep water dredged in 30-70 fathoms. Brady's material contained only dried shells so identification of these species using modern criteria is difficult. Both *P. arcuatum* and *P. flexuosum* have since been assigned to the genus *Paracytherois* Müller. As already shown by Horne and Whittaker (1985: 158-159) Brady occasionally confused very similar species of *Paradoxostoma* s. s. and in our opinion mistook *P. dispar,* a common species in the littoral zone of Madeira, for *P. hibernicum*. Finally, Hartmann (1959) described four new species, including two *Paradoxostoma, P. curtum* and *P. insigne,* from the littoral zone of Tenerife. *P. curtum,* which we did not encounter in this study, is an unusual species and clearly belongs to a different genus; *Paradoxostoma insigne* Hartmann, 1959, is a synonym of *Paradoxostoma sarniense* Brady, 1868 (see: Systematic description).

Clearly, the first step in the reclassification of *Paradoxostoma* s. l. required a detailed study of the type species and a exact definition of the genus *Paradoxostoma* s. s. However, the original (and only) description of the type, *P. dispar* Fischer from Madeira, is outdated. Fischer's (1855) illustrations are highly imperfect and one can only guess at relevant morphological details. Fortunately, the present material from the nearshore zone of Madeira and the Canary Islands contained a significant number of specimens of *P. dispar* as well as eleven species of *Paradoxostoma* s. l. We are confident that we have obtained the true *P. dispar* for a number of reasons: it is one of the most abundant species in the nearshore zone; the shell shows striking similarities in shape, proportions and presence of dark patches to the original figures (Fischer, 1855: Pl. 2, Fig. 2); sizes coincide: length of our specimens = 0.56-0.60 mm vs. length of Fischer's specimen = 0.30'''. The ventral margin of the ventrodistal lobe is also visible in Fischer's illustration of the penis (1855: Pl. 2, Fig. 4). The dorsodistal lobe (termed "Penis (?)" by Fischer) and large dorsodistal prehensile process (termed "hakenförmiges Haftorgan" by Fischer) are also quite similar. The present material provided an excellent opportunity to perform a detailed morphological study of *P. dispar* and provide up-to-date illustrations of the type, to designate neotype and paraneotypes, and to clearly define the genus *Paradoxostoma* s. s.

The remaining paradoxostomatid species in the present samples formed the basis for five new genera described below: *Bradystoma* gen. nov. (2 species); *Calcarostoma* gen. nov. (2 species); *Lanceostoma* gen. nov. (4 species); *Pontostoma* gen. nov. (11 species) and *Triangulostoma* gen. nov. (2 species). Our material from nearshore of Madeira contained only one female specimen of the type species of *Calcarostoma* gen. nov. However, at the last moment, in fact at the EOM-V in Cuenca, discussion with Dr. Karel Wouters (Royal Belgian Institute of Natural Sciences, Dept. of Invertebrates, Vautierstraat 29, B-1000 Brussels, Belgium; email: karel.wouters@naturalsciences.be) revealed that he had at his disposal two male specimens (and drawings) of the same species from the littoral of the Cape Verde Islands. We decided to pool our resources and describe *Calcarostoma calcaratum* Schornikov & Wouters sp. nov. in this paper.

MATERIAL, TERMINOLOGY AND METHODS

Material for this study consisted of four samples:

Sample 1. Tenerife, Canary Islands, collected by. Mr. Udo Schwarz near the town Puerto on 1 November 2001; depth up to 0.3 m, *Corallina* and other algae on rocks.

Samples 2, 3, 4. Madeira, collected by Dr. Peter Wirtz from Reis Magos, a small fishing village on the south-east coast of Madeira; depth up to 0.3 m; *Corallina*, *Padina* and other algae on rocks; Amphipoda: Gammaridea, Caprellidea; Isopoda, Ophiuroidea. Samples were collected on 3 April 2002 (Sample 2), 29 April 2002 (Sample 3), and 10 November 2002 (Sample 4).

Material on loan from the Royal Belgian Institute of Natural Sciences was collected by Th. Backeljau from a rock pool, Baia das Gatas, São Vicente (Cape Verde Is.) on 5 February 1996.

Material in the Crustacea Collection, Zoological Museum Hamburg was also examined for comparative purposes.

Abbreviations: * = live specimens; f = female; m = male; A-1, A-2 etc. = instars; s = shell; v = valve; RV, LV = right, left valves; A1, A2 = antennula, antenna; Md = mandibula; Mx = maxilla; P1, P2, P3 = pereiopods; Bo = brush-shaped organ; Ab = abdomen of female; Pe = penis; Bp = basipodite; cp = copulatory process; dej = ductus ejaculatorius; dpc = dorsodistal process of capsule; dph = dorsodistal prehensile process; dl, vl = dorsodistal and ventrodistal lobes.
and ventrodistal lobes.

Formulae (Fig. 1): Updated armature formulae for appendages as proposed by Schornikov & Gramm (1974) are used in generic descriptions. Figures without parentheses = podomeres numbered from proximal to distal; + = junction of podomeres. Figures wit-

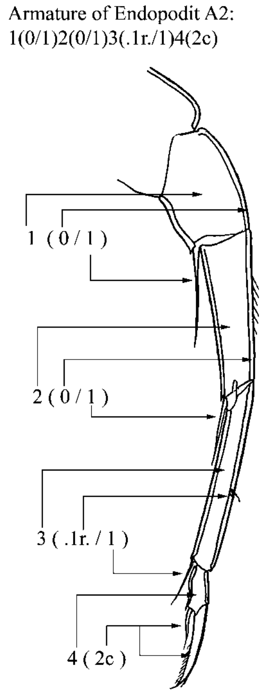


FIGURE 1–Schematic application of armature formula using exopodite A2 of *Lanceostoma* n. g.

hin parentheses = number of setae: numerator = setae on dorsal margin; denominator = setae on ventral margin; integer figures = lateral, medial or apical armature elements, from dorsal to ventral. Figures within parentheses without indexes = normally development setae; r = rudimentary; c = claw-shaped seta or claws; s = sensory seta; p = plumose seta or ray; re = reflexed seta or ray; a = atriumwards ray; t = tooth or tooth-shaped seta; l or m = lateral or medial seta. A dot indicates the presence of an interval between setae or between podomere ends; a colon indicates apical, lateral or medial setae; hyphen indicates variable elements. Commas are used for the sake of clarity e.g. to separate symbols by unarmed podomeres or setae without indexes.

Example: 1,2(1.1.1r.1/1,2c2-3:.1l.)+3(.1c.-1c/0: 2c1,1s1m) = originally 3-jointed appendage, 1st podomere unarmed, homologues of 2nd and 3rd podomeres fused. Dorsal margin of 2nd podomere with 1 proximal, 1 medial normally developed, 1 medial rudimentary and 1 distal seta, each with an interval inbetween. Ventral margin with 1 seta, 2 claws and 2-3 setae; laterally (:) 1 medial seta. Dorsal margin of 3rd podomere with 1 claw (in medial or distal position); ventral margin unarmed; distal margin (:) with 2 apical claws, 1 normal, 1 sensory apical seta, and 1 medial seta.

SOME MORPHOLOGICAL REMARKS

The shell of each Paradoxostomatinae genus has a distinctive shape. In a few cases the shape of the shell may deviate somewhat from the characteristic shape of the majority of species in the genus (as in *Brunneostoma*) but nevertheless, the general design of shell remains constant and recognisable. Sexual dimorphism is weakly expressed in the majority of the genera. In general, females are slightly higher and larger than males and more broadly rounded posteriorly. In *Boreostoma*, however, the opposite is true; males are larger and proportionally higher than females and the posterior margin of the male shell is broadly rounded.

The external shell surface of most Paradoxostomatidae is smooth and lustrous. Studies show that the primary sculpture (fossa-mural reticulation) was already reduced in the supposed ancestors of the group, the Keijicytherinae (Bythocytheridae), in the Palaeozoic (Schornikov, 1988; Schornikov & Michailova, 1990). Only a few genera iteratively developed secondary, mainly epicuticular sculpture which consists of fine, longitudinal or oblique striae, grooves, costulae or punctae. On the ventral part of the shell of *Acetabulastoma*, for example, oblique striae are clearly visible in transmitted light at medium magnification; in *Brunneostoma* longitudinal striae run parallel to the ventral margin but can only be distinguished at very high SEM magnifications; in *Pontostoma* the pattern consists of fine tubulae meandering inside the epicuticle**,** best seen under a light microscope at high magnification. Relatively large sculpture elements such as the longitudinal costae seen in "*Paradoxostoma*" *parallelicostatum* Hartmann, 1980 are very rarely found.

The free margin of the Paradoxostomatinae shells is usually smooth, but *Calcarostoma* has a small posteroventral spinula, *Echinophilus* a well-developed posteroventral spine and *Austroparadoxostoma* has a distinctly angular posteroventral projection. Okubo (1977) investigated the free margin of the Paradoxostomatinae shell in *Boreostoma pedale* (Hiruta, 1975) and reported the presence of an swelling, which "may be called" the flange, on the outer side of the selvage (seen in cross section). In our opinion this is not a real flange since this was already reduced in the Palaeozoic and is also absent on shells of Jonesiini and Pseudocytherini (Bythocytheridae) (Schornikov, 1981, 1988). Marginal pore canals do not open between the swelling and the selvage as in true marginal pore canals, but proximal to this swelling or on the swelling itself (Schornikov, 1993a). Therefore, we believe that this swelling is homologous to the selvage, and the homologue of the list is transposed onto the outer shell margin. This list may be poorly or well-developed. In addition, the inner lamella of Paradoxostomatinae bears two or three striae. In spite of the absence of a flange on shells of Jonesiini, Pseudocytherini and Paradoxostomatidae, marginal pore canals which reach of valve margin are apparently no different from 'real' marginal pore canals in other ostracod groups. The marginal zone (fused zone and vestibulum) usually has a distinctive shape not only in species, but also in groups of closely related genera. The number of marginal pore canals is often constant, usually 20, but is sometimes reduced to 15. Homologies are often difficult to make because of the very narrow fused zone near to the anterior margin and other areas. In order to facilitate orientation we selected two easily recognisable reference points: canal 10, the largest canal near the atrium area, and canals 13-14, which lie in the posterior third of the ventral margin and which are usually juxtaposed or fused proximally. Useful characters for specific identification are the arrangement and shape of real marginal pore canals, as well as the number and shape of false marginal pore canals. Sometimes false marginal pore canals are quite variable within species, for example in *Brunneostoma*. Occasionally one encounters individuals in which the number and arrangement is different, even between valves of the same specimen.

The hinge in *Paradoxostoma* s. l. is generally regarded as lophodont (Okubo, 1977; Horne & Whittaker, 1985). However, definitions for existing hinge types do not quite accommodate structures found in the Paradoxostomatinae. In many groups the terminal elements of the hinge consist of very delicate structures with vague boundaries, but terminal teeth of varying sizes and shapes are also common. Obviously, further investigation of the hinge structures in the Paradoxostomatinae is needed. In this paper we distinguish two types of hinges: hinges without teeth and hinges with terminal teeth.

There are three frontal scars in the Paradoxostomatinae: the frontal scar of the adductors (formed by a muscle from the endoskeleton), the frontal Md scar (formed by a muscle from the middle part of Md) and the fulcral point (Schornikov, 1993a). The frontal scar of the adductors is small and often difficult to locate because it lies far in front of the adductor muscle scars. The frontal Md scar and the fulcral point vary in position, shape and degree of expression, depending on the structure of Md coxa. In *Acetabulastoma*, *Austroparadoxostoma*, *Echinophilus* and *Boreostoma*, which have a relatively short and thick coxa, these scars are very clear, juxtaposed, and located just in front of the upper adductor muscle scar. In *Brunneostoma* scars are not large, but usually prominent. In *Obesostoma*, which has a very long and thin coxa, scars are hardly discernible above the adductor muscle scars: the fulcral point is located behind, and the frontal Md scar far in front of the adductors. In *Echinositus* the proximal part of the coxa is very short, and there is only one common scar. In many other genera, including the majority described herein, the coxa is of medium length and the fulcral point and the frontal Md scar are very small and indistinct, but the frontal scar of the adductors is comparatively clearly expressed.

Valves in the majority of Paradoxostomatinae are colourless and translucent, but opaque patches are visible in transmitted light in *Bradystoma*. In some genera valves are pale yellow or brown (*Brunneostoma*) in colour depending on the thickness of the epicuticle - the thicker it is, the more intensive the yellow-brown colour. Maybe the intensity also varies with the quantity of chitin in the calcified parts of the valves. The colour of living specimens originates mainly from the pigmented epidermis lining the outer lamella. The shape of the valve, its colour and the arrangement of patches are usually distinctive to many genera and differ in details in closely related species. Sex-based colour polymorphism is not uncommon. According to Hull & Rollinston (2000) males of *Boreostoma*, e.g. *B. variabile* (Baird, 1835), exhibit higher colour polymorphism than females. In *Lanceostoma* and some other groups, males and instars have a dark patch in the dorsomedial area, while females may be completely dark inside. Although peculiarities of colour are useful diagnostic features of living Paradoxostomatinae, pigment patches disintegrate and vanish some hours after the death of the animals. Therefore, it must be borne in mind that pigment patches in figures and descriptions in this paper are only approximate and precise contours can only be defined in living material.

In all known cases, the armature of A1 is 1,2+3,4(1/0)5(2/1)6(2/1)7(4) and the branchial plate of Mx bears 15 plumose rays. We regard both features as distinctive to the subfamily. The armature of A2 is 1(0/1)2(0/2-1m1-1)3(.1.-.1r.-0/1)4(1c1r1c-2c-1c1rc-1c)-4+1c; exopodite 2-3-jointed, often with additional, weakly developed subdivision of the proximal podomere. We consider the division into three podomeres and additional subdivision of the exopodite of A2 an innovation connected with the intensification of the function of this organ. Md: Coxa with or without dorsal seta; armature of palp: Bp (.1.-0/0),1-??+1,2 (.1.1-.1r1-1/1-0/0)3r(4). Mx: Palp similar to 2-jointed appendix or a large seta, rudimentary or absent; armature of first, second and third endites: 2-2c-1; 5-3; 6-3, respectively. First endite usually small, second and third ones long, sub-equal in length, with weakly developed subdivision in middle. In *Acetabulastoma* and *Echinophilus* the second endite is also shorter than the third; and in "*Paradoxostoma*" *maxillulahamatum* Hartmann, 1979 the first and second endites are reduced to small projections. Atriumwards rays have a common base of different lengths in each genera; proximal part usually sclerified with weakly developed subdivision. Rays also subdivided in two parts, except in *Acetabulastoma* and *Echinositus*. In *Echinophilus* the atriumwards rays are reduced to small projections. Armature of basal podomeres of P1, P2, P3: (.1.1c/0), (.1.1-1c/0), (1/0), respectively. In *Bradystoma* the dorsomedial seta of P1 is longer in the female than in the male. Up till now sexual dimorphism of the appendages was unknown in the Paradoxostomatinae. Bo biramous, rami rectangular, anterior one small, differing in form in each genus, in *Echinophilus* reduced to small projections with two plumose rays of different length. Furca of female usually with two setae, anterior one plumose; in *Obesostoma* setae are hypertrophied; in *Bradystoma* the smooth seta is rudimentary; in males of *Pontostoma* both setae are smooth and absent in females; in *Triangulostoma* there is only one smooth seta.

The gonads are usually housed entirely within the body, but in *Bradystoma* ripe eggs enter the duplicature, as in *Oviferocholus* Schornikov, 1981 (Sclerochilini).

In the Paradoxostomatidae the penis has an archaic rounded basal capsule similar to that of the Bythocytheridae. As in the Bythocytheridae, the copulatory processus of most Paradoxostomatinae is dorsally directed. Therefore, we think that this is the original position of the group. We distinguish the following processes in the distal part of the penis: (from dorsal to ventral) dorsodistal process of capsule, dorsodistal prehensile process, dorsodistal and ventrodistal lobes. In the Bythocytheridae the distal lobe bears a sensory seta, which is found on the ventrodistal lobe in Paradoxostomatidae. Bythocytheridae (in particular the Pseudocytherinae) have two dorsodistal prehensile processes on either side of the exit of the copulatory process (or ductus ejaculatorius). Apparently the inner one is transformed into the dorsodistal lobe in the Paradoxostomatinae, and the ventrodistal lobe of Paradoxostomatinae is homologous to the distal lobe of the Bythocytheridae. *Acetabulastoma*, *Boreostoma*, *Bradystoma*, *Calcarostoma*, *Echinositus* and some other Paradoxostomatinae have a dorsal extension of the dorsodistal lobe. A distally directed copulatory processus, as in *Triangulostoma*, may fuse with the ventrodistal lobe. In *Brunneostoma*, which has a long whip-like copulatory processus, the dorsodistal prehensile process is hypertrophied and acuminate, the dorsodistal lobe is reduced to a small projection that is often difficult to locate, and the ventrodistal lobe is slender, ventrally directed. In cases where the copulatory processus is ventrally directed, e.g. in *Boreostoma*, new processes have originated alongside it. Future investigations are necessary to differentiate these processes.

The morphological evolution of the Ostracoda (especially Podocop?) is extremely mosaical. Elements of the soft parts, mainly the appendages (with the exception of those connected with reproduction), evolved by way of reduction. The appendages of genera within families are extremely uniform, usually differing from each other by the reduction of a few elements; innovations are very rare and comparatively insignificant. On the other hand, evolution of the shell and copulatory appendages is mainly characterised by progressive complexity (Schornikov, 1986). This is especially true in the Paradoxostomatinae. At the generic level appendages are very similar, differing only in the degree of reduction in various parts of the antenna, mandible and maxillula. Innovations such as plumose, spinose, some hypertrophy or the particular shape of different elements are useful characters for specific identification. On the other hand, Paradoxostomatinae have developed a completely unique construction of the free margin of the shell; large-scale reconstructions are observed in the structure of the penis; and in *Bradystoma* ripe eggs are housed in the duplicature (normally eggs are retained in the body in the Cytherocopina).

SYSTEMATIC DESCRIPTION

All holotypes and a large number of paratypes are deposited in the Zoological Institute and Zoological Museum, Hamburg (code: ZMH); remaining specimens are deposited in the Museum of Institute of Marine Biology, Far East Branch, Russian Academy of Sciences, Vladivostok (code: MIBM); two paratypes are deposited in the Museum of Royal Belgian Institute of Natural Sciences, Brussels (code: O.C.). All new taxa are described by Schornikov & Keyser, except *Calcarostoma calcaratum* Schornikov & Wouters sp. nov.

Class OSTRACODA Latreille, 1806
Subclass PODOCOPA Sars, 1866
Order PODOCOPIDA Sars, 1866
Suborder CYTHEROCOPINA Gründel, 1967
Family PARADOXOSTOMATIDAE
Brady & Norman, 1889
Subfamily PARADOXOSTOMATINAE Brady & Norman, 1889;
emend. Schornikov, 1993
Genus *Paradoxostoma* Fischer, 1855 s.s.

Type species.–Paradoxostoma dispar Fischer, 1855.

Description.–Shell elongate subovate or ovate, with broadly rounded anterior and posterior margins; weakly inflated or compressed; female slightly higher and larger than male. Hinge without teeth. Fused zone very narrow anteriorly, relatively narrow and even ventrally and posteriorly. Number of marginal pore canals 19-20, canal 20 often not well expressed, canals 13 and 14 usually not fused. Fulcral point and frontal Md scar vague, frontal scar of the adductors clear. Valves colourless, fresh specimens with blue-black transverse bands. Armature of endopodite A2: 1(0/1)2(0/1)3(.1r./1)4(2c), exopodite 3-jointed, with proximal podomere subdivided. Md coxa straight, moderately long, without dorsal seta; armature of palp: Bp, 1,2(1/1)3r(4), apical podomere indistinctly divided from 2nd podomere. Mx palp reduced to rudimentary seta; armature of first, second and third endites: 2, 5, 6 respectively; first endite very small, 4 times shorter than second and third ones. Base of atriumwards rays moderately long, well sclerified. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1c/0; 1/0; third podomere of P3 with strongly spinose anterior margin. Bo biramous, rami rectangular, anterior one small. Furca with two medium setae, anterior seta plumose. Pe with moderately short, dorsally directed copulatory process; proximal part of ductus ejaculatorius unsclerified, long and curved, often looped. Dorsodistal process of capsule not large, dorsodistal prehensile process, dorsodistal and ventrodistal lobes present. Dorsodistal lobe large, lamellar, cuneiform, ventrally directed, sometimes with dorsal extension; ventrodistal lobe lamellar, subovate, dorsally directed, overlapping dorsodistal one.

Remarks.–*Paradoxostoma* s.s. resembles *Lanceostoma* gen. nov. in the structure of Pe, but may be distinguished by the structure of the shell, Md and Mx.

Composition.–9 species: *Paradoxostoma dispar* Fischer, 1855; *Paradoxostoma hibernicum* Brady, 1868; *Paradoxostoma flaccidum* Schornikov, 1975; *Paradoxostoma rarum* Müller, 1894; *Paradoxostoma rotundatum* Müller, 1894; *Paradoxostoma sarniense* Brady, 1868; *Paradoxostoma tauricum* Schornikov, 1965; *Paradoxostoma trieri* Horne & Whittaker, 1985; *Paradoxostoma wirtzi* sp. nov.

Distribution.–Temperate and subtropical waters of the NE Atlantic and NW Pacific (Japan).

Paradoxostoma dispar Fischer, 1855
(Fig. 2; Pl. 1, Fig. 1)

1855 *Paradoxostoma dispar* sp. nov. Fischer, p. 654-656; Pl. 2 (20), Figs 1-8.
?1911 *Paradoxostoma hibernicum* Brady, 1868. Brady, p. 595.

Neotype.–ZMH K-40437, male dry with soft parts, not dissected; Madeira, Sample 2.

Neoparatypes.–ZMH K-40438-40445; MIBM 8722. 10*f, 9*2vm, 4*1vA-1 (Sample 1); 17*f, 11*m, 11*1vA-1, 8*A-2, 3*A-3, 4*A-4, 4*A-5, 2*A-6 (Sample 2); 4*f, 7*m, 8*A-1, 4*A-2 (Sample 3); 5*f, 1*1vA-1 (Sample 4).

Description.–Shell subovate, weakly inflated; ratio between length, height and width in female = 43:23:14; male = 43:22:14. Anterior and posterior margins broad and evenly rounded, dorsal margin weakly convex, ventral margin convex in posterior part and slightly concave in atrium area. Length of females and males 0.56-0.60 mm. Length ratio between distal podomeres of A1 = 21:15:32:7:4; length ratio between podomeres of endopodite A2 and apical claws = 14:21:26:4:8:5. Knee seta of P1 a little longer than second podomere, one in P2 half as long as the second podomere. Pe with comparatively large dorsodistal process of capsule, length of dorsodistal prehensile process almost equal to height of dorsodistal lobe. Acuminate end of dorsodistal lobe with smooth ledge on inner margin. Proximal part of ductus ejaculatorius looped.

Remarks.–The shell of the type species of *Paradoxostoma* s. s. resembles *P. hibernicum* in outline, but differs in details of shell structure and Pe. Apparently Brady (1911) thought that *P. dispar* from the littoral zone of Madeira was *Paradoxostoma hibernicum* Brady, 1868 (see: Introduction).

Paradoxostoma sarniense Brady, 1868
(Fig. 3; Pl. 1, Fig. 2)

1868 *Paradoxostoma sarniense* sp. nov. Brady, p. 460, Pl. 35, Figs. 26-29, Pl. 40, Fig. 9.
1889 *Paradoxostoma hibernicum* Brady. Brady & Norman (pars), p. 232, Pl. 21, Fig. 17 only (non Brady, 1868).
1957 *Paradoxostoma hibernicum* Brady. de Vos, p. 60, 62, Pl. 24, Figs. 1a-h.
1959 *Paradoxostoma insigne* sp. nov. Hartmann, p. 169, Figs. 26-31; nov. syn.
1969 *Paradoxostoma sarniense* Brady. Yassini, p. 119, Pls. 15, 17.
1985 *Paradoxostoma sarniense* Brady. Horne & Whittaker, p. 177, Figs. 28A-H, 29A-I, 42C-D.
1989 *Paradoxostoma sarniense* Brady. Athersuch, Horne & Whittaker, p. 300, Figs. 12D, E; 130.

Material.–ZMH K-40446- 40452; MIBM 8723. 1*f, 4*2vm, 2*2vA-1 (Sample 1); 10*f, 7*m, 1*A-2 (Sample 2); 2*1vf, 7*m, 1*A-1 (Sample 3).

FIGURE 2–*Paradoxostoma dispar* Fischer, 1855. Male, valves, A1, A2, Md, P2, Pe, ZMH K-40441; P1, Bo, ZMH K-40442b; female, RV, Ab, Mx, P3, ZMH K-40443; F, PeF, original illustrations from Fischer (1855, Pl. 2, Figs. 2, 4). 7-20, marginal pore canals. Scale bars = 0,2 mm (valves); 0,1 mm (P1-3, Ab); 0,05 mm (all others).

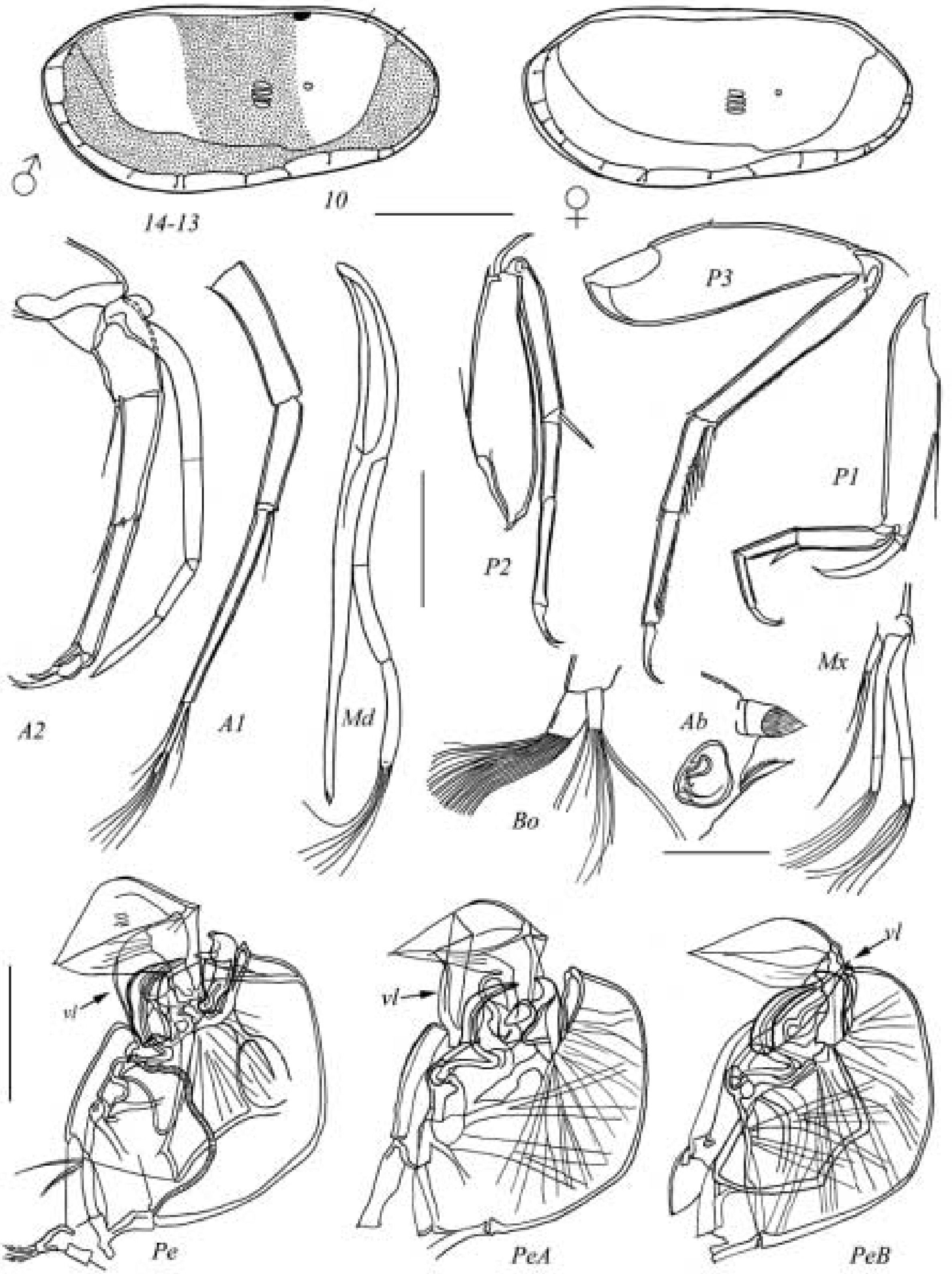


FIGURE 3–*Paradoxostoma sarniense* Brady, 1868. Male, RV, A2, Bo, Pe, Md, ZMH K-40446; A1, P1-P3, ZMH K-40447b; female RV, Mx, ZMH K-40448; Ab, ZMH K-40449b; *Paradoxostoma insigne* Hartmann, 1959. PeA with cover slip, PeB without cover slip (syntypes, ZMH K-28042). Scale bars = 0,2 mm (valves); 0,05 mm (all others).

Remarks.–Our specimens agree well with the description by Horne & Whittaker (1985). Length of females 0.58-0.60 mm, of males 0.56-0.60 mm. A study of the syntypes of *P. insigne* (ZMH-28042) disclosed that Hartmann's (1959: 169-171, Figs. 26, 27, 30) illustrations of the male valve and penis are not exact because the valve was decalcified and the penis was drawn without a cover slip. Our figures (Figs. 3 PeA & B) show that *Paradoxostoma insigne* Hartmann, 1959 is a synonym of *Paradoxostoma sarniense* Brady, 1868.

Paradoxostoma wirtzi sp. nov.
(Fig. 4 A; Pl. 1, Fig. 3)

Holotype.–ZMH K-40453a, b, male; Madeira, Sample 2.

Derivation of name.–After Dr. Peter Wirtz, who collected the samples.

Description.–Shell elongate subovate, weakly inflated; ratio between length, height and width male = 24:11:8. Anterior margin cut off in upper part, posterior margin wide and evenly rounded, dorsal margin gently arched, ventral margin almost straight. Length of male 0.48 mm. Length ratio between distal podomeres of A1 = 14:20:5:4; length ratio between podomeres of endopodite A2 and apical claws = 12:16:16:4:7:5. Knee seta of P1 equal to second podomere, one in P2 shorter than 1/3 second podomere. Pe with very small dorsodistal process of capsule, dorsodistal prehensile process large and broad. End of dorsodistal lobe acuminate beak-like. Proximal part of ductus ejaculatorius looped.

Remarks.–The new species resembles *P. rarum* Müller, 1894 but clearly differs in the structure of shell and Pe.

Genus *Paradoxostoma* Fischer, 1855 s. l.
Paradoxostoma planum Müller, 1894
(Fig. 4 B)

1894 *Paradoxostoma planum* sp. nov. Müller, p. 314, Pl. 23, Figs. 19, 17.

1912 *Paradoxostoma planum* Müller. Müller, p. 284.

Non 1988 *Paradoxostoma planum* Müller. Ruan & Hao, p. 338, Pl. 60, Figs. 26-28.

Non 1988 *Paradoxostoma planum* Müller. Ruan & Hao, p. 338, Pl. 60, Figs. 26-28.

Material.–ZMH K-40454a, b, 1 female shell with remains of appendages; Madeira, Sample 3.

Remarks.–Our specimen agrees well with the description by Müller (1894), however, it is significantly smaller (length 0.38 mm) than indicated by Müller from the Gulf of Naples (length 0.44-0.50 mm). Based on peculiarities of the shell and Pe structure, *P. planum* clearly belongs to a new genus. However, owing to the lack of knowledge concerning morphological details of this species, it is provisionally left in *Paradoxostoma* s. l.

Genus *Lanceostoma* gen. nov.

Type species.–*Lanceostoma tenerifense* sp. nov. here designated.

Derivation of name.–A reference to the lance-like shell of this paradoxostomatine genus.

Description.–Shell lanceolate, with narrowly rounded anterior and posterior margins and weak caudal process above mid-height; weakly inflated or compressed; female slightly higher and larger than male. Hinge without teeth. Fused zone narrow anteriorly, very broad ventrally and posteriorly, with characteristic posteroventral embayment. Number of marginal pore canals 20, canals 13 and 14 fused. Fulcral point and frontal Md scar vague, frontal scar of adductors clear. Valves yellow or pale-brown; fresh specimens of males and instars with dark patch in dorsomedial area, female valves dark for the most part or fully dark inside. Armature of endopodite A2: 1(0/1)2(0/1)3(.1r./1)4(2c), exopodite 3-jointed. Md coxa straight, moderately long, without dorsal seta; armature of palp: Bp+1,2(1/1)3r(4); apical podomere distinctly divided from 2nd podomere. Mx palp absent; armature of first, second and third endites: 1r1, 5, 6 respectively; first endite very small, second and third ones long. Base of atriumwards rays long, well sclerified. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1c/0; 1/0. Bo biramous, rami rectangular, anterior one small. Furca with two medium setae, anterior seta plumose. Pe with moderately long, dorsally directed copulatory process; proximal part of ductus ejaculatorius unsclerified and curved. Dorsodistal prehensile process present. Dorsodistal lobe large, lamellar, cuneiform, ventrally curved; ventrodistal lobe lamellar, subovate, dorsally directed, overlapping dorsodistal lobe.

Remarks.–The new genus resembles *Paradoxostoma* s. s. in the structure of Pe, but differs strongly in the structure of shell, Md and Mx. A great number of species from different parts of the World Ocean superficially resemble *Lanceostoma* but differ in the structure of the appendages and Pe.

Further study on the morphology and classification of this large complex of apparently closely related species groups is needed.

Composition.–4 species: *Lanceostoma intermedium* (Müller, 1894) nov. comb.; *Lanceostoma parallelum* (Müller, 1894) nov. comb.; *Lanceostoma taeniatum* (Müller, 1894) nov. comb.; *Lanceostoma tenerifense* sp. nov.

Distribution.–Temperate and subtropical waters of NE Atlantic.

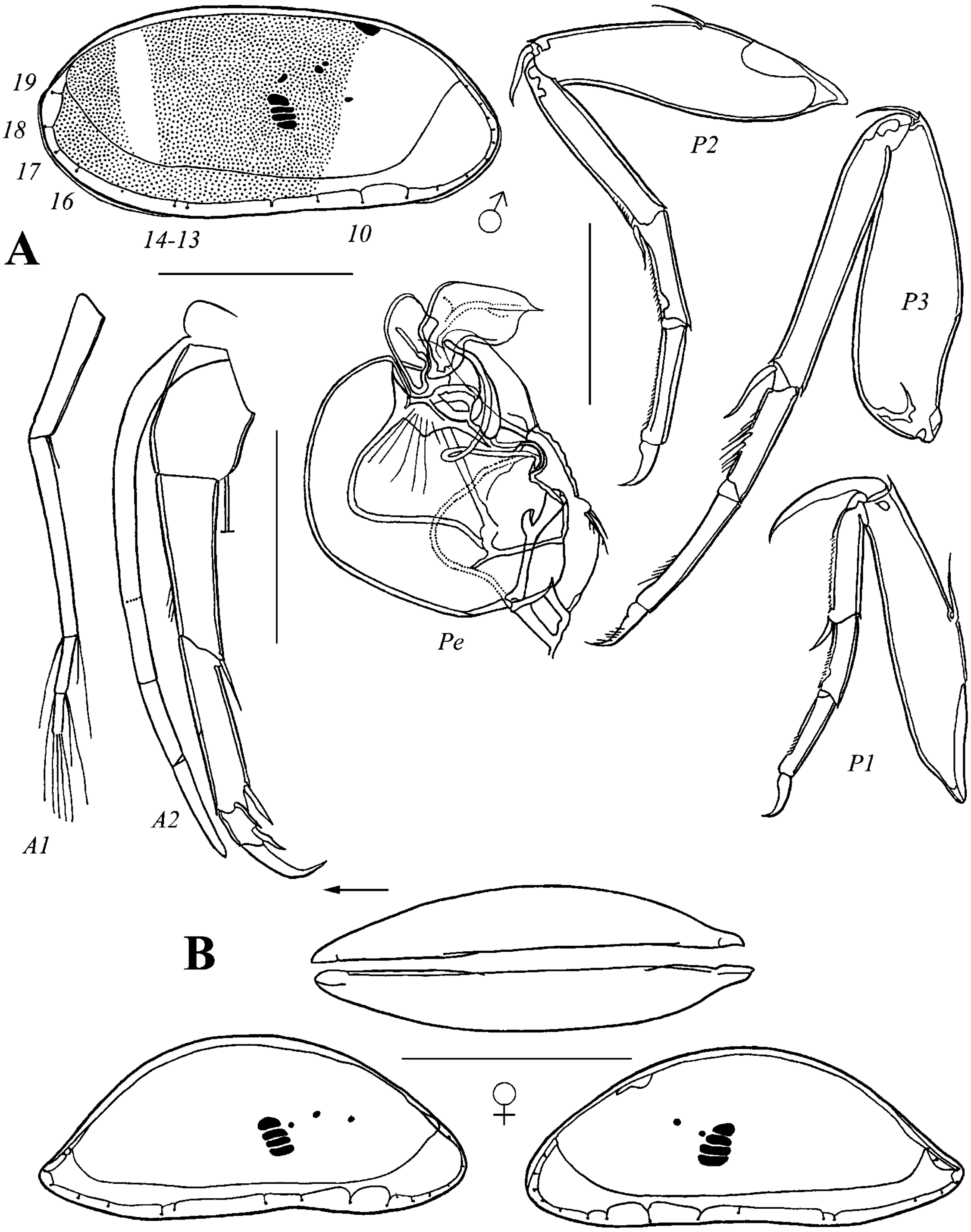


FIGURE 4–A, *Paradoxostoma wirtzi* sp. nov. Male, holotype. B, *Paradoxostoma planum* Müller, 1894. Female, ZMH K-40454a. Scale bars = 0,2 mm (valves); 0,05 mm (all others).

Lanceostoma tenerifense sp. nov.
(Fig. 5; Pl. 1, Fig. 4)

Holotype.–ZMH K-40455a, b, male; Tenerife Is., Sample 1.

Paratypes.–ZMH K-40456- 40458, 1vf, 3*m, 1*A-1 (Sample 1); ZMH K-40459-40460, 3*f, 3*m (Sample 2); ZMH K-40461, MIBM 8724, 87*1s2vf, 47*m, 48*2vA-1, 38*1vA-2, 4*A-3, 1*A-4 (Sample 3); 66*f, 71*m, 42*1vA-1, 34*A-2, 11*A-3 (Sample 4).

Derivation of name.–For the island where the type was collected.

Description.–Shell widely lanceolate, weakly inflated; ratio between length, height and width female = 27:12:8, in male = 27:11:6. Anterior extremity rounded, posterior more acuminate, caudal process almost at mid-height; dorsal margin moderately convex, slightly more so in females than males; ventral margin convex in posterior part, slightly concave in atrium area. Line of concrescence fused to inner margin in atrium area, in front and behind marginal pore canal pair 13-14. Length of females and males 0.48-0.54 mm. Length ratio between distal podomeres of A1 = 19:15:22:8:4; length ratio between podomeres of endopodite A2 and apical claws = 12:16:20:5:10:5. Knee seta of P1 a little longer than second podomere, acuminate beak-like; one in P2 a little shorter than half the second podomere. Pe with small, thin dorsodistal prehensile process, and comparatively short but very thick copulatory process.

Remarks.–The new species resembles *L. intermedium* (Müller, 1894), but clearly differs in the structure of shell and Pe.

Genus *Calcarostoma* gen. nov.

Type species.–*Calcarostoma calcaratum* Schornikov & Wouters sp. nov. here designated.

Derivation of name.–L. *calcar*, spine. A reference to the small spine on the ventral margin of this paradoxostomatine genus.

Description.–Shell elongate, subovate, with broadly rounded anterior and posterior margins and small posteroventral spinula; weakly inflated; female slightly larger than male. Hinge without teeth. Fused zone narrow anteriorly, even and relatively narrow or moderately broad ventrally and posteriorly. Number of marginal pore canals 20, canals 13 and 14 usually not fused. Fulcral point located above upper adductor muscle scar, frontal Md scar and frontal scar of adductors clear. Valves colourless, fresh specimens with dark-grey transverse bands or completely dark-grey inside. Armature of endopodite A2: 1(0/1)2(0/1)3(0/1)4(2c), exopodite 3-jointed. Md coxa straight, moderately long, with dorsal seta; armature of palp: Bp+1,2,3r(4), apical podomere distinctly divided from 2nd podomere. Mx palp reduced to rudimentary seta; armature of first, second and third endites: 1r1, 5, 6 respectively; first endite medium sized, second and third ones long. Base of atriumwards rays moderately long, well sclerified. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1c/0; 1/0; third podomere of P3 with spinose anterior margin. Bo biramous, rami rectangular, anterior one slender. Furca with two medium setae, anterior seta plumose. Pe with dorsally directed copulatory process; proximal part of ductus ejaculatorius unsclerified and looped or fully sclerified. Dorsodistal prehensile process present. Dorsodistal lobe large, lamellar, cuneiform, ventrally curved, with dorsal extension; ventrodistal lobe small, lamellar.

Remarks.–The new genus resembles *Paradoxostoma* s. s. in the structure of shell, but is easily distinguished by the posteroventral spinula and differences in the structure of Md and Mx.

Composition.–*Calcarostoma calcaratum* sp. nov. and *Calcarostoma denticulatum* (Okubo, 1977) nov. comb.

Distribution.–Subtropical and tropical waters of the NE Atlantic (Madeira and Cape Verde Is.) and NW Pacific (Japan).

Calcarostoma calcaratum Schornikov & Wouters sp. nov.
(Fig. 6; Pl. 1, Fig. 5)

Holotype.–ZMH K-40462a, b, female; Madeira, Sample 3.

Paratypes.–O.C. 2768a, b; O.C. 2769a, b, 2*m; Baia das Gatas, São Vicente (Cape Verde Is.)

Derivation of name.–L. *calaratus*, spinose.

Description.–Shell comparatively wide-subovate, weakly inflated; ratio between length, height and width in female = 26:13:10, in males = 25:12:9. Anterior margin cut off in upper part, posterior margin broad and evenly rounded, dorsal margin weakly convex, ventral margin convex in the posterior part and slightly concave in atrium area. Length of female 0.52 mm, males 0,48-0,50 mm. Length ratio between distal podomeres of A1 = 16:15:23:6:3; length ratio between podomeres of endopodite A2 and apical claws = 13:17:23:5:8:5. Knee seta of P1 equal to second podomere, one in P2 shorter than 1/3 second podomere. Pe with short copulatory process; proximal part of ductus ejaculatorius unsclerified and looped.

Remarks.–Type species differs from the second known species of the genus, *C. denticulatum* (Okubo, 1977), in the structure of the shell.

Genus *Bradystoma* gen. nov.

Type species.–*Bradystoma bradyforme* sp. nov. here designated.

Derivation of name.–A paradoxostomatine genus in honour of G. S. Brady.

Description.–Shell subrhomboidal, with broadly rounded anterior margin strongly cut off in upper part, caudal process not large but well-defined, above mid-height; strongly inflated and thick-walled; female slightly higher and larger than male. Hinge with terminal teeth. Fused zone narrow and even. Ca. 15 distinct

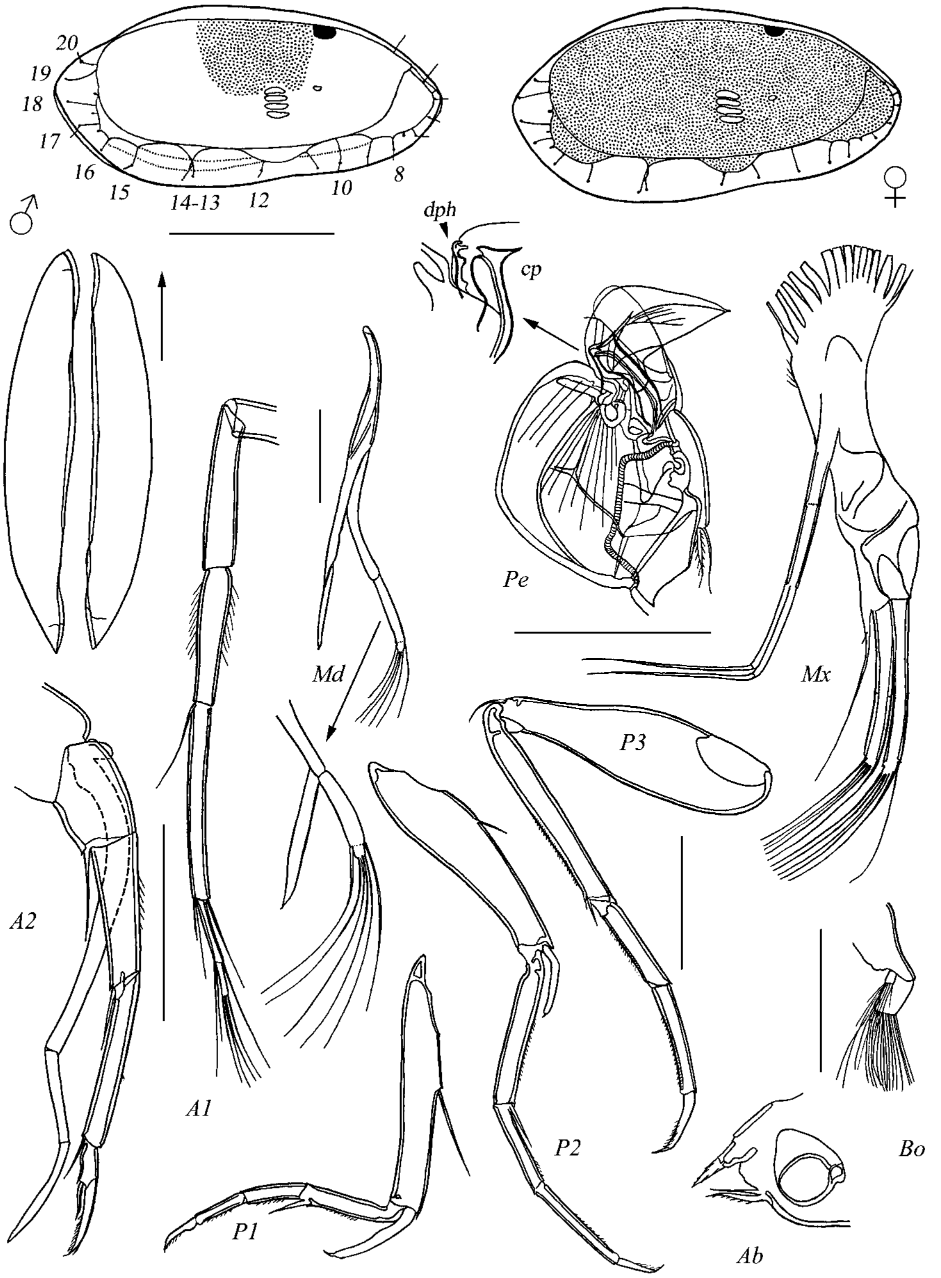


FIGURE 5–*Lanceostoma tenerifense* sp. nov. Male, valves, A2, Mx, P1, Pe, holotype; A1, Md details, P2, P3, Bo, Pe details, ZMH K-40456; female RV, ZMH K-40457; Md, Ab, ZMH K-40460b. Scale bars = 0,2 mm (valves & Bo); 0,05 mm (all others).

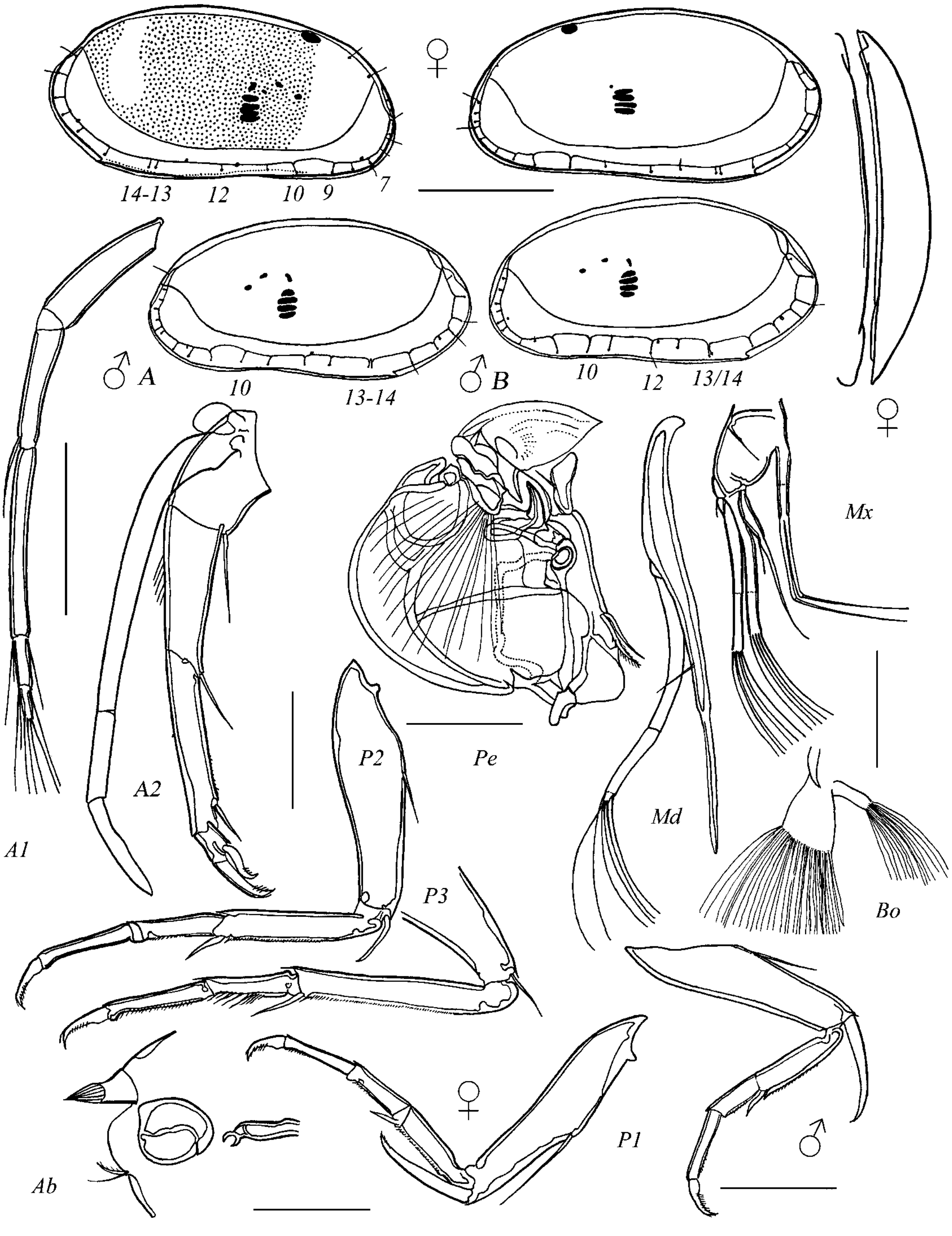


FIGURE 6–*Calcarostoma calcaratum* Schornikov & Wouters sp. nov. Female, valves, A1, A2, P1-P3, Ab, Mx, holotype. Male A, LV, Pe, P1, Bo, O.C. 2769; B, LV, Md, O.C. 2768. Scale bars = 0,2 mm (valves), 0,05 mm (all others).

marginal pore canals, canals 1-3, 14 and 20 not well expressed. Fulcral point immediately above anterior margin of upper adductor muscle scar, frontal Md scar not far in front and above it, frontal scar of adductors vague. Valves yellow or pale-brown, with opaque patches; fresh specimens strongly pigmented, olive- or chestnut-brown, with indistinct transverse bands. Armature of endopodite A2: 1(0/1)2(0/2)3(.1r./1)4(1c1r?), exopodite 3-jointed. Md coxa straight or slightly curved, moderately long, without dorsal seta; armature of palp: Bp,1,2(.1r1/1)3r(4), apical podomere indistinctly divided from 2nd podomere. Mx palp similar to large seta; armature of first, second and third endites: 2, 5, 6 respectively; first endite large, not shorter than one-half of second and third endites. Base of atriumwards rays moderately short, proximal part sclerified, distal part very short, unsclerified. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1c/0; 1/0; dorsomedial seta of basal podomere P1 in female longer than in male. Bo biramous, rami rectangular, anterior one comparatively long, subdivided in two parts**.** Furca with rudimentary smooth seta. Ripe eggs housed in the duplicature. Pe with short, dorsally directed copulatory processus; ductus ejaculatorius fully sclerified. Dorsodistal lobe with bicuspidate dorsoproximal extension and lamellar extension ventrally; ventrodistal lobe distally directed, very long and narrow.

Remarks.–The new genus differs from other genera of the subfamily by structure of shell, A2, Md, Mx and by the presence of ripe eggs in the duplicature.

Composition.–*Bradystoma bradyforme* sp. nov. and *Bradystoma bradyi* (Sars, 1928) nov. comb.

Distribution.–Temperate and subtropical waters of the NE Atlantic.

Bradystoma bradyforme sp. nov.
(Fig. 7-8; Pl. 1, Fig. 6)

Holotype.–ZMH K-40463a, b, male; Madeira, Sample 3.

Paratypes.–ZMH K-40464- 40471; MIBM 8725. 1*f, 1*m (Sample 2); 9*f, 11*m (1 pair in copulation), 10*3vA-1, 15*1vA-2, 12*1vA-3, 10*A-4, 4*1vA-5, 1*A-6 (Sample 3); 1*m, 1vA-1 (Sample 4).

Derivation of name.–L. From the resemblance of this species to *B. bradyi* (Sars, 1928).

Description.–Shell subrhomboidal, with comparatively weakly convex dorsal and widely rounded anterior margin; ratio between length, height and width in female = 29:16:15, in male = 56:29:26. Length of females 0.58-0.62 mm, males 0.56-0.58 mm. Length ratio between distal podomeres of A1 = 21:17:33:10:4; length ratio between podomeres of endopodite A2 and apical claws = 18:20:22:5:8:4. Knee seta of P1 a little shorter than the second podomere. Pe with comparatively small dorsoproximal extension of dorsodistal lobe and large ventrodistal lobe.

Remarks.–The type species differs from the second known species of the genus, *B. bradyi* (Sars, 1928), in the structure of shell and Pe (Fig. 7).

Genus *Pontostoma* gen. nov.

Type species.–*Pontostoma paraponticum* sp. nov. here designated.

Derivation of name.–L. *pons, pontis* = bridge + stoma, belonging to the Paradoxostomatinae.

Description.–Shell lunate, compressed, greatest height close to mid-length, dorsal margin evenly convex, ventral margin almost straight, anterior and posterior broadly rounded, almost equal, but sometimes more narrowly rounded posteriorly. Females higher and larger than males. Hinge without teeth. Fused zone narrow anteriorly and relatively broad ventrally and posteriorly. 20 marginal pore canals, canals 13 and 14 usually fused. Fulcral point located immediately above anterior margin of upper adductor muscle scar, frontal Md scar not far in front it, frontal scar of adductors vague. External shell surface smooth, but fine tubulae visible meandering inside epicuticle. Valves colourless, males and instars of fresh specimens with very broad blue-black transverse band in the middle, females sometimes partly or completely dark inside. Armature of endopodite A2: 1(0/1)2(0/2)3(.1r./1)4(1c), exopodite 3-jointed, proximal podomere very long, 2nd podomere very short. Md coxa straight, moderately long, without dorsal seta; palp long, extending beyond end of coxa, armature of palp: Bp,1,2(1/1)3r(4); apical podomere distinctly divided from 2nd podomere. Mx palp similar to medium-sized seta; armature of first, second and third endites: 2, 5, 6 respectively; first endite medium-sized, second and third ones long. Proximal part of base of atriumwards rays very short, sclerified, distal part long or short. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1c/0; 1/0. Bo biramous, rami rectangular, anterior one small. Furca in female absent, male with 2 smooth setae. Pe with moderately long, dorsally directed copulatory processus; ductus ejaculatorius fully sclerified. Dorsodistal process of capsule large, lamellar. Dorsodistal prehensile process overlapping capsule, often serrated on outer margin. Dorsodistal lobe lamellar, rounded or subtriangular, ventrally curved. Homologue to ventrodistal lobe not established.

Remarks.–The new genus resembles *Calcarostoma* gen. nov. in the outline of the shell, but differs strongly in the absence of a posteroventral spinula and in the structure of A2, Md and Mx. The new genus partly corresponds to the *arcuatum*-group established by Hartmann (1978), but not all species recorded in that group are included in the new genus.

Composition.–11 species: *Pontostoma arcuatum* (Hartmann, 1964) nov. comb.; *Pontostoma atlanticum* sp. nov.; *Pontostoma honssuense* (Schornikov, 1975) comb. nov. = *Paradoxostoma lunatum* Okubo, 1977 nov. syn.; *Pontostoma moonga* (Behrens, 1991) nov. comb.; *Pontostoma ornatum* (Hartmann, 1954) nov. comb.; *Pontostoma paenearcuatum* (Hartmann, 1978) nov. comb.; *Pontostoma paraponticum* sp. nov.; *Pontostoma ponticum* (Klie, 1942) nov. comb.; *Pontostoma pulche*

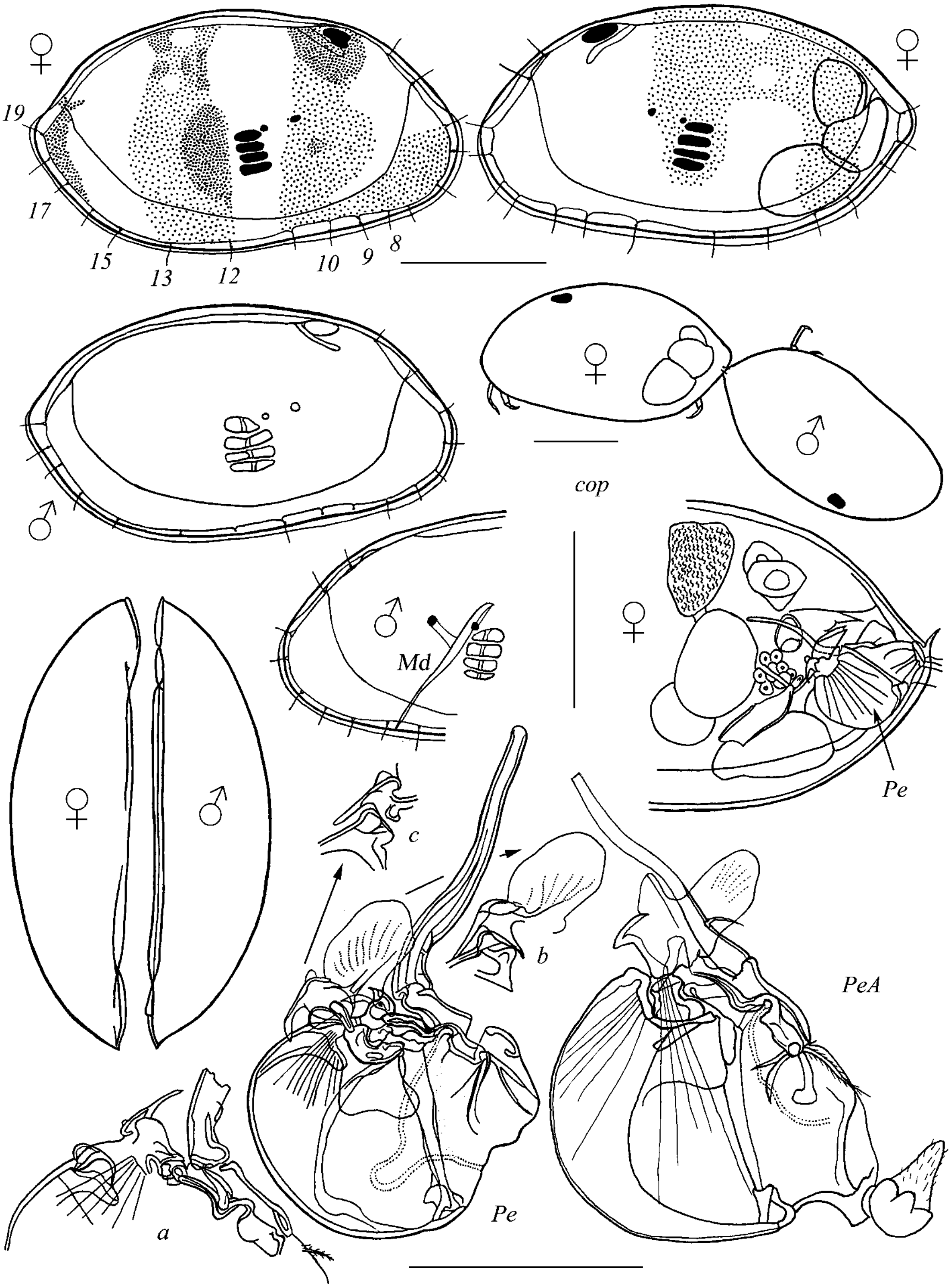


FIGURE 7–*Bradystoma bradyforme* sp. nov. Female, RV with epidermal colour patches, LV with opaque patches and ripe eggs inside duplicature, ZMH K-40470; male, valves, Pe, Pe detail a, holotype; Pe details b, c, ZMH K-40465b; cop = copulation position, Pe in female (ZMH K-40467), Md, frontal Md scar and fucral point in male (ZMH K-40468). *Bradystoma bradyi* (Sars, 1928) from Abereiddy Bay, S. Wales, PeA. Scale bars = 0,2 mm (valves); 0,1 mm (all others).

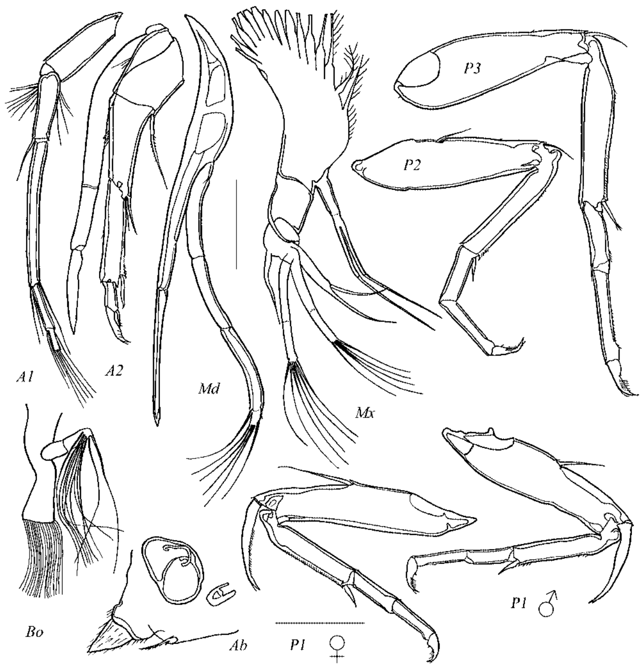


FIGURE 8–*Bradystoma bradyforme* sp. nov. Male, A2, Md, Mx, P1, P2, Bo, holotype; A1, ZMH K-40465b; female, P1, P3, Ab, ZMH K-40466b. Scale bars = 0,05 mm.

llum (Sars, 1866) nov. comb.; *Pontostoma striatum* (Müller, 1894) nov. comb.; *Pontostoma pararcuatum* (Hartmann, 1978) nov. comb.

Distribution.–Temperate and subtropical waters of NE Atlantic, Red Sea, nearshore of Japan and Australia.

Pontostoma paraponticum sp. nov.
(Fig. 9; Pl. 1; Fig. 7)

Holotype.–ZMH K-40472a, b, male; Madeira, Sample 3.

Paratypes.–ZMH K-40473- 40477; MIBM 8726. 2*f (Sample 2); 17*1sf, 7*m, 7*A-1, 10*A-2, 4*A-3, 1*A-4 (Sample 3); 9*1sf, 13*m, 9*A-1, 9*A-2, 3*A-3 (Sample 4).

Derivation of name.–From the resemblance of this species to *P. ponticum* (Klie, 1942).

Description.–Shell subovate lunate, compressed; ratio between length, height and width in female = 52:23:12, in male = 24:11:5. Anterior and posterior margins very widely and evenly rounded, dorsal margin weakly convex, ventral one almost straight, slightly concave in atrium area. Length of females 0.52-0.58 mm, males 0.48-0.50 mm. Length ratio between distal podomeres of A1 = 20:17:18:5:5; length ratio between podomeres of endopodite A2 and apical claw = 12:20:19:6:9. Knee seta of P1 a little longer than the second podomere, one in P2 half as long as second podomere. Pe with comparatively small dorsodistal lobe with narrowly rounded end.

Remarks.–The new species resembles *P. ponticum* (Klie, 1942), but clearly differs in the structure of shell and Pe.

Pontostoma atlanticum sp. nov.
(Fig. 10; Pl. 1, Fig. 8)

Holotype.–ZMH K-40478a, b, male; Madeira, Sample 4.

Paratype.–ZMH K-40479a, b, female; Madeira, Sample 4.

Derivation of name.–A reference to the occurrence of this species in the Atlantic Ocean.

Description.–Shell subovate lunate, compressed; ratio between the length, height and width in female = 32:15:10, in male = 29:13:8. Anterior and posterior margins very widely and evenly rounded, dorsal margin moderately convex, ventral one almost straight, slightly concave in atrium area. Length of female 0.64 mm, male 0.58 mm. Length ratio between distal podomeres of A1 = 23:18:21:5:4; length ratio between podomeres of endopodite A2 and apical claw = 11:19:19:5:8. Knee seta of P1 a little longer than the second podomere, one in P2 a little shorter than half the second podomere. Pe with large subtriangular dorsodistal lobe.

Remarks.–The new species resembles *P. paraponticum* sp. nov., but clearly differs in the structure of shell and Pe

Genus *Triangulostoma* gen. nov.

Type species.–*Triangulostoma madeirense* sp. nov. here designated.

Derivation of name.–Referring to the triangular shell of this paradoxostomatine genus.

Description.–Shell subtriangular, with greatest height close to mid-length, dorsum highly arched to angulate, narrowly rounded anterior and posterior margins; inflated. Females proportionally higher than males. Hinge with terminal teeth. Fused zone narrow anteriorly, very broad in isthmus area and posteriorly, relatively broad or very narrow in posterior part of ventral margin. 19-20 marginal pore canals, canal 20 often not well expressed; canal 11 directed anteriorly, canals 13 and 14 not fused. Fulcral point and frontal scar of adductors vague, frontal Md scar small, not far in front and above upper adductor muscle scar. Valves pale-brown; fresh specimens of males and ins-

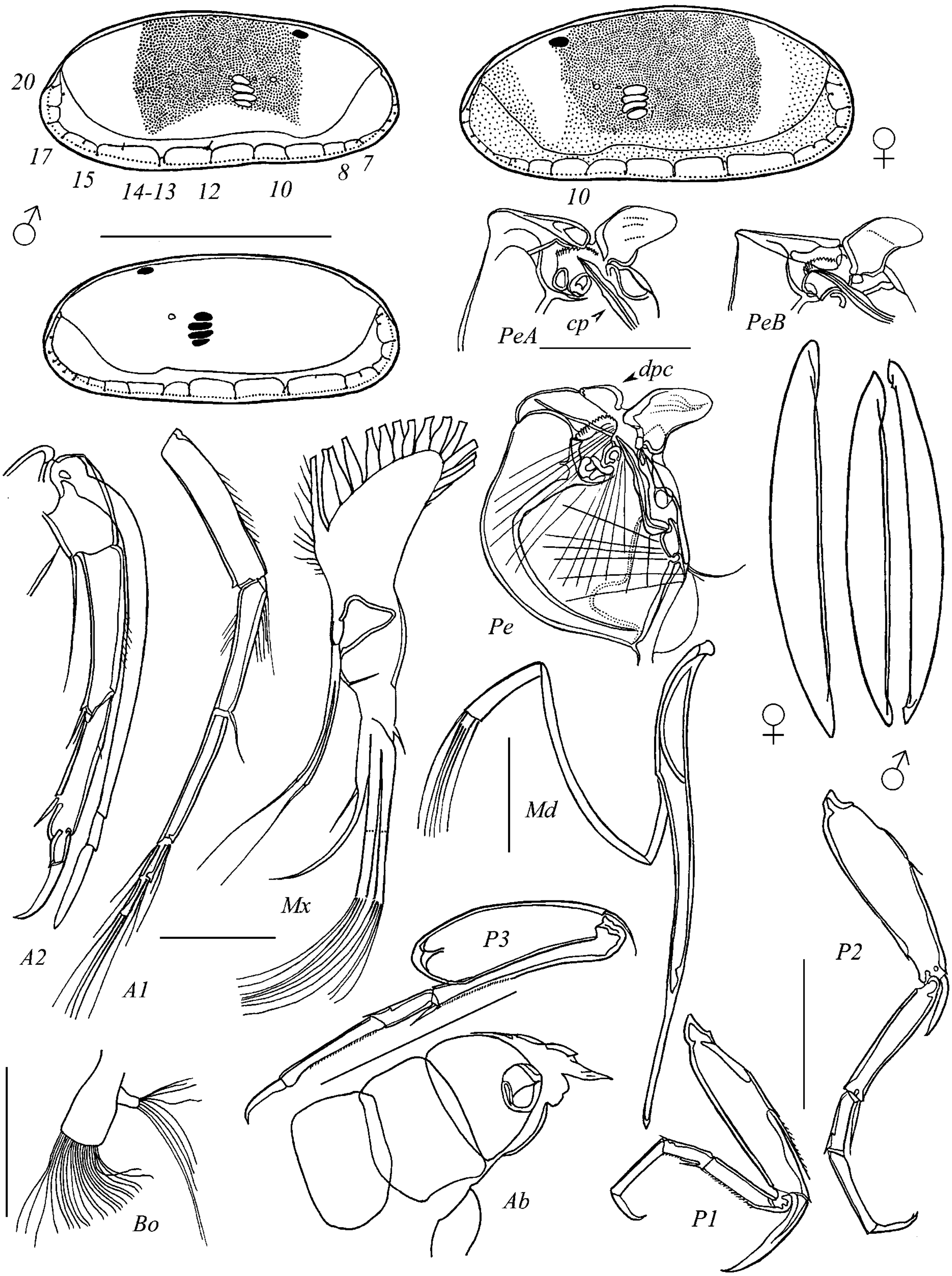


FIGURE 9–*Pontostoma paraponticum* sp. nov. Male RV, A1, A2, Md, P1-P3, Bo, Pe, holotype; male LV, ZMH K-40476a; Mx, Pe details A, B (different dpc positions on slides), ZMH K-40473b; female LV, ZMH K-40474; Ab with ripe eggs, ZMH K-40475b. Scale bars = 0,3 mm (valves); 0,03 mm (A1, A2, Mx, Md); 0,1 mm (all others).

tars with dark patch in dorsomedial area, females usually completely dark inside of valve. Armature of endopodite A2: 1(0/1)2(0/1)3(0/1)4(1c), exopodite 2-jointed, proximal podomere very long. Md coxa very short and thick, without dorsal seta; armature of palp: Bp+1,2(.1.1/1)3r(4); apical podomere distinctly divided from 2nd podomere. Mx palp absent; armature of first, second and third endites: 2, 5, 6 respectively; first endite small, second and third ones long. Base of atriumwards rays short. Armature of basal podomeres of P1, P2, P3: .1.1c/0; .1.1/0; 1/0. Bo biramous, rami rectangular, anterior one very small. Furca with 1-2? smooth seta. Pe with moderately short, distally directed copulatory process fused to ventrodistal lobe; ductus ejaculatorius fully sclerified.

Remarks.–The new genus is easily differentiated from other genera of the subfamily by its subtriangular, inflated shell, 2-jointed exopodite of A2, structure of Md, Mx, furca and Pe with copulatory process fused to ventrodistal lobe.

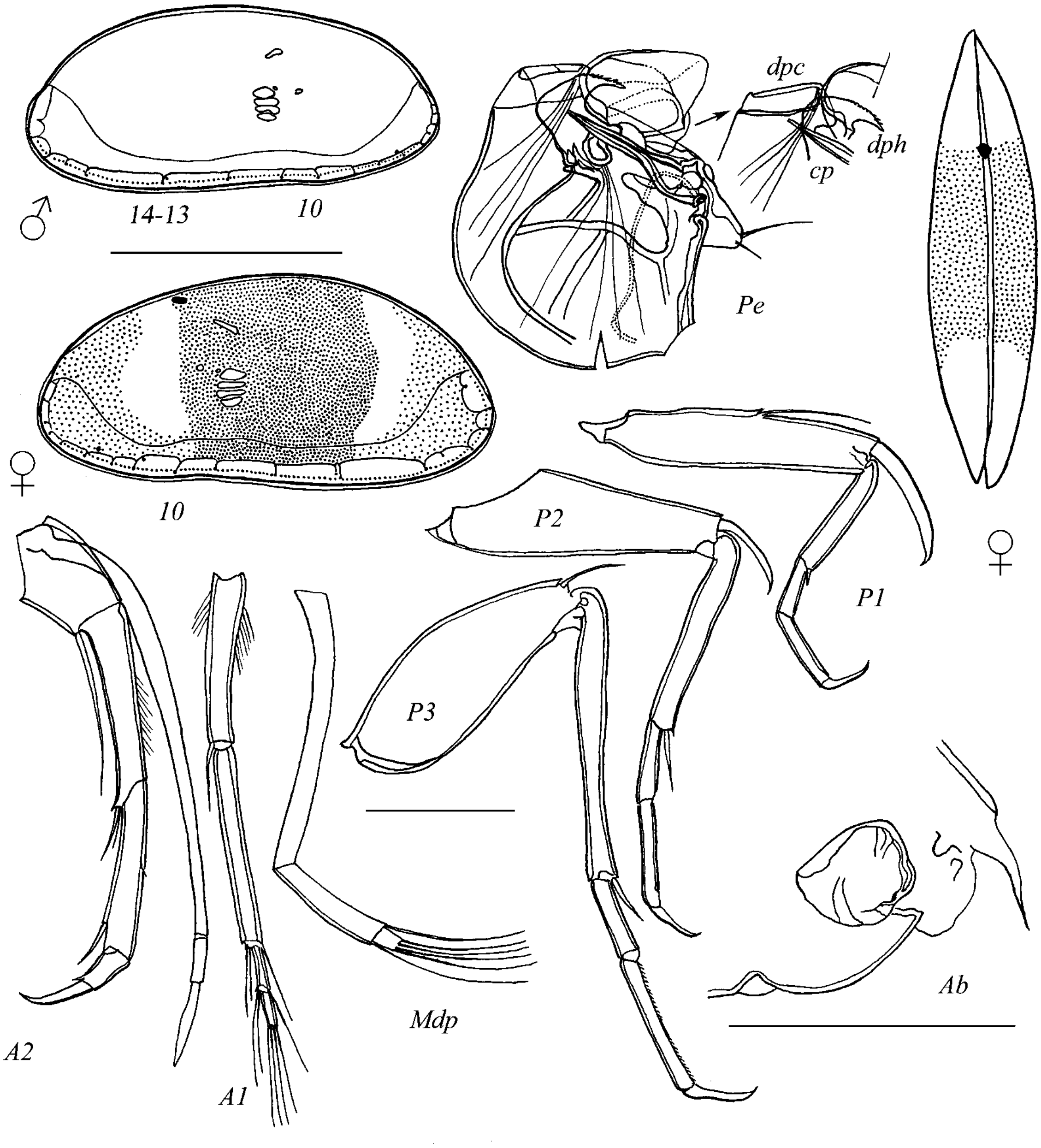


FIGURE 10–*Pontostoma atlanticum* sp. nov. Female LV, Ab, ZMH K-40479; all others, holotype. Scale bars = 0,3 mm (valves); 0,1 mm (Ab); 0,04 mm (all others).

Composition.–*Triangulostoma gibberum* (Schornikov, 1975) comb. nov. and *Triangulostoma madeirense* sp. nov.

Distribution.–Subtropical waters of NE Atlantic and NW Pacific (Japan).

Triangulostoma madeirense sp. nov.
(Fig. 11; Pl. 1, Fig. 9)

Holotype.–ZMH K-40480a, b, male; Madeira, Sample 3.

Paratypes.–ZMH K-40481- ZMH K-40483; MIBM 8727. Madeira, 2*f, 2*m (Sample 2); 22*2vf, 19*1vm, 1*A-1, 1*A-2 (Sample 3); 20*2vf, 15*m, 1*A-1, 2*A-2 (Sample 4).

Derivation of name.–For Madeira, where the type occurs.

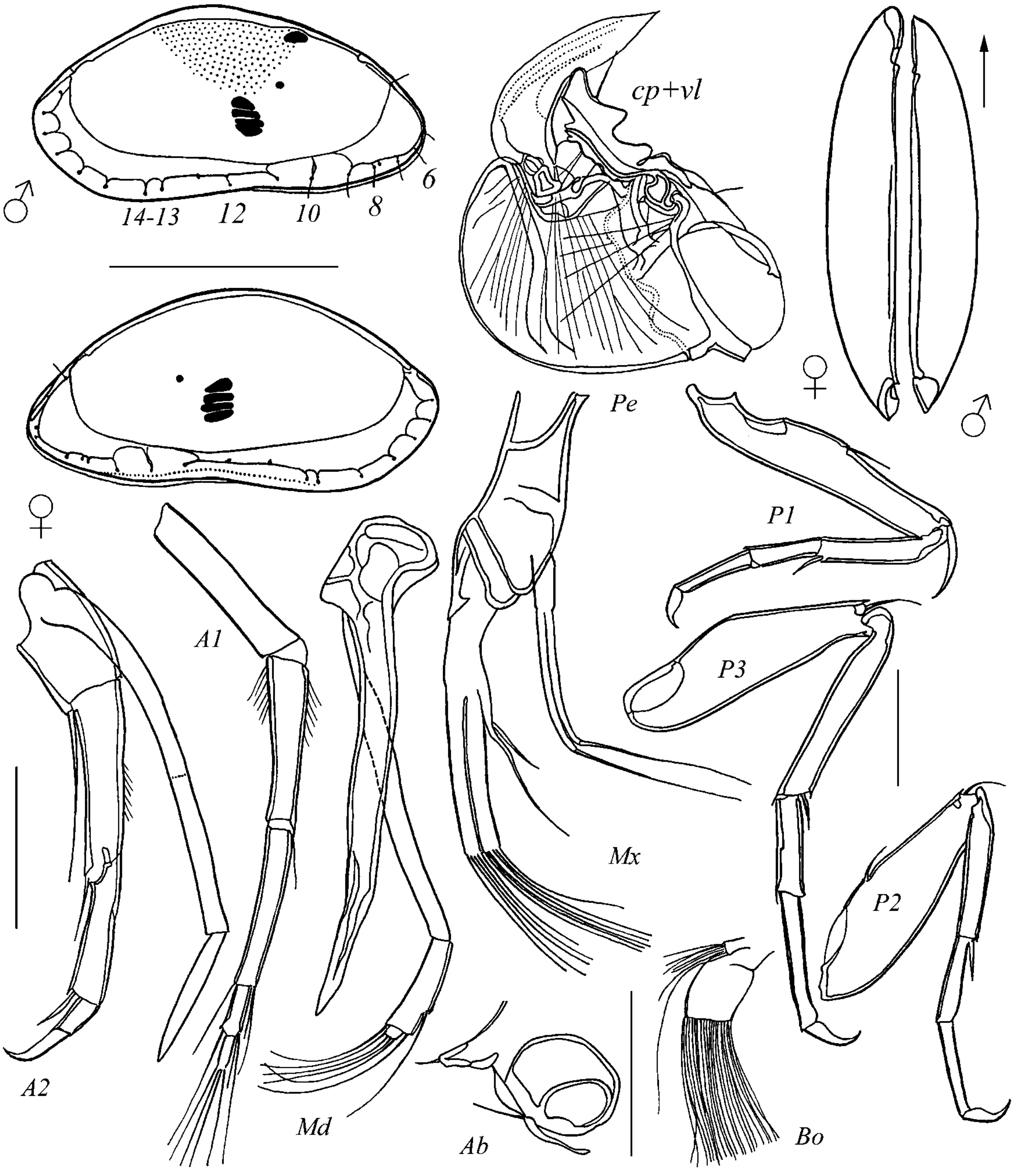


FIGURE 11–*Triangulostoma madeirense* sp. nov. Male, RV, P3, Bo, holotype; female, LV, Md, Ab, ZMH K-40482; all others, male ZMH K-40481b; Scale bars = 0,2 mm (valves); 0,03 mm (all others).

Description.–Shell subtriangular, dorsal margin comparatively strongly convex, anterior narrow, posterior margin cut off in lower part; ratio between length, height and width in female = 19:9:6, in male = 36:17:12. Length of females 0.36-0.38 mm, of males 0.34-0.36 mm. Length ratio between distal podomeres of A1 = 16:13:12:4:3; length ratio between podomeres of endopodite A2 and apical claw = 11:13:13:3:6. Knee seta of P1 a little shorter than half the second podomere. Pe without dorsodistal process of capsule. End of dorsodistal lobe acuminate.

Remarks.–The type species differs from the second known species of the genus, *T. gibberum* (Schornikov, 1975), in details of shell structure and Pe.

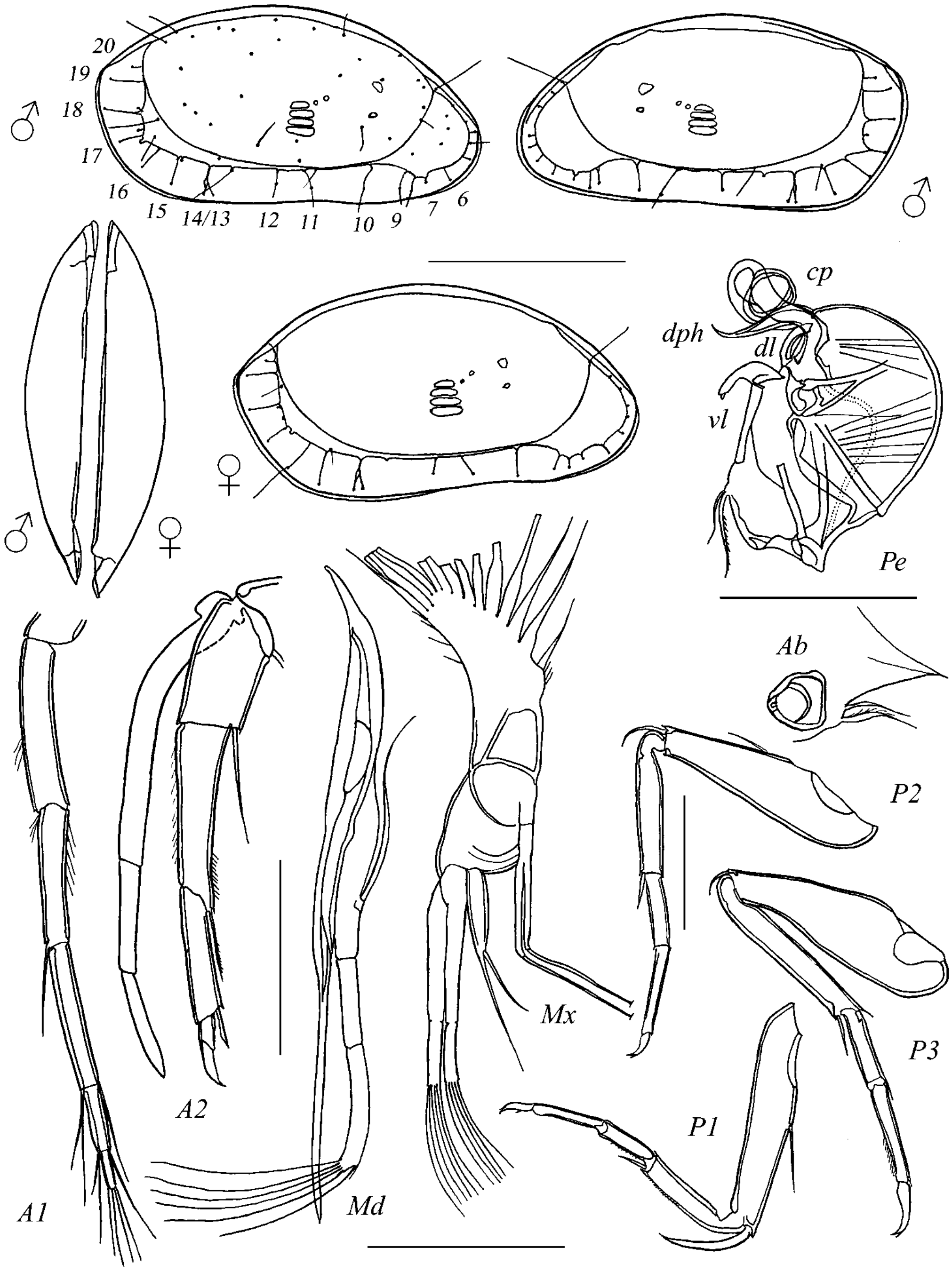


FIGURE 12–*Brunneostoma littorale* sp. nov. Female, RV, P1, Ab, holotype; male valves, ZMH K-40485; all others, male ZMH K-40488b; Scale bars = 0,2 mm (valves); 0,03 mm (P2-3); 0,05 mm (P1 & all others).

Genus *Brunneostoma* Schornikov, 1993

Type species.–*Paradoxostoma brunneum* Schornikov, 1974

Brunneostoma littorale sp. nov.
(Fig. 12; Pl. 1, Fig. 10)

Holotype.–ZMH K-40484a, b, female; Tenerife Island, Sample 1.

Paratypes.–ZMH K-40485- 40487. 6*2vf, 4*m (Sample 1.); ZMH K-40488- 40490; MIBM 8728. 7*1sf, 1*m, 6*A-1, 5*A-2, 2*A-3 (Sample 2); 3*f, 5*m, 2*A-1 (Sample 3).

Derivation of name.–L. Referring to the occurrence of this species in the littoral zone.

Description.–Shell ovate subcuneiform; ratio between length, height and width in female = 22:12:7, in male = 20:11:6. Anterior comparatively widely rounded, dorsal margin strongly convex, ventral margin slightly concave in atrium area, posterior almost straight, cut off in lower part. Length of females 0.42-0.44 mm, of males 0.38-0.40 mm. Length ratio between distal podomeres of A1 = 18:15:16:8:4; length ratio between podomeres of endopodite A2 and apical claw = 15:18:14:4:7. Knee seta of P1 a little shorter than 2/3 second podomere. Pe with very pointed dorsodistal prehensile process, very small dorsodistal lobe and curved ventrodistal one.

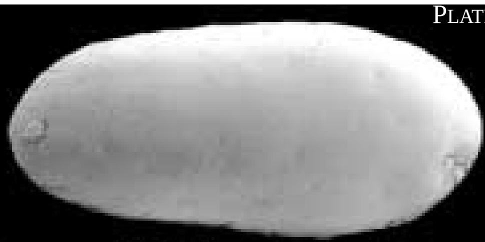
Remarks.–The new species resembles *B. porlockense* (Horne & Whittaker, 1985), but clearly differs in details of shell structure and Pe.

→

PLATE 1–*1, Paradoxostoma dispar* Fischer, LV female (ZMH K-40438). *2, Paradoxostoma sarniense* Brady, LV female (ZMH K-40451). *3, Paradoxostoma wirtzi* sp. nov., LV (holotype). *4, Lanceostoma tenerifense* sp. nov., LV female (ZMH K-40460). *5, Calcarostoma calcaratum* Schornikov & Wouters sp. nov., LV (holotype). *6, Bradystoma bradyforme* sp. nov., LV female (ZMH K-40470). *7, Pontostoma paraponticum* sp. nov., LV female (ZMH K-40474). *8, Pontostoma atlanticum* sp. nov., LV female (ZMH K-40479). *9, Triangulostoma madeirense* sp. nov., LV female (ZMH K-40482). *10, Brunneostoma littorale* sp. nov., LV female (ZMH K-40489). 11, *Brunneostoma cuneatum* sp. nov., LV female (ZMH K-40493).

PLATE 1

1 Paradoxostoma dispar



2 Paradoxostoma sarniense

3 Paradoxostoma wirtzi

4 Lanceostoma tenerifense

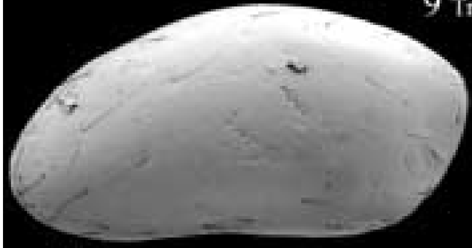
5 Calcarostoma calcaratum

6 Bradystoma bradyforme

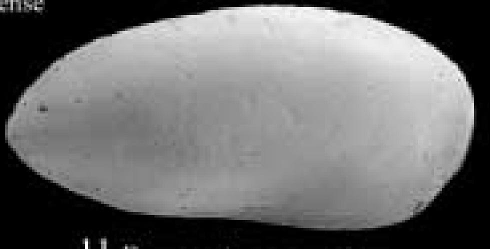
7 Pontostoma paraponticum

8 Pontostoma atlanticum

9 Triangulostoma madeirense



10 Brunneostoma littorale



11 Brunneostoma cuneatum

Brunneostoma cuneatum sp. nov.
(Fig. 13; Pl. 1, Fig. 11)

Holotype.–ZMH K-40491a, b; male. Madeira, Sample 3.

Paratype.–ZMH K-40492a, b; female. Madeira, Sample 3.

Derivation of name.–L. *cuneus*, referring to the wedge-shaped shell.

Description.–Shell subcuneiform; ratio between length, height and width in female = 22:11:7, in male = 22:11:6. Anterior margin narrowly rounded, dorsal one slightly convex, ventral margin almost straight, posterior very widely rounded. Length of female and male 0.44 mm. Length ratio between distal podomeres of A1= 20:18:16:7:5; length ratio between podomeres of endopodite A2 and apical claw = 16:16:15:5:6. Knee seta of P1 a little shorter than 2/3 second podomere. Pe with modera-

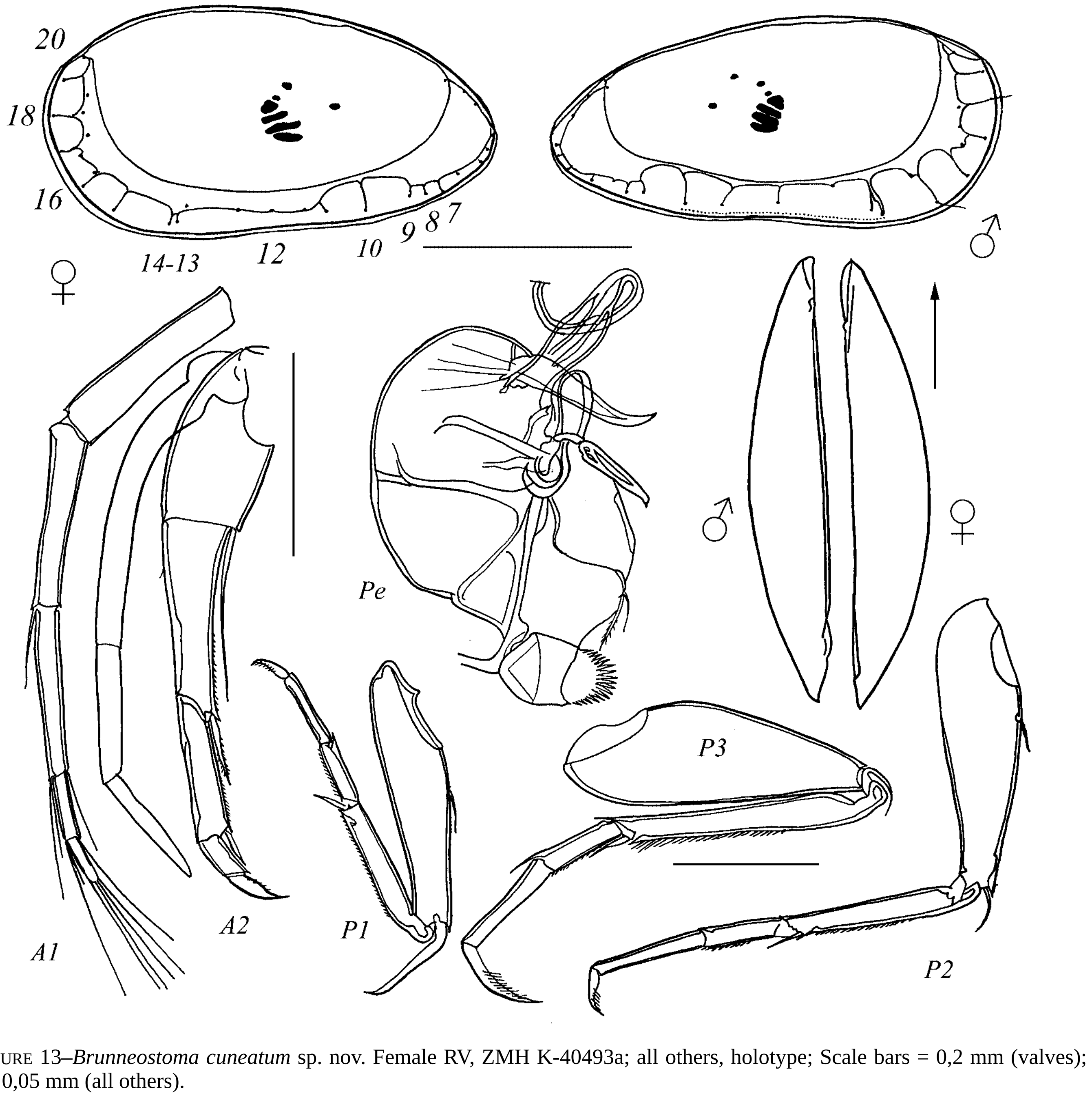


FIGURE 13–*Brunneostoma cuneatum* sp. nov. Female RV, ZMH K-40493a; all others, holotype; Scale bars = 0,2 mm (valves); 0,05 mm (all others).

tely pointed dorsodistal prehensile process, medium-sized dorsodistal lobe and straight ventrodistal one.

Remarks.–The new species resembles *B. littorale* sp. nov., but clearly differs in details of the shell structure and Pe.

ACKNOWLEDGEMENTS

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OSTRACOD SPECIES OF THE GENUS *CYTHEROPTERON* FROM LATE PLEISTOCENE, HOLOCENE AND RECENT SEDIMENTS OF THE LAPTEV SEA (ARCTIC SIBERIA)

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Abstract

Sixteen species of the genus *Cytheropteron* from the Laptev Sea Late Pleistocene, Holocene deposits and Recent surface sediments have been described. Analysis of the literature on this subject and the collections of O.M.Lev from St. Petersburg, together with our own material from the Laptev Sea, allowed us to introduce certain changes in the taxonomy of this genus. One species *Cytheropteron laptevensis* Stepanova sp. nov. is described as new.

Key words: Ostracoda, *Cytheropteron*, taxonomy, Late Pleistocene, Holocene, Recent, Laptev Sea.

Resumen

Se describen dieciséis especies del género *Cytheropteron* procedentes de sedimentos del Pleistoceno Superior, Holoceno y del Reciente del mar de Laptev. El análisis de la literatura referente a este tema, junto con las colecciones del O.M. Lev de San Petersburgo, así como nuestro material del mar de Laptev, nos ha permitido introducir algunas modificaciones en la taxonomía de este género. Una especie nueva, *Cytheropteron laptevensis* Stepanova sp. nov., es descrita en este trabajo.

Palabras clave: Ostracoda, *Cytheropteron*, taxonomía, Pleistoceno Superior, Holoceno, Reciente, mar de Laptev.

INTRODUCTION

Various species of the genus *Cytheropteron* are common in high latitudinal benthic assemblages. There are certain difficulties in identification of the species belonging to this genus, primarily due to high species diversity and the existence of closely related species with similar morphology and, hence, numerous synonyms. Another problem is that Russian publications on Arctic ostracods (Lev, 1972, 1983; Schneider, 1962) are not well known abroad, and collections from the Russian institutions and museums have never been compared to other collections.

Different scientists have described species of genus *Cytheropteron* from many regions: North Atlantic (Whatley & Coles, 1987), Great Britain and Ireland (Brady, 1868a; Brady *et al.*, 1874; Brady & Norman, 1889; Neale & Howe, 1973; Whatley & Masson, 1979; Athersuch *et al.*, 1989), Gulf of Alaska (Brouwers, 1994), Northeastern North America (Cronin, 1981, 1989). Lev (1972, 1983) gave descriptions of ostracod species from the Quaternary marine sediments of the high-latitude areas of the Arkhangel'sk Region (northeastern Russian Plain) and Taimyr Peninsula. We analyzed most of the publications dealing with taxonomic descriptions of *Cytheropteron* species. Although we have not yet had the opportunity to study original collections in non-Russian Institutions, we studied in detail the collections of O.M. Lev stored in "VNIIOkeangeologiya", St. Petersburg, Russia. This allowed us to resolve some controversial taxonomic problems.

In this paper we describe sixteen ostracod species of genus *Cytheropteron* from Late Pleistocene and Holocene deposits and surface sediments of the Laptev Sea. Of these one species is referred to as a new species.

MATERIAL

We analyzed specimens of *Cytheropteron* species from coretop and downcore sediment samples collected in the Laptev Sea during several Russian-German TRANSDRIFT expeditions, mainly, TRANSDRIFT V in August 1998 (aboard R/V Polarstern). Coretop samples, the uppermost one centimetre of sediments, were taken from box and kasten cores. These were obtained in different parts of the Laptev Sea at 26 stations covering a water depth range from 11 to 276 m (Fig. 1, see also Stepanova *et al*., 2003a).

Fossil ostracods were studied in four sediment cores, PS-51/135-4, PS-51/138-12, PS-51/080-13, and PS-51/154-11 from different parts of the Laptev Sea shelf and continental slope (Fig. 1). All cores were AMS^{14}C dated (Bauch *et al*., 2001). Cores from the middle eastern Laptev Sea shelf, PS-51/135-4 (water depth 51 m) and PS-51/138-12 (water depth 45 m), date back to 11.2 and 11.3 cal. ka, respectively; core PS-51/080-11 from the inner shelf (water depth 21 m) – to 6.3 cal. ka; and core PS-51/154-11 from the upper continental slope of the western Laptev Sea shelf (water depth 270 m) – to more than 15.7 cal. ka.

All specimens are stored at Moscow State University, Geological Faculty, Chair of Palaeontology, collection No. 292/1-287. Electronic photomicrographs were made at the Palaeontological Institute RAS.

For taxonomic description and comparison, we studied the collections of O.M. Lev stored in the All-Russian Institute for Geology and Mineral Resources of the World Ocean ("VNIIOkeangeologiya", former NIIGA), St. Petersburg, Russia.

When describing modern and fossil distribution of species we included our data on Recent and Holocene ostracods from the Kara Sea (Stepanova *et al*., 2003b; Taldenkova *et al*., 2003), but did not describe any of them here. Recent ostracods were identified from 30 surface samples obtained in the eastern part of the sea from water depths ranging between 10 and 295 metres. Holocene ostracods originate from core BP-00/07-5, eastern Kara Sea (water depth 43 m) that dates back to more than 8 cal. ka (Simstich *et al*., submitted).

SYSTEMATIC DESCRIPTIONS

We follow the supragenetic taxonomy provided by Nikolaeva (1989) and the morphological terminology of Nikolaeva (1989) and Athersuch (1989). Size groupings of *Cytheropteron* are based on the following carapace length standard: small: 0.3-0.4 mm; medium: 0.4-0.6 mm; large: > 0.6 mm. We distinguish between fossil and modern distribution of ostracods. By modern distribution we mean all ostracods found in surface sediments, but not necessarily living ones.

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Sars, 1866
Family CYTHERURIDAE G. Müller, 1894
Genus *Cytheropteron* Sars, 1866

1868 *Cytheropteron* Sars - Brady, 1868a, p. 447.
1874 *Cytheropteron* Sars - Brady *et al*., p. 201.
1880 *Cytheropteron* Sars - Brady, p. 135.
1928 *Cytheropteron* Sars, p. 223.
1961 *Cytheropteron* Sars - Reyment *et al*., p. 292.
1963 *Cytheropteron* Sars - Swain, p. 816.
1969 *Cytheropteron* (*Cytheropteron*) - Elofson, p. 88.
1979 *Cytheropteron* Sars - Whatley & Masson, p. 224-225.
1983 *Cytheropteron* Sars - Lev, p. 116.
1989 *Cytheropteron* Sars - Nikolaeva *et al*., p. 133.
1989 *Cytheropteron* Sars - Athersuch *et al*., p. 221.

Type species.–Cythere latissima Norman, 1864, Recent, North Atlantic (SD Brady & Norman, 1889).

Diagnosis.–Small to medium size. Carapace ovate to subrhomboidal or triangular in lateral view. Commonly, it possesses a caudal process upturned towards dorsal margin and a wing-like lateral process, or may be tumid ventro-laterally, highly variable morphologically in size and shape. Valves are unequal, right valve overlaps left valve dorsally. Surface smooth, wrinkled or ornamented: punctate, often reticulate, it may bear weak ribs, ridges or tubercules. Ala expansion may terminate in a spine. Eye tubercules absent. Usually four ovate elongated muscle scars forming a subvertical row in the midlength of valve, right above ventral margin. Hinge antimerodont: in right valve with two terminal dentate hinge bars and a median crenulate groove, left valve complementary.

The genus includes more than 200 species.

Stratigraphical range.–Jurassic - Recent, global distribution

Cytheropteron arcuatum Brady, Crosskey and Robertson, 1874
Pl. I, Figs. 1, 2

- 1874 *Cytheropteron arcuatum* Brady, Crosskey and Robertson, p. 203, Pl. VIII, Figs. 16-18; Pl. XIV, Figs. 19-22.
- 1889 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Brady & Norman, p. 213, Pl. XX, Figs. 28-30.
- 1979 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Whatley & Masson, p. 229, Pl. 1, Figs. 1-5.
- 1980 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Lord, Pl. 2, Figs. 13-15.
- 1981 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Cronin, p. 402, Pl. 7, Fig. 1.
- 1983 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Lev, p. 117, Pl. XI, Fig. 6.
- 1989 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Cronin, Pl. V, Fig. 12.
- 1996 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Whatley *et al*., Pl. 1, Fig. 16.
- 1999 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Kupriyanova, Pl. 2, Fig. 10.
- 2001 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Didié, Pl. 2, Figs. 7-8.
- 2003 *Cytheropteron arcuatum* Brady, Crosskey and Robertson - Stepanova *et al*., 2003a, Pl. II, Figs. 13, 14.

Type series.–Brady *et al*., 1874, p. 203, Pl. VIII, Figs. 16-18; Scotland, Errol; Pleistocene; Pl. XIV, Figs. 19-22; Scotland, Drylers; Pleistocene.

Description.–Carapace small, subtriangular in lateral view, with flattened anterior and posterior margins. Dorsal margin strongly convex, gradually passing into anterior margin through the obtuse cardinal angle, and into posterior margin through slight concavity. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, caudate, upturned towards dorsal margin. Greatest length at mid height, greatest height in the center of valve. Ala with rounded anterior edge and subvertical posterior. Ala extremity terminates with a spine, a round punctum occurs in the central part of ala expansion. Surface is pierced by pore canals aligned in subvertical rows forming stream-like pattern. Fine ribs form weakly developed fossae on anterior and posterior margins.

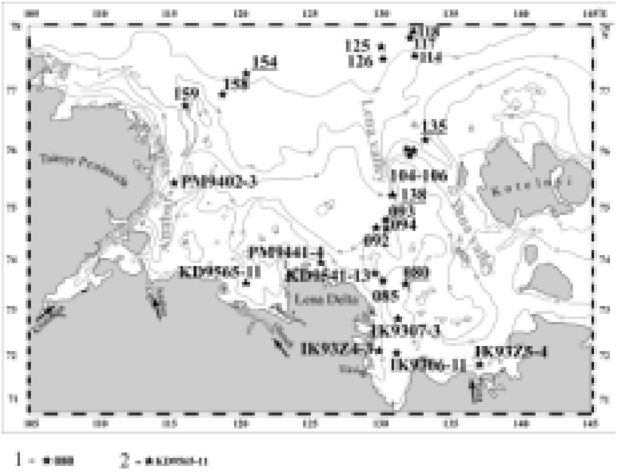


FIGURE 1–Site locations in the Laptev Sea.
1 – stations of TRANSDRIFT V expedition; underlined are sediment cores used in this study; 2 – stations of the previous TRANSDRIFT expeditions (I-IK93, II-PM94, III-KD95).

Measurements, mm.–

	L	H
MSU292/77	0.29	0.2
MSU292/78	0.35	0.21
MSU292/79	0.28	0.18

* L - maximum length; H – maximum height.

Comparison.–*Cytheropteron arcuatum* differs from *C. foresteri* Brouwers, 1994 from the Pleistocene-Holocene deposits of the Gulf of Alaska (Brouwers, 1994, Pls. 24-25, Pl. 17, Figs. 13-18, Pl. 18, Figs. 2, 3, 6, Pl. 19, Figs. 1-4, Pl. 20, Figs. 10, 11, 22, 23) in more convex dorsal margin, presence of fine ribs on posterior and anterior margins, and smaller pore puncta.

Variability.–Carapaces may differ in height. Weak ornamentation of the margins varies from fine ribs to almost smooth surface.

Fossil distribution.–Neogene through Quaternary marine sediments: Lower Severnaya Dvina River, Novaya Zemlya, Lower Pechora River, Lower Ob River, Lower Yenisei River; Pleistocene: Scotland, Ireland, Norway, North Sea, Laptev Sea, Champlain Sea, coastal Maine, Boston "blue clay", western Goldthwait Sea (Quebec); Holocene: eastern Kara Sea, Laptev Sea (Fig. 2).

Modern distribution.– Greenland Sea, Barents Sea, Kara Sea, Laptev Sea, East-Siberian Sea, Beaufort Sea, Canadian Arctic, Baffin Sea (Fig. 2).

FIGURE 2–Distribution of *Cytheropteron arcuatum*. 1 – fossil distribution; 2 – modern distribution.

Description.–Carapace small, fragile, subtriangular in lateral view. Dorsal margin slightly arched, gradually beveled towards anterior and posterior margins. Ventral margin straight, slightly concave in anterior third. Anterior margin flattened, arcuate and evenly rounded. Posterior margin also flattened, caudate, upturned towards dorsal margin. Caudal process convex in postero-dorsal part and straight or slightly concave in postero-ventral part. Greatest length at mid height, greatest height in the center of valve. Ala with rounded anterior edge and subvertical posterior. Two round puncta occur at the base of ala expansion close to its edges. Lateral valve surface bears two fine loop-like ribs. The first one stretches in a broad arc from the mid-dorsal point through lateral surface and ends at the base of anterior edge of ala. The second rib forms a loop convex upwards, its endings reach anterior and posterior edges of ala. This rib nearly touches dorsal margin. Distinct fine rib is developed along anterior edge of ala, the second fine rib, less distinct, extends along its posterior edge. Lateral valve surface between ribs is smooth. Several weak subvertical stream-like ribs occur on posterior margin.

Material.–Eighty-four valves and 32 carapaces from Late Pleistocene through Holocene deposits of the Laptev Sea.

Cytheropteron biconvexa Whatley and Masson, 1979
Pl. I, Figs. 3, 4

1979 *Cytheropteron biconvexa* Whatley & Masson, 1979, p. 229, Pl. 3, Figs. 5, 10, 14-16, 18-20.
1980 *Cytheropteron* sp. A - Lord, Pl. 2, Figs. 20-22.
1989 *Cytheropteron biconvexa* Whatley & Masson - Cronin, Pl. V, Figs. 5-6.
1993 *Cytheropteron biconvexa* Whatley & Masson - Lord *et al.*, Pl. 3, Fig. 4.
1999 *Cytheropteron biconvexa* Whatley & Masson - Kupriyanova, Pl. 2, Fig. 5.
2003 *Cytheropteron biconvexa* Whatley & Masson - Stepanova *et al.*, 2003a, Pl. II, Figs. 7, 8.

Holotype.–Micropalaeontology Collections stored in the Palaeontology Department, National History Museum, London, OS 10800; adult left valve, borehole, Forties Field, North Sea, Lat. 57º43’54.5”N, Long. 00º58’25.5”E. Type level – 5 m depth in borehole; Pleistocene.

FIGURE 3–Distribution of *Cytheropteron biconvexa*. See key Fig. 2.

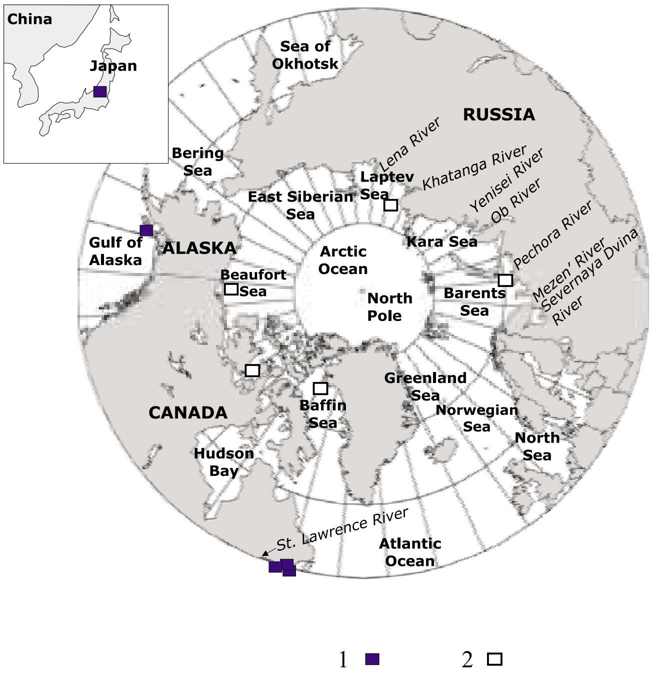


FIGURE 4–Distribution of *Cytheropteron champlainum.* See key Fig. 2.

Measurements, mm.–

	L	H
MSU292/76	0.4	0.23
MSU292/262	0.36	0.22

Comparison.–Cytheropteron biconvexa differs from *C. inornatum* Brady and Robertson, 1872 in the number of fine ribs on the lateral surface (two against three, fine ribs on the ala edges are not considered) and their pattern.

Variability.–Carapaces differ slightly in height in the center due to variations in convexity of the dorsal margin. Also, the height of the posterior margin varies slightly.

Remarks.–Specimens of this species from the Quaternary deposits of the western Russian Arctic are stored in VNIIOkeangeologia (St. Petersburg), collection of O.M. Lev. She did not identify them to species level.

Fossil distribution.–Pleistocene: North Sea, Northern Ireland, Norway, Goldthwait Sea (Quebec); Pleistocene-Holocene: Pechora Sea, Laptev Sea; Holocene of the eastern Kara Sea (Fig. 3).

Modern distribution.–Western Laptev Sea, Gulf of Alaska, Beaufort Sea, Canadian Arctic, Greenland Sea (Fig. 3).

Material.–Five valves and 4 carapaces from Late Pleistocene through Holocene deposits and from Recent surface sediments of the Laptev Sea.

Cytheropteron champlainum Cronin, 1981
Pl. I, Figs. 5, 6

1981 *Cytheropteron champlainum* Cronin, 1981, p. 404, Pl. 8, Figs. 7, 8.
1987 *Cytheropteron champlainum* Cronin - Cronin & Ikeya, p. 84, Pl. 3, Figs. 3, 6.
1989 *Cytheropteron champlainum* Cronin, Pl. IV, Fig. 7.
1994 *Cytheropteron champlainum* Cronin - Brouwers, p. 17, Pl. 17, Figs. 1-6.
1994 *Cytheropteron tarrensis* Brouwers, p. 36, Pl. 21, Fig. 1; Pl. 22, Figs. 4-10, 25.
2003 *Cytheropteron champlainum* Cronin - Stepanova *et al*., 2003a, Pl. II, Fig. 2.

Holotype.–U.S. National Museum (USNM), Department of Palaeobiology, USNM311142; female right valve; Canada, Ontario, north end of gravel pit, west side of road, 5.6 km N of Kars, Ontario, Canada; Pleistocene.

FIGURE 5–Distribution of *Cytheropteron dimlingtonensis.* 1 – fossil distribution; 2 – modern distribution; 3 – probable fossil distribution.

Description.–Carapace medium sized. Trapeziform in lateral view. Dorsal margin arcuately convex, gradually beveled towards anterior and posterior margins. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuate and evenly rounded. Posterior margin lower than anterior, caudate, flattened, upturned towards dorsal margin. Greatest length at mid height, greatest height in the center of valve. Broad wing-like process with rounded edge overhangs ventral margin. Ala is subdivided by depression of slightly variable size. Valve surface with subvertical rows of puncta and fossae, or only fossae. Fine rib along ala edge extends from the lower section of anterior part of valve and merges with fossae muri at the posterior part of valve. Fine rib equal in length to dorsal margin runs slightly below and parallel to it. Below ala process, several fine ribs parallel to ventral margin stretch from anterior part of valve and eventually merge with fossae muri at posterior part of valve. The whole valve surface, besides fossae muri, is pierced by pore canals.

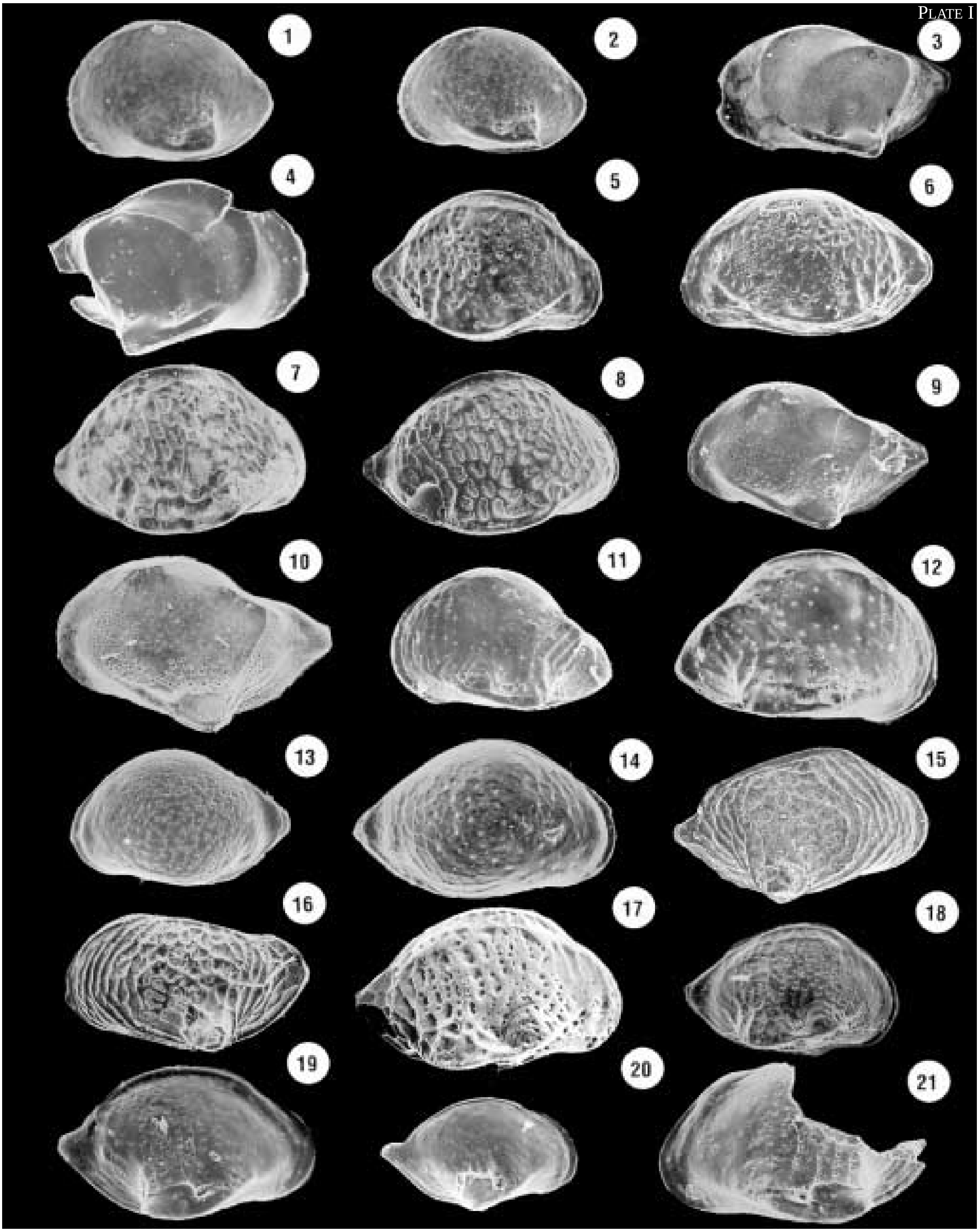
Sexual dimorphism.–Cronin (1981) pointed to strong sexual dimorphism: male carapace is higher and shorter. Our specimens demonstrate a similar pattern.

FIGURE 6–Distribution of *Cytheropteron discoveria.* See key Fig. 2.

→

PLATE 1–*1, 2, Cytheropteron arcuatum* Brady, Crosskey and Robertson, 1874; *1,* left valve, external view, MSU292/77, x140; *2,* left valve, external view, MSU292/78, x97; recent surface sediments of the western-central Laptev Sea. *3, 4, Cytheropteron biconvexa* Whatley and Masson, 1979; *3,* left valve, external view, MSU292/76, x100; *4,* right valve, external view, MSU292/262, x130; recent surface sediments of the western-central Laptev Sea. *5, 6, Cytheropteron champlainum* Cronin, 1981; *5,* right valve, external view, MSU292/59, x86; *6,* left valve, external view, MSU292/263, x80; recent surface sediments of the western-central Laptev Sea. *7, 8, Cytheropteron dimlingtonensis* Neale and Howe, 1973; *7,* right valve, external view, MSU292/277, x90; *8,* right valve, external view, MSU292/279, x80; late Pleistocene of the western Laptev Sea. *9, 10, Cytheropteron discoveria,* Brouwers 1994; *9,* left valve, external view, MSU292/270, x100; *10,* left valve, external view, MSU292/271, x115; Holocene of the western Laptev Sea. *11, 12, Cytheropteron elaeni* Cronin, 1989; *11,* left valve, external view, MSU292/268, x115; *12,* right valve, external view, MSU292/282, x110; recent surface sediments of the eastern Laptev Sea. *13, 14, Cytheropteron inflatum* Brady, Crosskey and Robertson, 1874; *13,* left valve, external view, MSU292/71, x70; *14,* right valve, external view, MSU292/281, x130; recent surface sediments of the western-central Laptev Sea. *15, 16, Cytheropteron montrosiense* Brady, Crosskey and Robertson, 1874; *15,* right valve, external view, MSU292/180, x94; *16,* left valve, external view, MSU292/266, x90; recent surface sediments of the southern Laptev Sea. *17, 18, Cytheropteron nodosoalatum* Neale and Howe, 1973; *17,* right valve, external view, MSU292/213, x87; recent surface sediments of the southern Laptev Sea; 18, right valve, external view, MSU292/81, x90; recent surface sediments of the western-central Laptev Sea. *19-21, Cytheropteron porterae* Whatley and Coles, 1987; *19,* right valve, external view, MSU292/61, x87; *20,* right valve, external view, MSU292/74, x70; *21,* left valve fragment, external view, MSU292/283, x100; recent surface sediments of the western-central Laptev Sea.

PLATE I



Measurements, mm.–

	L	H
MSU292/59	0.53	0.3
MSU292/260	0.41	0.23
MSU292/263	0.57	0.31

*Variability.–*Ornamentation is highly variable ranging from small puncta (0.01 mm) to fossae (0.016 mm).

Comparison.–Cytheropteron champlainum differs from *C. dimlingtonensis* Neale and Howe, 1973, in ornamentation: *C. champlainum* carapace has both puncta and fossae, while *C. dilmingtonensis* – only fossae densely punctate inside.

*Remarks.–*Close examination of the published illustrations of *C. dimlingtonensis* Neale and Howe, 1973, *C. champlainum* Cronin, 1981 and *C. tarrensis* Brouwers, 1994 allowed us to include them in one group of species, since they have nearly identical shape and dimensions. Surface ornamentation within this group varies markedly, from small puncta to fossae. *Cytheropteron tarrensis* has the smoothest surface with puncta grading into elongated fossae towards posterior margin. The ornament of *C. champlainum* is identical but more distinct than that of *C. tarrensis*, therefore, we consider these species to be synonyms. Moreover, *C. dimlingtonensis* has solely reticulate surface sculpture (Pl. I, Figs. 7, 8).

*Fossil distribution.–*Plio-Pleistocene of Japan; Pleistocene of the Gulf of Alaska, Champlain Sea, Goldthwait Sea, Western Newfoundland, coastal Maine, Massachusetts and Nova Scotia (Fig. 4).

Modern distribution.– Barents Sea, western Laptev Sea, Beaufort Sea, Canadian Arctic, Baffin Sea (Fig. 4).

*Material.–*Twelve valves from Late Pleistocene and Holocene deposits and recent surface sediments of the Laptev Sea.

Cytheropteron dimlingtonensis Neale and Howe, 1973

Pl. I, Figs. 7, 8

1961 *Cytheropteron* cf. *pyramidale* Brady - Swain, Fig. 2, N28.

1963 *Cytheropteron pyramidale* Brady - Swain, p. 816, Pl. 97, Fig. 19, Pl. 98, Fig. 9.

1973 *Cytheropteron dimlingtonensis* Neale & Howe, p. 242, Pl. 1, Figs. 3, 5.

1978 *Cytheropteron dimlingtonensis* Neale & Howe - Robinson, Pl. 2, Fig. 4.

FIGURE 7–Distribution of *Cytheropteron elaeni.* See key Fig. 2.

1979 *Cytheropteron dimlingtonensis* Neale & Howe - Whatley & Masson, p. 232, Pl. 6, Figs. 11, 13-16.

1999 *Cytheropteron champlainum* Cronin - Kupriyanova, Pl. 2, Fig. 2.

*Holotype.–*University of Hull; HU.50.Q.1.9.; left valve; England, Yorkshire, Dimlington; Pleistocene.

*Description.–*Carapace medium sized. Trapeziform in lateral view. Dorsal margin arcuately convex, gradually beveled towards anterior and posterior margins. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuate and evenly rounded. Posterior margin lower than anterior, caudate, flattened, upturned towards dorsal margin. Greatest length at mid height, greatest height in the center of valve. Broad wing-like process with rounded edge overhangs ventral margin. Ala is subdivided by rounded depression (about 0.03 x 0.02 mm). Valve surface with distinct subvertical rows of fossae. Fine rib along ala edge extends from the lower section of anterior part of valve and merges with fossae muri at the posterior part of valve. Fine rib equal in length to dorsal margin runs slightly below and parallel to it. Below the ala process, several fine ribs parallel to ventral margin stretch from anterior part of valve and eventually merge with fossae muri at posterior part of valve. The whole valve surface, besides fossae muri, is densely punctate.

Measurements, mm.–

	L	H
MSU292/229	0.4	0.21
MSU292/235	0.44	0.25
MSU292/277	0.51	0.34
MSU292/279	0.58	0.37

*Variability.–*The degree of reticulation is slightly variable. Shape of fossae varies from elongated to more rounded. Some carapaces are higher and shorter with more convex dorsal margin, possibly due to sexual dimorphism (published photomicrographs are not separated into sexes).

*Comparison.–*Comparison with *Cytheropteron champlainum* Cronin, 1981 is given above (see description of *C. champlainum*).

Cytheropteron dimlingtonensis differs from *C. latissimum* (Norman, 1864) from the Pleistocene deposits of the North Sea (Whatley & Masson, 1979, pp. 225-227, Pl. 6, Figs. 7, 9, 12) by the presence of more distinct subvertical rows of puncta, more convex dorsal margin, and more evenly rounded ala edge.

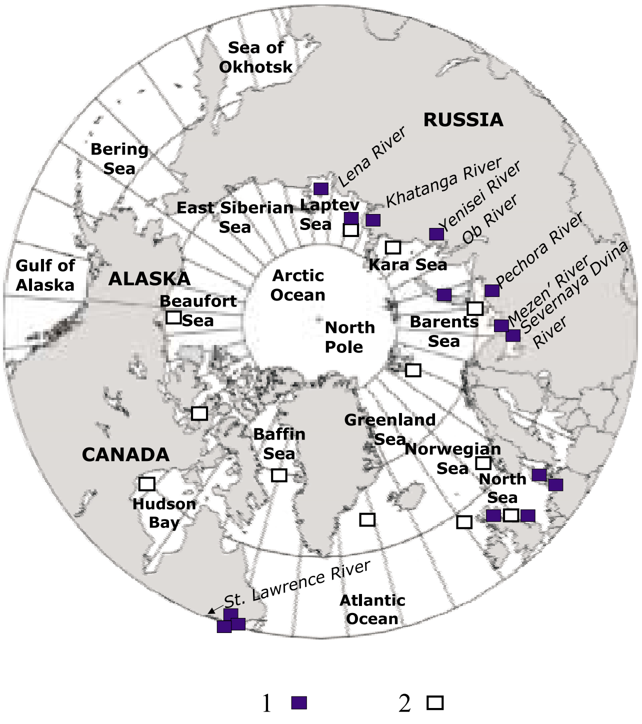


FIGURE 8–Distribution of *Cytheropteron inflatum*. See key Fig. 2.

*Remarks.–*Ostracods identified as *Cytheropteron subcircinatum* Sars 1866, (Lev, 1983, pp. 119-120, Pl. XVI, Figs. 1-2) from Pleistocene – Holocene deposits of the Lower Severnaya Dvina and Mezen' Rivers, and Kola Peninsula could be probably referred to *C. dimlingtonensis*. However, since descriptions of these specimens are not given in the publication of Lev (1983), we can not be absolutely sure that these species are synonyms. Therefore, we did not include *C. subcircinatum* sensu Lev (1983) in the list of synonyms.

We consider that the specimens attributed by Kupriyanova (1999) to *C. champlainum* (Kupriyanova, 1999, Pl. 2, Fig. 2) should be referred to as *C. dimlingtonensis*, since these specimens bear only reticulate ornament.

*Fossil distribution.–*Pleistocene: Great Britain; Pleistocene-Holocene of the Laptev Sea, Denmark, Pechora Sea; Pleistocene of northern Alaska (Gubik Formation); Probably, Pleistocene - Holocene: Lower Severnaya Dvina and Mezen' Rivers, Kola Peninsula; Holocene of the eastern Kara Sea (Fig. 5).

*Modern distribution.–*Laptev Sea, Spitsbergen coast (Fig. 5).

*Material.–*Sixteen valves from Late Pleistocene and Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron discoveria Brouwers, 1994
Pl. I, Figs. 9, 10

1994 *Cytheropteron discoveria* Brouwers, p. 20, Pl. 11, Fig. 5, Pl. 13, Figs. 1-6, 9.
2003 *Cytheropteron inornatum* Brady & Robertson - Stepanova *et al*., 2003a, Pl. II, Fig. 9.

*Holotype.–*U.S. National Museum (USNM); USNM 408516; left valve, Gulf of Alaska, locality DC2-80-EG-195; Pleistocene-Holocene (original information about age is not exact).

*Description.–*Carapace small, thin-shelled, subtriangular in lateral view. Dorsal margin strongly and arcuately convex, gradually beveled towards anterior margin, and passes into posterior margin through slight concavity. Ventral margin straight, slightly concave in anterior third. Anterior margin flattened and evenly rounded. Posterior margin also flattened, caudate. Caudal process convex in postero-dorsal part and slightly concave in postero-ventral part. Greatest length at mid height, greatest height in the center of valve. Ala with straight anterior edge and subvertical posterior one. Protruding part of ala densely punctate with very small puncta, largest puncta occur rarely at its base and on lateral valve surface above it. Part of ala with small puncta and with larger ones divided by biconvex rib. Very small puncta occur on posterior and anterior parts of valve; punctate area ends in front of dorsal margin. Lateral surface bears four fine ribs. One short rib extends parallel to postero-dorsal margin just below its concavity. Another short one occurs below anterior hinge edge subparallel to dorsal margin. A third rib extends upwards from ala extremity with minor inclination towards posterior margin and meets the first rib. The fourth rib extends from the ala extremity along the leading ala edge towards the anterior margin and ends just short of anterior margin. Several fine ribs occur on the posterior end parallel to postero-ventral margin. They originate at posterior side of ala and disappear short of caudal process extremity. These ribs partly merge forming elongated fossae. Carapace in posterior and anterior parts is densely punctate.

Measurements, mm.–

	L	H
MSU292/270	0.44	0.22
MSU292/271	0.42	0.19
MSU292/84	0.4	0.22

*Variability.–*Some carapaces are considerably less punctate than others (Stepanova *et al*., 2003a, Pl. II, Fig. 9).

Comparison.–Cytheropteron discoveria Brouwers, 1994 differs from *C. inornatum* Brady and Robertson, 1872 from Recent sediments from waters around Scotland (Whatley & Masson, 1979, p. 238, Pl. 3, Figs. 1-3, 5-7) in having a punctate surface, in the number of fine ribs on the lateral surface (four against three) and in their pattern.

*Remarks.–*In Stepanova *et al.* (2003a) *C. discoveria* was mistakenly referred to as *C. inornatum* due to the poor material (two valves) on this species from the western Laptev Sea. Later we obtained more specimens from the Holocene deposits of the western

FIGURE 9–Distribution of *Cytheropteron montrosiense.* See key Fig. 2.

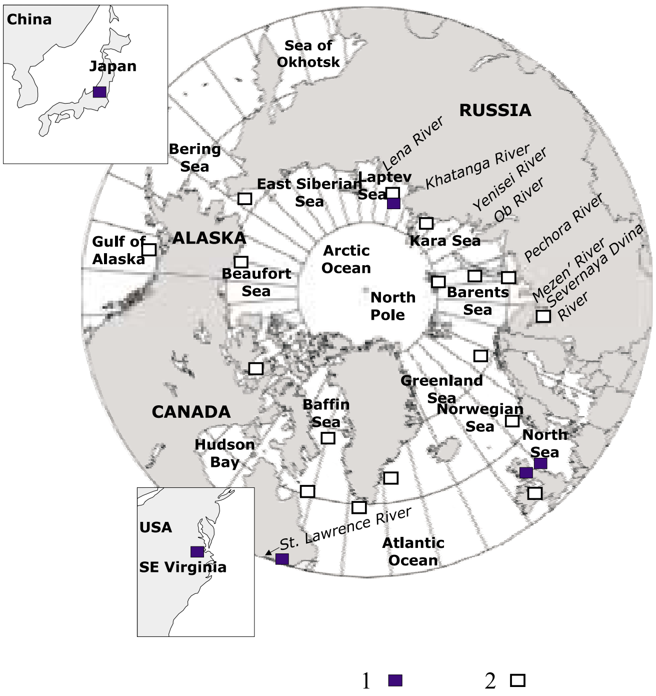


FIGURE 10–Distribution of *Cytheropteron nodosoalatum.* See key Fig. 2.

Laptev Sea which revealed a pronounced difference between these two species.

Fossil distribution.–Pleistocene-Holocene: Gulf of Alaska, Cook Inlet and Kodiak shelf, Pribilof Islands, western Laptev Sea (Fig. 6).

Modern distribution.–Gulf of Alaska, western Laptev Sea (Fig. 6).

Material.–Fourteen valves from Late Pleistocene to Holocene deposits of the western Laptev Sea and Recent surface sediment of the same area.

Cytheropteron elaeni Cronin, 1989
Pl. I, Figs. 11, 12

1975 *Cytheropteron* sp. nov.? - Neale & Howe, Pl. 6, Fig. 5.
1981 *Cytheropteron nealei* Cronin, p. 406, Pl. 7, Fig. 7.
1983 *Cytheropteron paralatissimum* Swain - Lev, p. 120, Pl. XVI, Fig. 15.
1989 *Cytheropteron elaeni* Cronin, Pl. V, Fig. 8.
1994 *Cytheropteron elaeni* Cronin - Brouwers, p. 23, Pl. 22, Figs. 11-13.
1999 *Cytheropteron paralatissimum* Swain - Kupriyanova, Pl. 2, Fig. 9.
1999 *Cytheropteron bronwynae* Joy & Clark - Didié *et al.*, Pl. I, Fig. 14.
2003 *Cytheropteron elaeni* Cronin - Stepanova *et al.*, 2003a, Pl. I, Fig. 14.

Holotype.–U.S. National Museum (USNM), Department of Paleobiology, USNM311151; female right valve?; Canada, Quebec, exposures on east side of Quebec Route 221, 7.2 km S of St. Remi; Pleistocene.

Description.–Carapace small, subtriangular in lateral view, with flattened anterior and posterior margins. Dorsal margin arcuate, strongly convex, slightly concave in front of posterior margin, passes into anterior margin through slight ledge. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, subtriangular. Greatest length at lower third, greatest height in front third of valve. Ala with straight anterior edge and subvertical posterior. Along ala base a row of four fossae, each contains a punctum. Anterior part of valve with fine ribs parallel to anterior margin. On posterior part of valve, above posterior ala edge, three fine subvertical ribs slightly curved towards anterior margin. At hinge edges some ribs

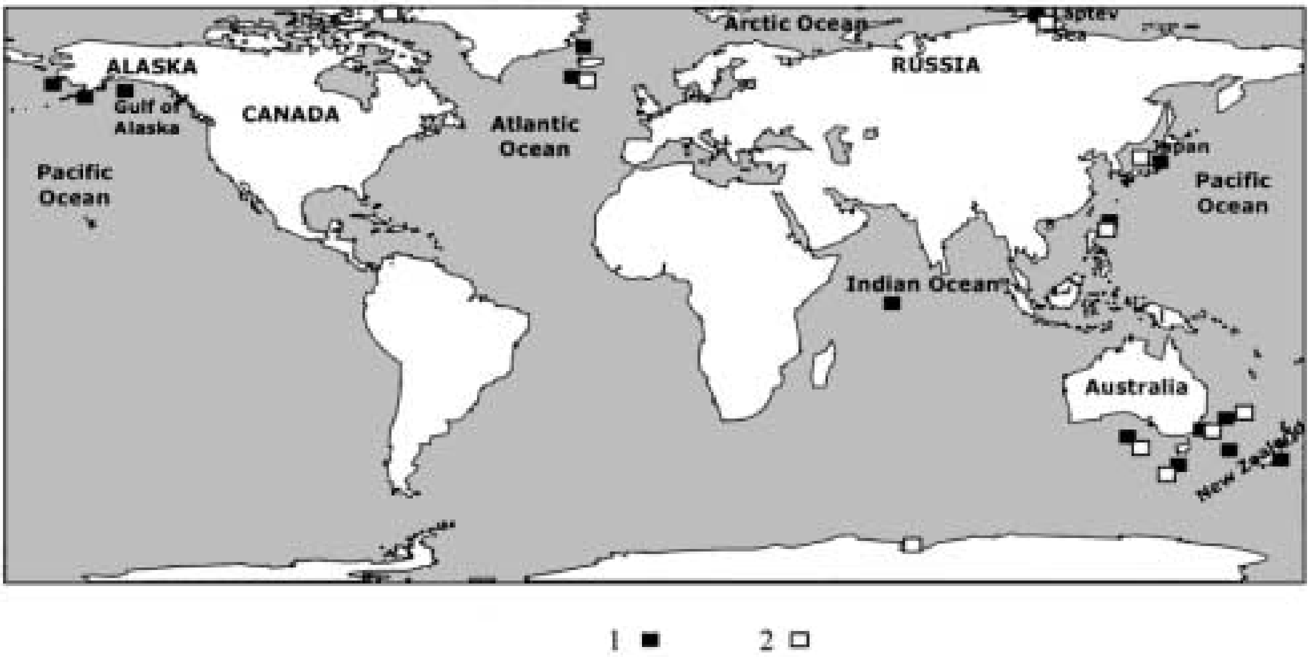


FIGURE 11–Distribution of *Cytheropteron perlaria.* See key Fig. 2.

merge forming two elongated nodes. Valves pierced by pore canals, pore puncta arranged in subvertical rows.

Measurements, mm.–

	L	H
MSU292/268	0.36	0.22
MSU292/282	0.39	0.25
MSU292/47	0.41	0.22

Variability.–Ornament of specimens is highly variable. Compared to our exemplars, specimens shown in most published micrographs possess more pronounced ribs on anterior part of valve and above posterior ala edge. Therefore, when these ribs merge, nodes they form on dorsal side are considerably bigger.

Comparison.–*Cytheropteron elaeni* differs from *C. nodosum* Brady, 1868 from surface sediments of the seas around Great Britain and Ireland (Brady, 1868a, pp. 448-449, Pl. XXXIV, Figs. 31-34) in the absence of pronounced reticulation and presence of smaller nodes on dorsal side.

FIGURE 12–Distribution of *Cytheropteron porterae.* See key Fig. 5.

Remarks.–Cronin (1981) described species *Cytheropteron nealei* Cronin, 1981. Later this name was considered to be non-valid, being twice used earlier by other authors ("*Cytheropteron*" *nealei* Jarn, 1975, and *Cytheropteron*? *nealei* Joy and Clark, 1977), consequently Cronin (1989) gave this species a new name *Cytheropteron elaeni* Cronin, 1989.

The specimen from the Iceland Sea identified by Didié *et al.* (1999) as *Cytheropteron bronwynae* (Didié *et al.*, 1999, Pl. I, Fig. 14) we would refer to as *C. elaeni*.

Fossil distribution.–Neogene-Quaternary: Novaya Zemlya; Pleistocene: Kola Peninsula, Lower Severnaya Dvina River, Lower Pechora River, Taimyr Peninsula, Gulf of Alaska, Bering Sea, Beaufort Sea, Champlain Sea, Goldthwait Sea (Quebec); Holocene: Laptev Sea, eastern Kara Sea (Fig. 7).

Modern distribution.– Greenland Sea, Iceland Sea, Norwegian Sea, White Sea, Barents Sea, Kara Sea, eastern Laptev Sea, Chukchi Sea, Canadian Arctic, Beaufort Sea, Hudson Bay, Labrador Sea (Fig. 7).

Material.–One hundred thirty-seven valves, 20 carapaces and 25 juvenile valves from the Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron inflatum Brady, Crosskey and Robertson, 1874
Pl. I, Figs. 13, 14

1868 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Brady, 1868b, Pl. V, Figs. 8-10 (nomen nudum).

1874 *Cytheropteron inflatum* Brady, Crosskey and Robertson, p. 204, Pl. VIII, Figs. 24-27, Pl. XIV, Figs. 26-29.

1889 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Brady & Norman, p. 209, Pl. XX, Figs. 19-21.

1928 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Sars, p. 231, Pl. CVI, Fig. 2.

1962 *Cytheropteron testudo* Sars - Woszidlo, Pl. 5, Fig. 15.

1979 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Whatley & Masson, p. 237, Pl. 8, Figs. 8, 13-16.

1981 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Cronin, p. 404, Pl. 2, Figs. 3-4.

1983 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Lev, p. 118, Pl. XV, Figs. 7-8.

1989 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Cronin, Pl. V, Fig. 11.

1996 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Whatley *et al.*, Pl. 2, Figs. 1-2.

1998 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Whatley *et al.*, Pl. 1, Figs. 20, 21.
2003 *Cytheropteron inflatum* Brady, Crosskey and Robertson - Stepanova *et al.*, 2003a, Pl. II, Fig. 1.

Type series.–Brady *et al*, 1874, p. 204, Pl. VIII, Figs. 24-27; Scotland, Errol; Pleistocene; Pl. XIV, Figs. 26-29; Scotland, Drylers; Pleistocene.

Description.–Carapace medium, subtriangular in lateral view, with flattened anterior and posterior margins. Dorsal margin arcuately convex, gradually beveled towards anterior and posterior margins. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, subtriangular. Greatest length at mid-height, greatest height in the center of valve. Strongly inflated lateral expansion above ventral margin. Several fine ribs follow its outline and form weakly developed fossae on posterior margin of valve. Valve surface bears numerous sporadically distributed puncta with pore canals.

Measurements, mm.–

	L	H
MSU292/71	0.55	0.25
MSU292/119	0.36	0.21
MSU292/73	0.37	0.18
MSU292/281	0.33	0.22

Variability.–Ornamentation is slightly variable. Some specimens of *C. inflatum* given in publications differ from our exemplars in occurrence of fine ribs not only on ventral, anterior and posterior margins, but on the whole valve surface where they form weakly developed fossae.

Comparison.–*Cytheropteron inflatum* differs from *C. walli* Whatley and Masson, 1979 from Pleistocene through Recent sediments of Great Britain (Whatley & Masson, 1979, p. 256, Pl. 8, Figs. 1, 3-6) in absence of distinct reticulation, more inflated carapace, and less defined lateral expansion.

Compared to *Cytheropteron testudo* Sars, 1869 (Sars, 1928, p. 230, Pl. CVI, Fig. 1), *C. inflatum* has a more laterally inflated carapace, less abundant pore puncta, and no wing-like process.

Remarks.–In Brady (1868b) only illustrations of *Cytheropteron inflatum* are given. The first description of this species was published in 1874. That is why this year is considered as the year of its attribution.

In the publication devoted to the Pleistocene ostracods of Germany, Woszidlo (1962) identified species *Cytheropteron testudo* (Woszidlo, 1962, Pl. 5, Fig. 15), which we consider to be *Cytheropteron inflatum* (see also remarks in Whatley & Masson, 1979).

FIGURE 13–Distribution of *Cytheropteron pseudomontrosiense.* See key Fig. 2.

Fossil distribution.–Quaternary: Cheshskaya Bay coast, Lower Severnaya Dvina River, Lower Pechora River, Novaya Zemlya, Lower Yenisei River, Taimyr Peninsula, North Sea; Pleistocene: Scotland, Northern Germany (Schleswig-Holstein), Denmark, Champlain Sea, Goldthwait Sea (Quebec), Monreal (Canada); Holocene of the Laptev Sea (Fig. 8).

Modern distribution.–North Atlantic, Greenland Sea, Norwegian Sea, Great Britain coast, Barents Sea, Spitsbergen coast, Kara Sea, western Laptev Sea, Beaufort Sea, Canadian Arctic, Baffin Sea, Hudson Bay (Fig. 8).

Material.–Twenty-six valves from Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron montrosiense Brady, Crosskey and Robertson, 1874
Pl. I, Figs. 15, 16

1868 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Brady, 1868b, Pl. 5, Figs. 1-3 (not Pl. 5, Figs. 4-5) (nomen nudum).

1874 *Cytheropteron montrosiense* Brady, Crosskey and Robertson, p. 205, Pl. 8, Figs. 28-32 (not Pl. 8, Figs. 33-36, Pl. 14, Figs. 13-16).
1962 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Woszidlo, Pl. 5, Fig. 13.
1972 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Lev, Pl. 1, Figs. 18-19.
1978 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Robinson, Pl. 6, Fig. 5a (not 5b).
1979 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Whatley & Masson, p. 240, Pl. 2, Figs. 1-4, 6.
1983 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Lev, p. 117, Pl. XV, Fig. 4, Pl. XVI, Figs. 8-9.
1986 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - McDougall *et al.*, Pl. 12, Figs. 3, 5 (not Pl. 12, Figs. 1, 2, 4, 6, 7).
1989 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Cronin, Pl. V, Fig. 2.
1993 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Lord *et al.*, Pl. 3, Figs. 1-2.
1996 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Whatley *et al.*, Pl. 2, Figs. 3-4.
1999 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Kupriyanova, Pl. 2, Fig. 3.
2003 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Stepanova *et al.*, 2003a, Pl. I, Fig. 15.

FIGURE 14–Distribution of *Cytheropteron sulense*. See key Fig. 2.

Type material.–Type specimens are stored in the Hancock Museum in Newcastle, type locality – Scotland, Drylers, Montrose; Pleistocene.

Description.–Carapace medium, subrhomboidal in lateral view, with flattened anterior and posterior margins. Dorsal margin straight, gradually passing into anterior margin through obtuse cardinal angle, and into posterior margin through slight concavity. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, caudate, slightly upturned towards dorsal margin. Greatest length at mid height, greatest height in center of valve. Valves differ in outline: right valves with more convex dorsal margin. Caudal process slightly convex in postero-dorsal part in left valves, and concave in right valves. Laterally inflated expansion above ventral margin, with extremity shaped as a massive spine in posterior third of valve. Surface reticulate: subvertically elongated fossae at anterior and posterior margins, and rounded ones in central part.

Measurements, mm.–

	L	H
MSU292/130	0.34	0.18
MSU292/180	0.51	0.25
MSU292/266	0.47	0.24

Variability.–Reticulation slightly varies in its degree, possibly due to preservation.

Comparison.–*Cytheropteron montrosiense* differs from *C. sulense* Lev, 1972 in presence of massive spine on lateral expansion.

Remarks.–In Brady (1868b) only illustrations of *Cytheropteron montrosiense* are given. The first description of this species was published in 1874 that is why this year is considered as the year of its attribution.

Fossil distribution.–Neogene-Quaternary marine deposits: Lower Izhma river, Lower Severnaya Dvina River, Vaigach Island, Novaya Zemlya, Lower Ob River, Lower Yenisei River; Quaternary: North Sea, Pechora Sea; Pleistocene: Ireland, Scotland, Northern Germany (Schleswig-Holstein), Great Britain, Boston “blue clay” (Massachusetts); Late Pleistocene-Holocene

FIGURE 15–Distribution of *Cytheropteron suzdalskyi*. See key Fig. 2.

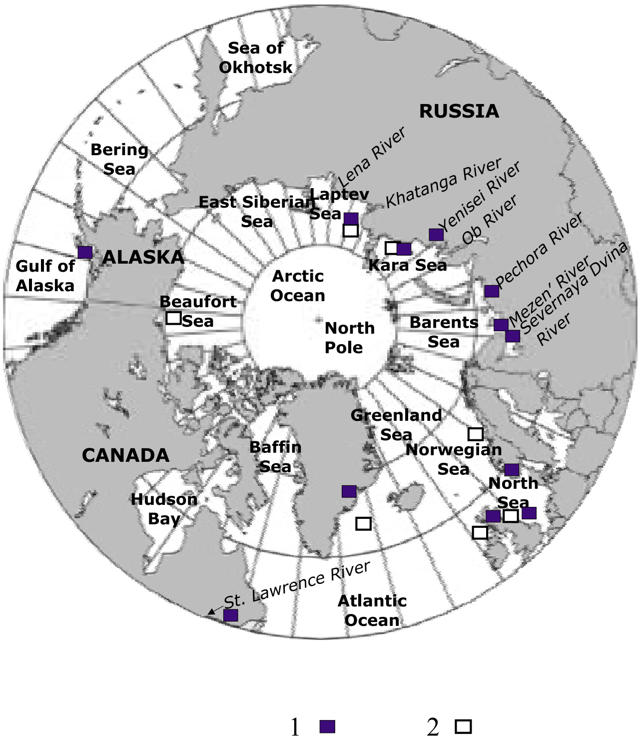


FIGURE 16–Distribution of *Cytheropteron tumefactum*. See key Fig. 2.

of the Beaufort Sea; Holocene: Laptev Sea, eastern Kara Sea (Fig. 9).

Modern distribution.–Greenland Sea, Norwegian Sea, Great Britain coast, White Sea, Barents Sea, Kara Sea, eastern Laptev Sea, East Siberian Sea, Beaufort Sea, Baffin Sea (Fig. 9).

Material.–Twelve valves and 5 carapaces from Holocene deposits and surface Recent sediments of the Laptev Sea.

Cytheropteron nodosoalatum Neale and Howe, 1973
Pl. I, Figs. 17, 18

1973 *Cytheropteron nodosoalatum* Neale & Howe, p. 240, Pl. 1, Figs. 6, 7a, b.

1975 *Cytheropteron nodosoalatum* Neale & Howe, Pl. 6, Figs. 8, 10, Pl. 7, Figs. 2, 4, 10, 11.

1979 *Cytheropteron nodosoalatum* Neale & Howe - Whatley & Masson, p. 242, Pl. 6, Figs. 3, 5, 6, 10.

1980 *Cytheropteron nodosoalatum* Neale & Howe - Lord, Pl. 2, Fig. 16.

1987 *Cytheropteron nodosoalatum* Neale & Howe - Cronin & Ikeya, p. 84, Pl. 3, Figs. 1, 2.

1989 *Cytheropteron nodosoalatum* Neale & Howe - Cronin, Pl. IV, Figs. 1-4.

2003 *Cytheropteron nodosoalatum* Neale & Howe - Stepanova *et al.*, 2003a, Pl. II, Figs. 3, 4.

Holotype.–University of Hull, HVH 9787; left valve; England, Yorkshire, Dimlington; Pleistocene.

Description.–Carapace medium, subrhomboidal in lateral view, with flattened anterior and posterior margins. Dorsal margin slightly convex, gradually beveled towards anterior and posterior margins, and slightly concave passing into them. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded and bent towards ventral margin. Posterior margin lower than anterior, caudate, slightly upturned towards dorsal margin. Greatest length at mid height, greatest height in center of valve. Valves differ in outline: right valves shorter and higher with more convex dorsal margin. Caudal process straight or slightly convex in postero-dorsal part in left valves, and slightly concave in right valves. Broad lateral wing-like expansion, subdivided by a depression in its central part, overlaps ventral margin. On ala edges massive nodes flank this depression and give it a bipartite appearance. Surface reticulate and punctate, fossae and puncta in subvertical rows, fossae predominantly restricted to posterior part of valve, and puncta over the entire surface. In central part round puncta prevail, on anterior and posterior margins they are considerably smaller and occur more densely. Elongated subvertical fossae with low muri above posterior node of ala. Fine rib stretches from lower part of anterior margin of valve, runs along ala edge, and ends at its posterior edge. Here it splits into two or three upward branches; at mid-height point of valve they merge with fossae muri. Fine rib equal in length to dorsal margin runs slightly below and parallel to it. Several fine ribs parallel to ventral margin, below ala expansion, run from lower anterior part of valve and merge with fossae muri on posterior part. Thread-like ribs forming fossae with puncta inside occur on posterior third of valve and anterior margin.

Measurements, mm.–

	L	H
MSU292/39	0.55	0.29
MSU292/81	0.43	0.23
MSU292/213	0.56	0.34

1 ■ 2 □

FIGURE 17–Distribution of *Cytheropteron laptevensis* Stepanova sp. nov. See key Fig. 2.

*Variability.–*Ornamentation varies from densely punctate surface to well developed fossae with puncta within them.

Comparison.–Cytheropteron nodosoalatum differs from *C. champlainum* Cronin, 1981 from Pleistocene deposits of the Goldthwait Sea and Presumpscot formation (Maine), in having massive nodes on the alate expansion.

*Fossil distribution.–*Plio-Pleistocene of Japan; Pleistocene: Great Britain, North Sea, SE Virginia, Goldthwait Sea and Presumpscot formation (Maine); Holocene of the Laptev Sea (Fig. 10).

*Modern distribution.–*Irish Sea, Norwegian Sea, White Sea, Barents Sea, Franz Josef Land coast, Novaya Zemlya coast, Kara Sea, Laptev Sea, Chukchi Sea, Gulf of Alaska, Beaufort Sea, Canadian Arctic, Baffin Sea, Davis Strait, Labrador Sea, southern and eastern coasts of Greenland (Fig. 10).

*Material.–*Thirteen valves and one carapace from Holocene deposits and surface Recent sediments of the Laptev Sea.

Cytheropteron perlaria Hao, 1988

Pl. II, Figs. 32, 33

1987 *Cytheropteron testudo* Sars - Whatley & Coles, Pl. 3, Fig. 1.
1988 *Cytheropteron testudo* Sars - Whatley & Ayress, Pl. 1, Figs. 7-8.
1988 *Cytheropteron perlaria* Hao sp. nov. - Hao, p. 280, pl. 47, Figs. 4-9.
1994 *Cytheropteron carolae* Brouwers, 1994, p. 17, Pl. 8, Figs. 12-14.
1999 *Cytheropteron perlaria* Hao - Swanson & Ayress, Pl. I, Figs. 7-13; Pl. II, Figs. 1-3.
1999 *Cytheropteron* sp. aff. *perlaria* Hao - Swanson & Ayress, Pl. 7, Figs. 1-6; Pl. 8, Fig. 1.
2003 *Cytheropteron testudo* Sars - Stepanova *et al.*, 2003a, Pl. II, Figs. 5, 6.

*Holotype.–*Chinese University of Geosciences in Beijing; left valve, N 40212; Okinawa Trough, station 919, 865; Late Pleistocene.

*Description.–*Carapace small, subtriangular in lateral view, with flattened anterior and posteroir margins. Dorsal margin slightly convex, more convex in right valves, strongly bent towards posterior margin, so that it almost touches ventral margin. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded, bent towards ventral margin. Posterior margin considerably lower than anterior, caudate. Caudal process in postero-dorsal part straight or slightly convex in left valves, and slightly concave in right ones. Greatest length right above ventral margin, greatest height at anterior hinge edge. Wing-like expansion with rounded edge above ventral margin, flat, peak-like, subvertical to valve surface. Rib along ala edge. Two fine ribs right above ala expansion. At anterior margin one or several (maximum 3) thread-like ribs. They stretch from ala base parallel to anterior margin, reach dorsal margin, where they turn toward posterior margin and extend further parallel to dorsal margin. These ribs do not reach posterior part of valve. Valve surface evenly densely punctate. Puncta small, round.

Measurements, mm.–

	L	H
MSU292/69	0.37	0.21
MSU292/70	0.34	0.18
MSU292/71	0.36	0.2

*Variability.–*Number of fine ribs parallel to anterior and dorsal margins varies from one to three.

Comparison.–Cytheropteron perlaria Hao, 1988 differs from *Cytheropteron testudo* Sars, 1869 from Australian waters (Swanson & Ayress, 1999, p. 157, Pl. 4, Figs. 1-12; Pl. 5, Figs. 1-13; Pl. 6, Figs. 10-12) in having considerably smaller size, not exceeding 0.5 mm, while maximum carapace length of C. *testudo* is usually more than 0.5 mm.

*Remarks.–*Swanson & Ayress (1999) included *Cytheropteron perlaria* into the “species group” *Cytheropteron testudo*, that also includes: *C. delphinium*, *C. bikurangiensis*, *C. sarsi*, *C. taciturnum*, *C. testudo*, *C. wellmani*. All these species are morphologically very similar, and some of them are cosmopolites. Both *C. perlaria* and *C. testudo* were reported from the Arctic and North Atlantic. From our point of view the only obvious difference in carapace morphology between these two species is the carapace size. Previously we mistakenly attributed our specimens to *C. testudo* Sars, 1869, but according to Swanson & Ayress (1999), they should be referred to as *C. perlaria* Hao, 1988, since all of them do not exceed 0.5 mm.

Swanson & Ayress (1999) consider distribution of *C. perlaria* Hao, 1988 to be subordinated by that of *Cytheropteron testudo* Sars, 1869, but in their paper they mainly list findings of *C. perlaria* in the Southern Hemisphere. Therefore, we suppose that most findings of *Cytheropteron testudo* might also contain specimens of *C. perlaria,* since distinguishing of these species is very complicated.

We consider *Cytheropteron carolae* Brouwers (1994, p. 17, Pl. 8, Figs. 12-14) from Pleistocene through Holocene deposits of the Gulf of Alaska to be a synonym of *Cytheropteron perlaria* Hao, 1988. In original description of *C. carolae* there is no comparison with *C. perlaria* and also, in our opinion, the reference list does not include any publication with illustrations of *C. perlaria*. Therefore, we conceive it to be expedient to attribute specimens shown in Brouwers (1994) to *C. perlaria* Hao, 1988.

*Fossil distribution.–*Late Paleogene and Neogene deposits of: SW Pacific Ocean, Indian Ocean, North Atlantic Ocean. Late Eocene (Ototara limestone, Ashley mudstone) of New Zealand; Miocene-Pleistocene: New Caledonia basin, Lord Howe Rise, Challenger Platean; Pleistocene-Holocene: North Atlantic, Gulf of Alaska, Cook Inlet, Pribilof Islands, South Australian continental slope, East Australian continental slope, Tasman Sea; Holocene: Queensland Plateau, western Laptev Sea, Denmark Strait (Fig. 11).

*Modern distribution.–*North Atlantic, western Laptev Sea, China Sea, Okinawa Trough, Queensland Plateau, New Caledonia basin, Lord Howe Rise, Challenger Plato, East Australian continental slope, South Australian continental slope, Kerguelen Plateau, Prydz Bay (Antarctica) (Fig. 11).

*Material.–*Fourteen valves and 10 carapaces from Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron porterae Whatley and Coles, 1987
Pl. I, Figs. 19-21

1987 *Cytheropteron porterae* Whatley & Coles, p. 64, Pl. 2, Figs. 21-23.
1996 *Cytheropteron porterae* Whatley & Coles - Whatley *et al*., Pl. 2, Figs. 7, 9.
1998 *Cytheropteron porterae* Whatley & Coles - Whatley *et al*., Pl. 2, Figs. 1-2.
2001 *Cytheropteron porterae* Whatley & Coles - Didié, Pl. 2, Figs. 19-21.
2003 *Cytheropteron porterae* Whatley & Coles - Stepanova *et al*., 2003a, Pl. II, Figs. 10, 11.

*Holotype.–*Micropalaeontology Collections stored at Palaeontological Department, National History Museum, London, OS 12536; adult right valve, North Atlantic, DSDP site 607, Lat. 41º00’07”N, Long. 32º54’44” W, core 15 c.c., NN Zone 16, Late Pliocene.

*Description.–*Carapace medium, subrhomboidal in lateral view, with flattened anterior and posterior margins. Dorsal margin arcuately convex, in right valves stronger than in left ones, gradually beveled towards anterior and posterior margins. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded and bent towards ventral margin. Posterior margin lower than anterior, strongly caudate, slightly upturned towards dorsal margin. Greatest length at mid-height, greatest height at mid-length. Ala with gently rounded anterior edge and subvertical posterior edge. At ala base, a row of several (4-6) subvertically elongated fossae punctate within. The nearest to anterior margin fossa contains a large pit. Above the row of fossae, ala surface is smooth. Central part of valve bears subvertical rows of puncta. On posterior and, rarely, anterior margins, thread-like ribs run parallel to them forming weakly developed fossae.

Measurements, mm.–

	L	H
MSU292/61	0.59	0.28
MSU292/74	0.52	0.23
MSU292/89	0.4	0.17

*Variability.–*Reticulation varies in its degree on anterior and posterior margins; on anterior margin often not developed.

Comparison.–Cytheropteron porterae is distinguished from *C. carolinae* Whatley and Coles, 1987 from the Quaternary deposits of the North Atlantic (Whatley & Coles, 1987, p. 60-61, Pl. 2, Figs. 6, 7, 9) in its larger size and presence of puncta partially covering valve surface. *C. carolinae* has puncta over the entire surface and lacks reticulation and puncta at the base of the ala.

*Fossil distribution.–*Tentative findings in deep water Miocene deposits of the Indian Ocean; Pliocene-Quaternary: N. Atlantic; Pleistocene-Holocene: western Laptev Sea; Holocene of the eastern Kara Sea (Fig. 12).

*Modern distribution.–*Greenland Sea, Newfoundland, North Atlantic, Kara Sea and western Laptev Sea (Fig. 12).

*Material.–*Eighty valves and 13 carapaces from Late Pleistocene to Holocene deposits and Recent surface sediments of the western Laptev Sea.

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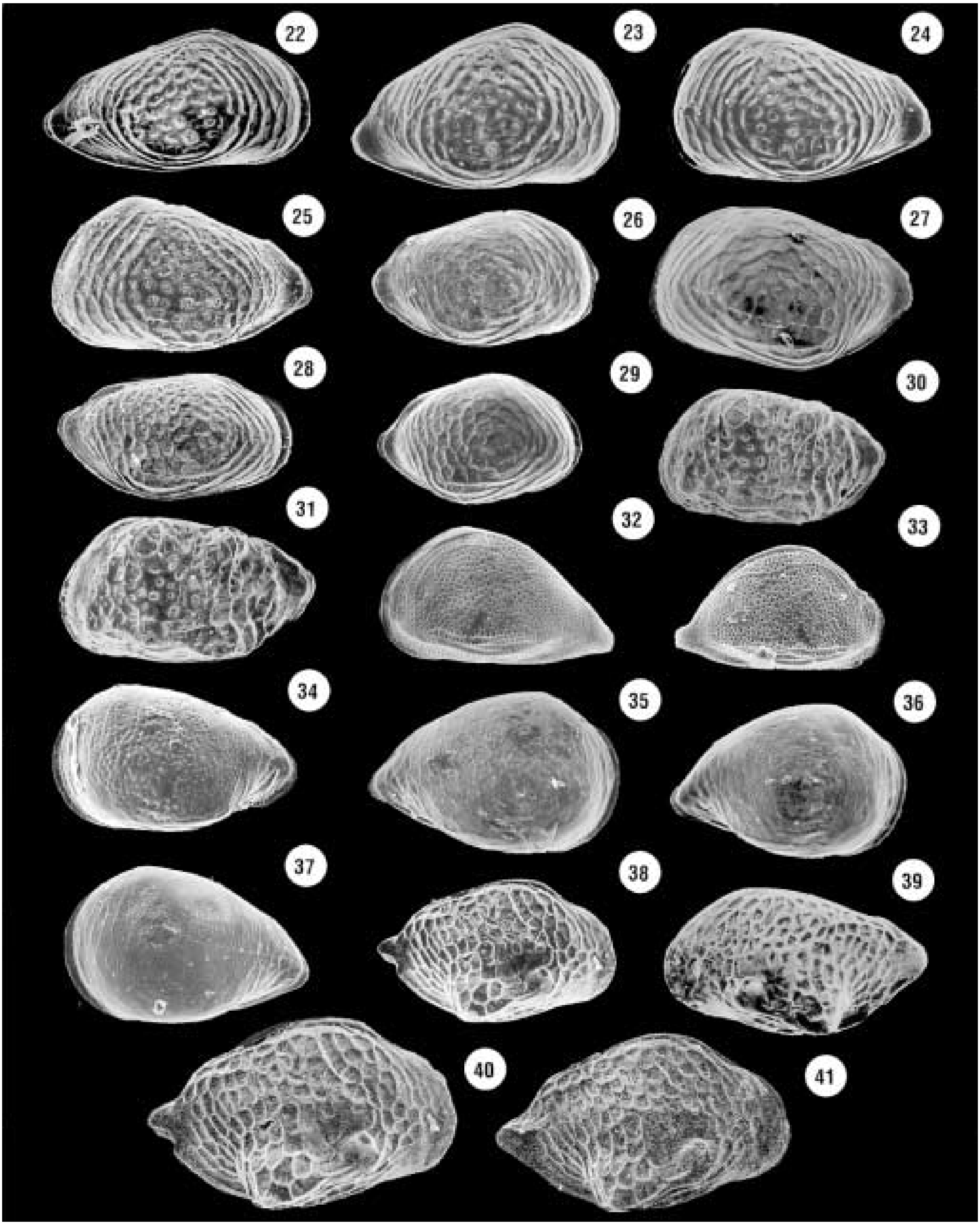
PLATE 2–*22-25, Cytheropteron pseudomontrosiense* Whatley and Masson, 1979; *22,* right valve, external view, MSU292/285, x135; *23,* right valve, external view, MSU292/286, x155; *24,* left valve, external view, MSU292/287, x120; late Pleistocene of the western Laptev Sea; *25,* left valve, external view, collection of Lev (NIIGA), from sample N18, x100, identified by O.M. Lev as *Cytheropteron sulense;* late Pliocene-Pleistocene of the Malozemel'skaya tundra. *26-29, Cytheropteron sulense* Lev, 1972; *26,* right valve, external view, collection of Lev (NIIGA), N1183-69, x100; *27,* left valve, external view, collection of Lev (NIIGA), N1183-68, x100; late Pliocene-Pleistocene of the Malozemel'skaya tundra; *28,* right valve, external view, MSU292/179, x65; *29,* right valve, external view, MSU292/135, x85; Holocene and recent surface sediments of the eastern Laptev Sea. *30, 31, Cytheropteron suzdalskyi* Lev, 1972; *30,* left valve, external view, MSU292/49, x75; *31,* left valve, external view, MSU292/267, x85; Holocene and recent surface sediments of the eastern Laptev Sea. *32, 33, Cytheropteron perlaria* Hao, 1988; 32, left valve, external view, MSU292/71, x120; *33,* right valve, external view, MSU292/69, x96; recent surface sediments of the western-central Laptev Sea. *34-37, Cytheropteron tumefactum* Lev, 1972; *34,* left valve, external view, collection of Lev (NIIGA), from sample 2302 (identified by O.M. Lev as *Cytheropteron punctatum*), x105; *35,* right valve, external view, collection of Lev (NIIGA), from sample 2302 x105; late Pliocene-Eopleistocene of the Arkhangelsk region; *36,* right valve, external view, MSU292/60, x96; *37,* left valve, external view, MSU292/264, x115; recent sediments of the western-central Laptev Sea. *38-41, Cytheropteron laptevensis* Stepanova sp. nov.; *38,* right valve, external view, MSU292/278, x110; *39,* left valve, external view, MSU292/280, x135; *40,* right valve external view, MSU292/253, x145; *41,* right valve external view, MSU292/234, x125; Pleistocene-Holocene of the western Laptev Sea.

PLATE II



Cytheropteron pseudomontrosiense Whatley and Masson, 1979
Pl. II, Figs. 22-25

1874 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Brady *et al*., p. 205, Pl. VIII, Figs. 33-36 (not Pl. 8, Figs. 28-32, Pl. 14, Figs. 13-16).
1889 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Brady & Norman, p. 216, Pl. XIX, Figs. 26-27.
1963 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Swain, p. 817, Pl. 95, Fig. 14 (not Pl. 97, Fig. 21).
1977 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Cronin, Pl. III, Fig. 19.
1978 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Robinson, Pl. 6, Fig. 5b (not 5a).
1979 *Cytheropteron pseudomontrosiense* Whatley & Masson, p. 247, Pl. 2, Figs. 5, 7-10, 13, 14.
1980 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Lord, Pl. 2, Figs. 1-6.
1981 *Cytheropteron pseudomontrosiense* Whatley & Masson - Cronin, p. 404, Pl. 6, Figs. 5, 7.
1989 *Cytheropteron pseudomontrosiense* Whatley & Masson - Cronin, Pl. V, Fig. 4.
1991 *Cytheropteron pseudomontrosiense* Whatley & Masson - Brouwers *et al*., Pl. 3, Fig. 2.
1999 *Cytheropteron pseudomontrosiense* Whatley & Masson - Kupriyanova, Pl. 2, Fig. 8.

Holotype.–Micropalaeontology Collections stored at the Palaentological Department, National History Museum, London, OS 10830; adult left valve, North Sea, Forties Field borehole, DB 13, Lat. 57º43’54.5’’N, Long.00º58’25.5’’ E, depth in core 5 m, upper part of the Quaternary succession.

Description.–Carapace medium, subtriangular in lateral view, with flattened anterior and posterior margins. Dorsal margin almost straight, slightly concave in posterior part, gradually beveled towards anterior and posterior margins. Dorsal margin passes into anterior margin through obtuse cardinal angle. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, caudate. Greatest length at lower third, greatest height at anterior hinge edge. Valves differ in outline: right valves with more convex (distinct) cardinal angles, and left valves with gradually sloping cardinal angles. Caudal process in postero-dorsal part straight or slightly convex in left valves, and slightly concave in right valves. Rounded laterally inflated expansion above ventral margin. Surface is reticulate, fossae distributed concentrically; in the central part of valve fossae rounded, on margins elongated. Above ventral margin fossae muri merge into ribs contouring lateral expansion.

Measurements, mm.–

	L	H
From sample N18, Belush’e, Identified as C. sulense (collection of O.M. Lev, VNIIOkeangeologiya)	0.41	0.24
N 292/285	0.37	0.19
N 292/286	0.32	0.19
N 292/287	0.39	0.21

Variability.–The degree of reticulation is variable. Usually fossae are well expressed.

Comparison.–*Cytheropteron pseudomontrosiense* differs from *Cytheropteron sulense* Lev, 1972 (Lev, 1972, p. 18, Pl. 1, Figs. 14-17) from the Late Pliocene-Early Pleistocene deposits of Arkhangel’sk Region in having solely subtriangular lateral valve outline, while *C. sulense* is ovate or trapeziform in lateral view.

Remarks.–We consider *C. pseudomontrosiense* and *C. sulense* to be two distinct species. The most interesting fact is that in original descriptions of both species, their authors (Lev, 1972, Whatley & Masson, 1979) put the same illustrations in the synonym list (Brady *et al*, 1874, p. 205, Pl. 8, Figs. 33-36). We studied the collection of O.M. Lev stored in St. Petersburg in order to clearify this confusion. Most specimens shown in Lev (1972, 1983) are trapeziform, while *C. pseudomontrosiense* valves in published micrographs demonstrate a predominantly subtriangular outline. In Lev’s collection we found specimens of both morphotypes. Thus, we suppose that Lev considered only trapeziform carapaces as adults, while subtriangular ones she thought to be late moult stages. Originally Whatley & Masson (1979) published micrographs of subtriangular specimens, though some of them were almost trapeziform. Specimens of both morphotypes are present in our samples from the Laptev Sea. All surface samples and Holocene sediment samples from the eastern Laptev Sea mainly contain specimens of *C. sulense*, but the Late Pleistocene – Holocene sediments from the western Laptev Sea are dominated by *C. pseudomontrosiense*. At the same time, specimens of another morphotype are always present in small amounts. Since publications of Lev (1972, 1983) are in

Russian, they are not widely known abroad. Therefore, both morphotypes in foreign publications are named *C. pseudomontrosiense* (or *C. montrosiense*). Despite this fact we consider them as separate species (according with Whatley, pers. comm., 2003, and Briggs, pers. comm., 2003). Therefore, subtriangular specimens are referred to as *C. pseudomontrosiense,* and subovate and trapeziform ones - as *C. sulense*.

Fossil distribution.–Pliocene of Greenland; Quaternary: North Sea, Pechora Sea; Pleistocene: Great Britain, Norway, Champlain Sea; Pleistocene-Holocene: Norwegian Sea, western Laptev Sea (Fig. 13).

Modern distribution.– East Siberian Sea, Beaufort Sea, Baffin Sea, Spitsbergen coast (Fig. 13).

Material.–Fifty-three valves and 2 carapaces from Late Pleistocene to Holocene deposits of the western Laptev Sea.

Cytheropteron sulense Lev, 1972
Pl. II, Figs. 26-29

1868 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Brady, 1868b, Pl. 5, Figs. 4-5 (not Pl. 5, Figs. 1-3).

1963 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Swain, p. 817, Pl. 97, Fig. 21 (not Pl. 95, Fig. 14).

1972 *Cytheropteron sulense* Lev, p. 18, Pl. 1, Figs. 14-17.

1983 *Cytheropteron sulense* Lev, Pl. XVI, Figs. 12, 13.

1986 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - McDougall *et al.*, Pl. 12, Figs. 1, 2, 4, 6 (not Pl. 12, Figs. 3, 5, 7).

1988 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Siddiqui, Pl. 2, Fig. 4.

1991 *Cytheropteron* cf. *C. montrosiense* Brady, Crosskey and Robertson - Brouwers *et al.*, Pl. 2, Fig. 5.

1991 ?*Cytheropteron* sp. 3 - Brouwers *et al.*, Pl. 2, Fig. 7.

1999 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Schoning & Wastegärd, Pl. 1, Fig. 4.

2003 *Cytheropteron sulense* Lev - Stepanova *et al.*, 2003a, Pl. I, Figs. 12, 13.

Holotype.–Collection stored at VNIIOkeangeologiya, St. Petersburg, N1183-66; adult right valve; Russia, Arkhangel'sk Region, Malozemel'skaya tundra, Sula River, Kotkino, Late Pliocene-early Pleistocene.

Description.–Carapace medium, trapeziform to ovate in lateral view, with flattened anterior and posterior margins. Dorsal margin almost straight, slightly concave in posterior part, gradually beveled towards anterior and posterior margins. Dorsal margin passes into anterior margin very gradually. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, caudate. Greatest length slightly higher of mid-height, greatest height at anterior hinge edge. Valves differ in outline: right valves with more convex (distinct) cardinal angles, and left valves with gradually sloping cardinal angles. Caudal process in posteroventral part slightly convex in left valves, and slightly concave in right valves. Rounded laterally inflated expansion above ventral margin. Surface is reticulate, fossae distributed concentrically; in the central part of valve fossae rounded, on margins elongated. Above ventral margin fossae muri merge into ribs contouring lateral expansion.

Measurements, mm.–

	L	H
N1183-68 (collection of O.M. Lev, VNIIOkeangeologiya)	0.51	0.3
N1183-69 (collection of O.M. Lev, VNIIOkeangeologiya)	0.42	0.23
MSU292/135	0.44	0.27
MSU292/179	0.47	0.23

Variability.–The degree of reticulation is variable. Usually fossae are well expressed.

Comparison.–For comparison with morphologically similar species see description of *C. montrosiense* given above.

Remarks.–See remarks to *C. pseudomontrosiense. Cytheropteron sulense* was often confused with both *C. montrosiense* and *C. pseudomontrosiense*. Here we consider the specimens given in McDougall, 1986 (Pl. 13, Figs. 1, 2, 4, 6) from the Late Pleistocene – Holocene deposits of the Beaufort shelf as *C. sulense,* because all these specimens demonstrate solely subovate lateral outline.

Fossil distribution.–Pliocene of Greenland; Late Pliocene-Pleistocene of Malozemel'skaya tundra; Holocene of the eastern Laptev Sea; Late Pleistocene-Holocene of the Baltic Sea, Beaufort Sea (Fig. 14).

Modern distribution.–Novaya Zemlya coast, Kara Sea, eastern Laptev Sea, Chukchi Sea, Hudson Bay, Canadian Arctic, Beaufort Sea, Baffin Sea (Fig. 14).

Material.–One hundred twenty-five valves and 18 carapaces from Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron suzdalskyi Lev, 1972
Pl. II, Figs. 30, 31

1972 *Cytheropteron suzdalskyi* Lev, p. 19, Pl. 1, Figs. 1-5.
1975 *Cytheropteron* cf. *nodosum* Brady - Neale & Howe, Pl. 7, Fig. 5.
1983 *Cytheropteron suzdalskyi* Lev, Pl. XV, Figs. 13, 14.
1989 *Cytheropteron* cf. *suzdalskyi* Lev - Cronin, Pl. IV, Fig. 8.
1994 *Cytheropteron suzdalskyi* Lev - Brouwers, p. 35, Pl. 18, Figs. 4, 5.
1999 *Cytheropteron suzdalskyi* Lev - Kupriyanova, Pl. 2, Fig. 4.
2003 *Cytheropteron suzdalskyi* Lev - Stepanova *et al.*, 2003a, Pl. I, Fig. 11.

Holotype.–Collection VNIIOkeangeologiya, N1183-87; adult right valve, Russia, Arkhangel’sk Region, Lower Severnaya Dvina River, Ust’-Pinega; early Late Pleistocene.

Description.–Carapace medium, trapeziform in lateral view, with flattened posterior margin. Dorsal margin slightly convex, almost straight, gradually beveled towards margins. Ventral margin straight, parallel to dorsal margin. Anterior margin arcuately rounded and bent towards ventral margin. Posterior margin lower than anterior, caudate, slightly upturned towards dorsal margin. Greatest length at upper third of valve, greatest height at anterior hinge edge. Right valves higher and shorter, with more convex dorsal margin. Caudal process in postero-ventral part in left valves straight, and slightly concave in right ones. Broad lateral bipartite wing-like expansion, subdivided by depression into two massive nodes. Another two massive nodes in dorsal part are restricted to hinge margins, they are slightly bigger than ala nodes. Valve surface, except for posterior part of valve, reticulate. Fossae arranged in rows. Fossae subvertically elongated at anterior and posterior margins and rounded in central part of valve. Fossae punctate in base. On ventral margin high fossae muri form several ribs parallel to it and contouring ala outline.

Measurements, mm.–

	L	H
MSU292/49	0.54	0.32
MSU292/267	0.55	0.3
MSU292/143	0.53	0.3

Variability.–Reticulation may vary in its degree; sometimes fossae are not developed, but puncta are always present.

Comparison.–*Cytheropteron suzdalskyi* differs from *C. nodosum* Brady, 1868 from Recent marine sediments around Great Britain and Ireland (Brady, 1868a, p. 448, Pl. XXXIV, Figs. 31-34) in having more pronounced reticulation and considerably more massive nodes on the dorsal side of valve.

Fossil distribution.–Quaternary: Kola Peninsula, Cheshskaya Bay coast, Lower Severnaya Dvina River, Lower Pechora River, Taimyr Peninsula; Late Pleistocene of the Champlain Sea; Holocene: eastern Kara Sea, Laptev Sea, Gulf of Alaska (Fig. 15).

Modern distribution.–Eastern Laptev Sea, Kara Sea, Beaufort Sea, Novaya Zemlya (Fig. 15).

Material.–One hundred twenty-six valves and 9 carapaces from Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron tumefactum Lev, 1972
Pl. II, Figs. 34-37

1874 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Brady *et al.*, p. 205, Pl. 14, Figs. 13-16 (not Pl. 8, Figs. 28-36).
1972 *Cytheropteron tumefactum* Lev, p. 17, Pl. 1, Figs. 12-13.
1977 *Cytheropteron montrosiense* Brady, Crosskey and Robertson - Cronin, Pl. III, Fig. 17.
1979 *Cytheropteron simplex* Whatley & Masson, p. 252, Pl. 2, Figs. 11, 12, 19-21.
1980 *Cytheropteron montrosiense* juv. - Lord, Pl. 2, Figs. 7-8.
1981 *Cytheropteron simplex* Whatley & Masson - Cronin, p. 406, Pl. 6, Figs. 6, 8.
1983 *Cytheropteron tumefactum* Lev, p. 118, Pl. XV, Fig. 9, Pl. XVI, Fig. 14.
1983 *Cytheropteron punctatum* Brady - Lev, p. 120-121, Pl. XVI, Figs. 6-7.
1989 *Cytheropteron simplex* Whatley & Masson - Cronin, Pl. V, Fig. 1.
1991 *Cytheropteron simplex* Whatley & Masson - Brouwers *et al.*, Pl. 2, Fig. 3.

1993 *Cytheropteron simplex* Whatley & Masson - Lord *et al*., Pl. 3, Fig. 3.
1996 *Cytheropteron simplex* Whatley & Masson - Whatley *et al*., Pl. 3, Fig. 4.
1999 *Cytheropteron tumefactum* Lev - Kupriyanova, Pl. 2, Fig. 6.
1999 *Cytheropteron punctatum* Brady - Kupriyanova, Pl. 2, Fig. 7.
2003 *Cytheropteron simplex* Whatley & Masson - Stepanova *et al*., 2003a, Pl. II, Fig. 12.

Holotype.–Collection VNIIOkeangeologiya, N1183-74; adult right valve, Russia, Arkhangel’sk Region, Pechora River, Khongurei; Late Pliocene-Early Pleistocene.

Description.–Carapace medium, rounded-triangular, strongly inflated, with flattened anterior and posterior margins. Dorsal margin slightly convex, bent towards posterior margin. Ventral margin straight, slightly concave in anterior third. Anterior margin arcuately rounded. Posterior margin lower than anterior, caudate, slightly downturned towards ventral margin. Greatest length at lower third, greatest height at anterior hinge edge. Lateral wing-like inflation above ventral margin. Several fine ribs extend along the inflation and contour it. Their extension on anterior and posterior margins form weakly developed elongated fossae. The whole valve surface unevenly punctate.

Measurements, mm.–

	L	H
From sample N2302, Lower Severnaya Dvina River, *C. punctatum* (collection of O.M. Lev, VNIIOkeangeologia)	0.43	0.24
From sample N2302, Lower Severnaya Dvina River, *C. tumefactum* (collection of O.M. Lev, VNIIOkeangeologia)	0.43	0.27
MSU292/60	0.41	0.27
MSU292/68	0.45	0.28

Variability.–Number of puncta is variable; central parts of some specimens are practically devoid of them. Besides, smoother specimens are larger and more rounded, while more punctate specimens are lower and almost triangular in shape.

Remarks.–Diverse intraspecific morphological variability has led to a confusing taxonomy. Lev described smooth forms as a new species *C. tumefactum* in 1972. Punctate forms she attributed to *C. punctatum* Brady, 1868. We studied Lev’s collection stored at VNIIOkengeologia (St. Petersburg) and came to the conclusion that her *“C. punctatum”* does not correspond to G.S. Brady’s description (1868a, p. 449, Pl. XXXIV, Figs. 45-48). Whatley & Masson in 1979 included both (punctate and smooth) morphotypes into a single species that they described as new and named it *Cytheropteron simplex*. Whatley & Masson (1979) mentioned strong intraspecific variability, but did not describe smooth and punctate forms separately. We consider both morphotypes to be a single species and, according to ICZN, name it *C. tumefactum* Lev 1972 (also according with Briggs, pers. comm., 2003).

Comparison.–*Cytheropteron tumefactum* differs from *Cytheropteron montrosiense* in having a more laterally inflated carapace, and a caudal process downturned towards ventral margin. The valve surface of *C. tumefactum* bears puncta and fine ribs at posterior, ventral and anterior margins, while *C. montrosiense* is strongly reticulate.

Fossil distribution.–Pliocene of Greenland; Quaternary: North Sea, Scotland, Cheshskaya Bay coast, Lower Severnaya Dvina River, Lower Pechora River, Lower Yenisei River; Pleistocene of Norway, Champlain Sea, Goldthwait Sea; Late Pleistocene-Holocene of the western Laptev Sea; Holocene: Gulf of Alaska, eastern Kara Sea (Fig. 16).

Modern distribution.–Greenland Sea, Great Britain, Norwegian Sea, Kara Sea, western Laptev Sea, Beaufort Sea (Fig. 16).

Material.–One hundred nine valves and 22 carapaces from Holocene deposits and Recent surface sediments of the Laptev Sea.

Cytheropteron laptevensis Stepanova sp. nov.
Pl. II, Figs. 38-41

1979 *Cytheropteron*? *sedovi* Schneider - Whatley & Masson, p. 251, Pl. 7, Figs. 15-19.
1983 *Cytheropteron* ex gr. *sedovi* Schneider - Lev, p. 121, Pl. XV, Figs. 10-12.
1990 *Cytheropteron sedovi* Schneider - Penney, Pl. 1, Fig. 1.

Derivation of Name.–From its findings in the Laptev Sea.

Holotype.–Collection stored at the Geological Department, Moscow State University, MSU292/280; adult left valve, Laptev Sea; core PS51-154, Lat. 77^{o}16’61’’N, Long. 120^{o}36’03’’E, core depth 129 cm; Holocene.

Description.–Carapace medium, subrhomboidal in lateral view, with flattened anterior and posterior margins. Dorsal margin almost straight, with obtuse cardinal angles, gradually beveled towards anterior and posterior margins. Ventral margin slightly convex in posterior half and slightly concave in anterior third. Anterior margin evenly arcuately rounded. Posterior margin caudate, slightly upturned towards dorsal margin, lower than anterior margin. Left valves have more smoothed cardinal angles, and right valves have prominent cardinal angles and more convex dorsal margin. Caudal process in postero-dorsal part in left valves straight or slightly convex, in right valves concave. Greatest length at mid-height, greatest height at anterior hinge edge. Above anterior margin wing-like process, with straight anterior edge and subvertical posterior. The anterior part of the ala has a rounded swelling, and subvertically elongated socket behind it (0.02 x 0.015 mm). Surface reticulate, fossae irregularly shaped, mostly subvertically elongated. Solum of fossae punctate.

Measurements, mm.–

	L	H
MSU292/220	0.36	0.19
MSU292/234	0.41	0.25
MSU292/253	0.38	0.23
MSU292/278	0.4	0.22
MSU292/280	0.36	0.18

*Variability.–*Reticulation varies in its degree, but usually fossae are well developed.

Comparison.–Cytheropteron laptevensis differs from *C. sedovi* from Recent sediments of the Central Arctic Ocean (Schneider, 1962, p. 104, Pl. XII, Fig. 1) in having subrhomboidal instead of subtriangular outline, absence of ribs and presence of fossae. *C. sedovi* bears distinct parallel subvertical ribs on posterior margin. Its lateral valve surface is nearly completely covered with subvertical rows of puncta. Ala morphology is also different: *C. sedovi* has rounded anterior edge of ala and subvertical posterior, and it bears a subvertical row of four puncta, while ala of *C. laptevi* has a straight anterior edge and a swelling at its anterior base, behind which there is a socket.

*Remarks.–*Whatley & Masson (1979) questionably referred several specimens to *Cytheropteron*? *sedovi* Schneider, 1962 and pointed out that they failed to find the original description of Schneider. We studied illustrations given in Schneider (1962) and came to the conclusion, that specimens in publications of Whatley & Masson (1979) and Penny (1990), and those from our samples, do not correspond to the original description of *C. sedovi* Schneider and, therefore, it is necessary to distinguish a new species *C. laptevensis.*

*Fossil distribution.–*Pleistocene: Ireland, North Sea, Lower Pechora River, Lower Ob River; Late Pleistocene and Holocene of the western Laptev Sea (Fig. 17).

*Material.–*Thirteen adult and 1 juvenile valve from the Late Pleistocene-Holocene deposits of the western Laptev Sea.

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AN INTERSTITIAL OSTRACODA FROM A BEACH-SAND HABITAT IN KEAWE'ULA BAY, NORTHERN HAWAII

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Abstract

Beach deposits from the marine intertidal zone at Keawe'ula Bay, on the north-western flank of Kohala Volcano, north Hawaii, yield a population of *Semicytherura challengerae* sp. nov. that appear to have been living interstitially within the coarse- to very coarse-grained beach sand. The ostracods, which preserve part of their soft-anatomy, are systematically described.

Key words: Ostracoda, new species, marine interstitial environment, Recent, Hawaii.

Resumen

Unos depósitos de playa, procedentes de la zona intermareal marina de Keawe'ula Bay, en el flanco noroccidental del volcán Kohala, norte de Hawai, han proporcionado una población de *Semicytherura challengerae* sp. nov., ostrácodo que vive intersticialmente dentro de una arena de playa gruesa a muy gruesa. Los ostrácodos, que preservan en parte la anatomía de los tejidos blandos, son descritos taxonómicamente.

Palabras clave: Ostracoda, nueva especie, medio marino intersticial, Reciente, Hawai.

INTRODUCTION

On the north coast of Hawaii, to the northwest of Kohala Volcano, at Keawe'ula Bay (latitude 20° 6.5'N, longitude 155° 52.5'W) (Fig. 1), coarse- to very coarse-grained beach sands are preserved between boulders of the rocky, marine intertidal zone. Most of the sand grains are greater than 500 µm in size, but a small proportion of the deposit is finer. The monospecific ostracod community, which was collected from the 205 µm sieve fraction, comprised *Semicytherura challengerae* sp. nov. The new species is described and its mode of life is discussed. All figured specimens (MPK 12807-12813) and unfigured specimens (MPA 51924) are deposited in the collections of the British Geological Survey, Nottingham, England.

PREVIOUS WORK

Recent ostracods from Hawaii are poorly known. During the late 19th century, the Royal Navy Challenger Expedition collected a single grab sample off reefs of Honolulu, at a depth of 40 fathoms (approximately 73 m). It yielded 15 species belonging to the genera (by original designation) *Pontocypris, Bairdia, Cythere, Xestoleberis, Loxoconcha* and *Cytherella* (Brady, 1880). Bate (1963) catalogued those specimens collected during the cruise and now deposited at the Natural History Museum, London and Hancock Museum, Newcastle upon Tyne. Puri & Hulings (1976) designated lectotypes for some species. However, none of the ostracods collected from Hawaii at that time can be placed in the genus *Semicytherura*.

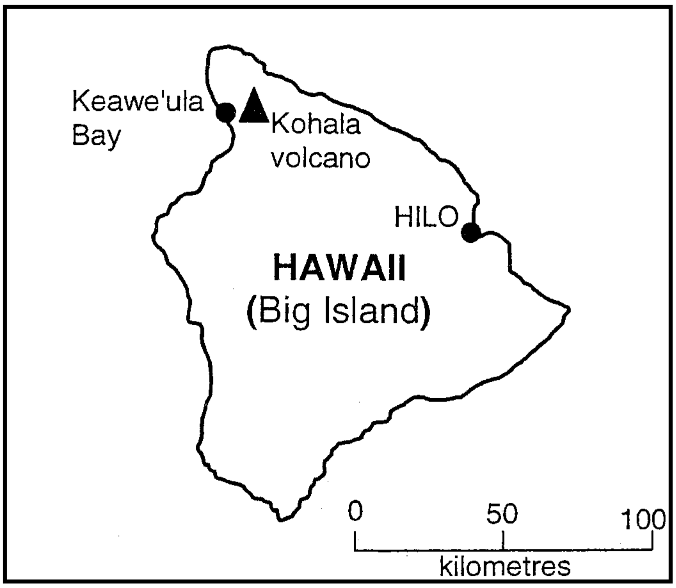


FIGURE 1–Sketch map of Big Island, Hawaii, to show the position of the study site at Keawe'ula Bay.

A biostratinomic analysis of living and sub-Recent algae- and sediment-dwelling ostracod associations from the neighbouring island of Oahu, was undertaken by Izuka & Kaesler (1986). Details of the assemblages were not given, but *Semicytherura* was not amongst the taxa mentioned. Hartmann (1991) described numerous interstitial taxa from several islands of the Hawaiian chain, including species of *Polycope, Paracobanocythere, Cobanocythere, Psammocythere, Cytheropteron, Xestoleberis, Paradoxostoma, Parvocythere, Aglaiocypris, Dolerocypria, Loxoconcha, Morkhovenia* and *Paracytheridea*. Only six species were recoverded from Big Island: *Polycope hawaiiensis* Hartmann, 1991; *Paracobanocythere hawaiiensis* Gottwald, 1973; *Cobanocythere konensis* Hartmann, 1991; *Psammocythere hawaiiensis* Hartmann, 1991; *Xestoleberis hawaiiensis* Hartmann, 1991, and *Dolerocypria minutissima* Hartmann, 1991. *Semicytherura* was not recorded.

Although modern literature on Recent Pacific ostracods is extensive, *Semicytherura* is surprisingly rare in the Recent faunal record. A selective literature search suggests that the genus is moderately diverse, although not common, off Japan, China and surrounding areas, but it is very rarely recorded off the Islands of Southeast Asia, the Coral Sea and the Pacific (e.g. Hanai *et al.*, 1977; Hanai *et al.*, 1980; Ikeya & Hanai, 1982; Quanhong & Pinxian, 1988; Whatley & Watson, 1988; Weissleader *et al.*, 1989; Ikeya & Itoh, 1991; Ikeya *et al.*, 1992; Whatley & Roberts, 1995; Whatley & Jones, 1999; Whatley *et al.*, 2000).

THE OSTRACOD COMMUNITY

The assemblage of ostracods recovered from beach sands at Keawe'ula Bay is essentially monospecific. Although two species were recorded, *S. challengerae* sp. nov. and *Xestoleberis hawaiiensis* Hartmann, 1991, the latter was represented by only a single, dead specimen, as discussed below.

Semicytherura challengerae sp. nov. (Pl. 1, Figs. 1-7) is considered to have been living at the time of sample collection, as indicated by the preservation of soft parts present in all the carapaces found. The sample was not collected specifically for ostracods and, unfortunately, steps to preserve the soft parts were not taken. Consequently, much of the thorax was missing in all of the specimens, but the appendages and soft parts around the central dorsal area remained in most (e.g. Text-Fig. 2). No data exist for the rate of decomposition of an ostracod carcass, but comparison of the degree of decay of *S. challengerae* sp. nov. with experiments on crustacea such as shrimps and prawns (e.g. Briggs & Kear, 1994), suggest that the specimens were almost certainly living at the time they were collected, approximately three months prior to examination. During the intervening time the specimens had been stored in wet sediment within a plastic container. All specimens found are adults and of a similar size (292-325 µm long). Juvenile instars were probably lost as a result of winnowing (there was very little sediment within the grain size 75 to 205 µm), but their absence may be a consequence of sample processing (the sample was washed through a 75 µm sieve).

The second species recorded, *Xestoleberis hawaiiensis* Hartmann, 1991 (text-fig. 3), is represented by a single carapace that was apparently dead at the time of collection. Unlike the specimens of *Semicytherura*, no soft-parts were observed and the lateral surface of the carapace is crossed by irregular, sinuous borings, suggesting it had been lying in the sediment for some time. Hartmann (1991) recovered *X. hawaiiensis* from coarse sediment in a sheltered embayment at Kealia Beach, Big Island, where it was living interstitially.

Semicytherura challengerae sp. nov. is considered to have been living interstitially in Keawe'ula Bay for three reasons. Firstly, the sediment is a coarse- to very coarse-grained sand that accumulated on an exposed coastline in a high energy environment. The sand

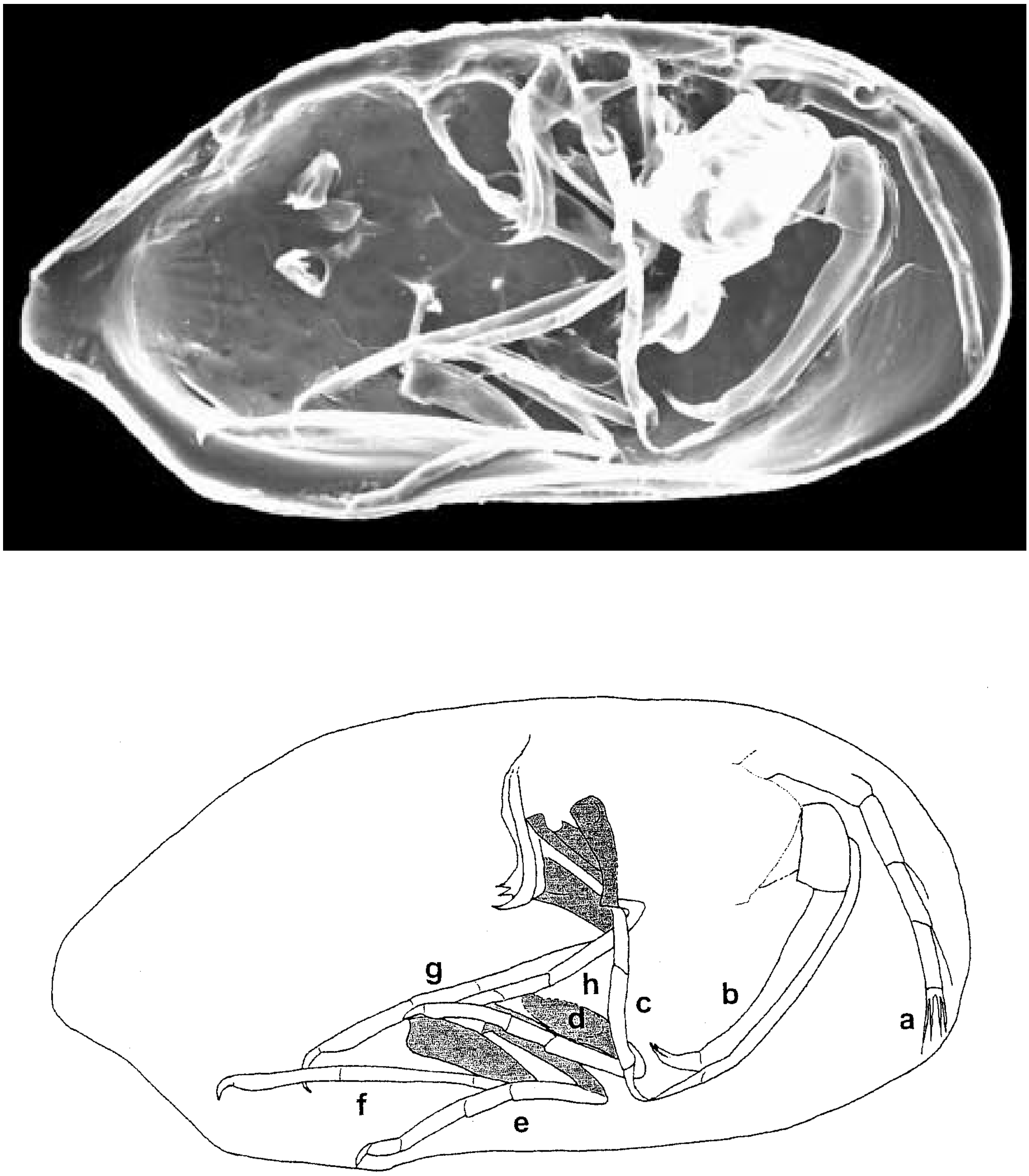


FIGURE 2–*Semicytherura challengerae* sp. nov. from Keawe'ula Bay, on the north-western flank of Kohala Volcano, northern Hawaii. For dimensions, see text.

Left valve, internal view and the preserved soft parts of a female paratype, MPK12810.

In the diagrammatic representation, the basipodites of each appendage are shaded. a. one of the paired uniramous antennulae (appendage 1) with four podomeres; b. second antenna (appendage 2) of which at least two podomeres on the endopodite are visible; c-h. six paired "walking legs" of the thorax (appendages 5-7), each comprising basipodite and three podomeres on the endopodite.

collected was preserved between large boulders near the low water mark. It is unlikely that the fragile and diminutive ostracods could have survived these adverse energy conditions and sediment substrate, and it is likely that they took refuge within the large interstices between the sediment grains. This strategy was described by Hartmann & Hartmann-Schröder (1975) who found that surface-ostracods were absent on exposed beaches of South Africa, Angola and Mozambique (where the high-energy environment is similar to that of Hawaii), but diverse assemblages were present in interstitial habitats. Secondly, the dimensions of *S. challengerae* sp. nov. are very small (adults did not exceed 325 µm), a characteristic of other interstitial ostracods described by, for example, Gottwald (1973), Bonaduce & Danielopol (1988) and Hartmann (1991). Finally, the notion is supported by the presence of *Xestoleberis hawaiiensis*, which, although only represented by a single dead specimen, is known to live interstitially.

SYSTEMATIC PALAEONTOLOGY

Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family CYTHERURIDAE Müller, 1894
Genus *Semicytherura* Wagner, 1957

Type species. *Semicytherura nigrescens* (Baird, 1838). Combined with *Semicytherura* by Wagner (1957) (see also Athersuch *et al*., 1989).

Semicytherura challengerae sp. nov.
(Pl. 1, Figs. 1-7; Fig. 2)

Derivatio nominis.–After the the Royal Navy's ship HMS Challenger. Recent Hawaiian ostracods were first collected during the Challenger Expedition of 1873 to 1876 and described by Brady (1880).

Diagnosis.–Small species of *Semicytherura* (adults between 292 and 325 µm long) with heavily fovoelate lateral surface; an anastomosing series of riblets around the anterior, ventral and posterior margins; and an anterior rib that thickens anterodorsally and extends along the dorsal margin to mid-length.

Holotype.–Carapace, female, MPK12807 (Pl. 1, Fig. 1).

Paratypes.–Carapace, male, MPK12808; right valve, female, MPK12809; left valve female, MPK12810; carapace, female, MPK12811; carapace male, MPK12812 (Pl. 1, Figs. 2-7).

Material.–At least 47 specimens.

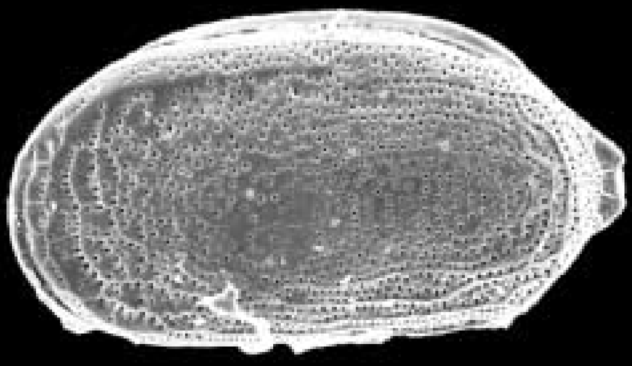
Locality and horizon.–Found living, probably interstitially, in beach sand in Keawe'ula Bay on the northwestern flank of Kohala Volcano, north coast of the Island of Hawaii (Fig. 1).

Description.–*Female*: Carapace small and elongate. Anterior margin broadly rounded. Dorsal margin weakly arched, flattened mid-dorsally, posterior cardinal angle moderately well formed. Posterodorsal margin weakly concave, merging into a blunt, caudal extension situated at mid-height. Dorsal margin weakly sinuous. Mid-lateral surface ornamented with a mesh of very weak reticulation, the almost vestigial muri comprise a thickened, non-foveolate network barely standing higher than the solus. Foveolae up to about 3 microns in diameter, situated in the sola. In the anterior, ventral and posterior marginal areas, the muri are raised into a series of sinuous and anastomosing riblets, which control the disposition of the foveolae into linear series. The anterior marginal rib is more prominent anterodorsally, extends along the dorsal margin to mid-length and continues to the caudal process as a very weak riblet. In dorsal view (Pl. 1, Fig. 5) the species is slightly inflated laterally, broadest anterior of mid-length and slightly compressed at mid-length forming a weak concavity in its outline. The posterior end of the inflation is abruptly terminated, so

→

PLATE 1–*Semicytherura challengerae* sp. nov. from intertidal beach deposits at Keawe'ula Bay, on the north-western flank of Kohala Volcano, northern Hawaii. For dimensions, see text.
1, Carapace, left valve, lateral view; female; MPK12807; holotype. *2*, Carapace, left valve, lateral view; male; MPK12808; paratype. *3*, Right valve, internal view; female; MPK12809; paratype. *4*, Central muscle scar group (highlighted with a pecked line) of specimen MPK12809 (see Fig. 3) (the figure measures 40 µm across). *5*, Carapace, dorsal view; female; MPK12811; paratype. *6*, Carapace, dorsal view; male; MPK12812; paratype. *7*, Magnified part of the lateral surface of the male MPK12808 (see Fig. 2), showing detail of reticulation, the disposition of the foveolae and the interrupted ornament in the area of the adductor muscle scars (the figure measures 65 µm across).

Plate 1



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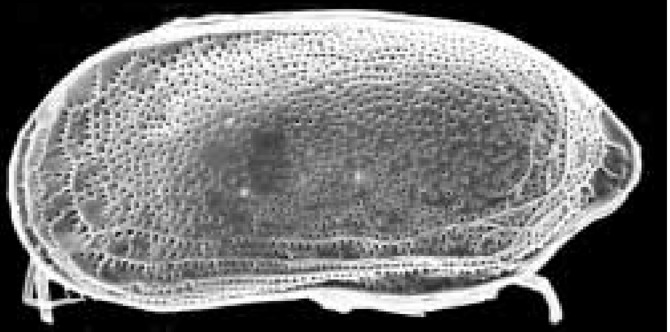

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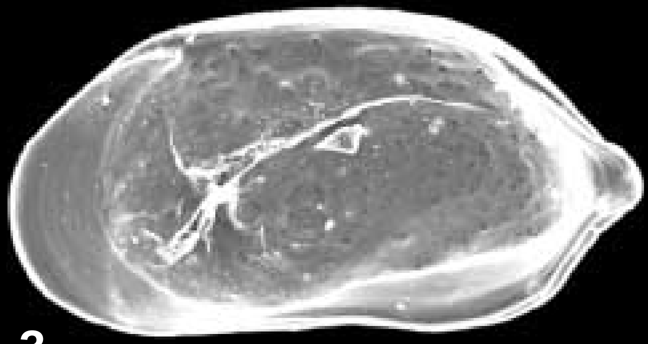

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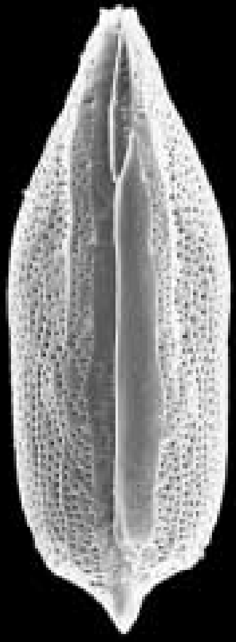

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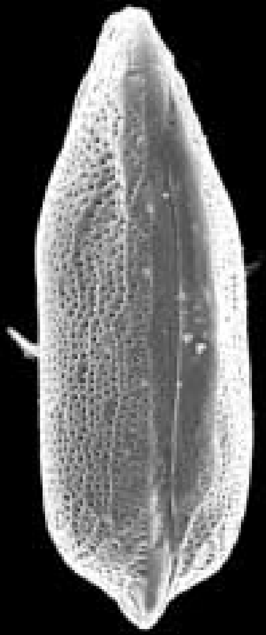

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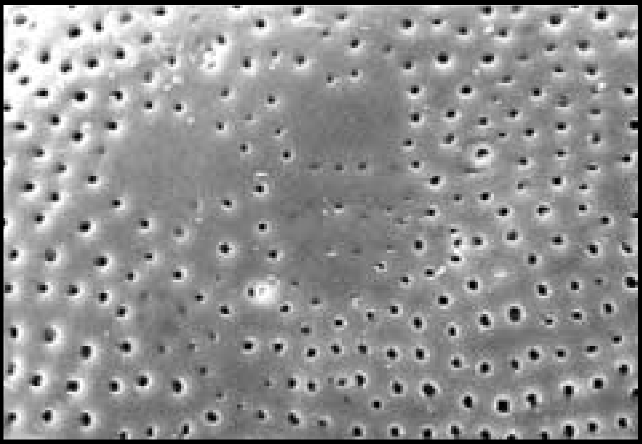

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that the outline between the posterior end of the lateral inflation and the caudal process is strongly concave. Dorsal margin thickened and, with the exception of the posterior end, free of foveolae. Right valve overlaps the left dorsally. Eye-tubercle absent. Normal pores widely scattered.

Inner lamella broad anteriorly and posteroventrally, but narrow at the caudal process and anterior of mid-length, at the weak ventral concavity. Normal pores small and widely scattered, but generally obscured by the foveolae when viewed externally. Approximately eighteen sinuous marginal pore canals disposed in groups anteriorly, and about five canals at the posterior margin. Adductor muscle scars comprise a vertical row of four scars, the dorsal one being ovate and the remainder elongate; a small, rounded slightly kidney-shaped frontal scar; and an obliquely disposed, elongate frontal scar. Hinge weak, comprising, in the right valve a narrow, median groove and very weakly developed denticulate teeth and, in the left valve, weakly developed elongate sockets separated by a smooth, narrow bar.

Male: Elongate. Anterior broadly rounded, dorsal margin very weakly arched, almost straight, merging into the blunt caudal process situated at mid-height. Unlike the female, the posterior cardinal angle is weakly developed. Ventral margin weakly sinuous. Lateral ornamentation as for female. The adductor muscle scars represented externally by a thickening of the carapace and an interruption of the reticulation (Pl. 1, Fig. 7), although foveolae continue between the individual scars. In dorsal view, the carapace is widest posterior of mid-length and the lateral outline is straight or very weakly concave; the distinct mid-length concavity of the female not present in the male. Posterior outline between the lateral inflation and the caudal process more rounded, when viewed dorsally, the concavity seen in the female less pronounced in the male.

Sexual dimorphism: Male carapace more elongate than the female and widest towards the posterior. The invagination of the inner lamella is also dimorphic; that in the female being wider immediately anterior to the caudal process, compared to that of the male.

Soft parts: Partially preserved soft anatomy is present in the majority of specimens, particularly the appendages which are more heavily scleritised and thus most resistant to decay. None of the specimens preserve the trunk or copulatory region of the animal, a situation which is consistent with the later stages of decay determined by experiments on crustacea, such as shrimps and prawns (see Briggs & Kear, 1994). Preservation prevents a full description of the morphology, but the best preserved specimen shows several appendages and other soft-tissue (Text-Fig. 2). At the anterior end is one of the paired uniramous antennulae (appendage 1), comprising 4 podomeres each of which is terminated with setae. Posterior of this, and partially hidden by soft anatomy around the central dorsal area is the second antenna (appendage 2), of which two podomeres of the endopodite are fully visible, the proximal-most podomere of the endopodite probably being partly hidden by other soft tissue. The mandible (appendage 3) and maxilla (first maxilla of some authors; appendage 4) are not visible and are either not preserved or obscured by the soft tissue in the central dorsal area. Posterior of this are the three paired "walking legs" (appendages 5-7; appendage 5 is referred to as the second maxilla by some authors) of the thorax, some of which have been displaced and are resting on the ventral margin of the valve. Each thoracic appendage comprises a basipodite and an endopodite with 3 podomeres.

Dimensions.–

			Length (μm)	Height (μm)	Width (μm)
MPK12807	Carapace	Female	300	167	100
MPK12808	Carapace	Male	325	150	87
MPK12809	Right valve	Female	300	167	—
MPK12810	Left valve	Female	303	167	—
MPK12811	Carapace	Female	292	167	100
MPK12812	Carapace	Male	316	150	100

Remarks.–The very small size and the ornament serve to separate this species from other members of the genus. It resembles *Semicytherura* sp. 2 of Ikeya & Itoh (1990), although that species is much more heavily costate compared to the Hawaiian species. *Semicytherura tetragona* (Hanai, 1957) is more highly arched compared to the present species, and lacks the anastomosing marginal riblets and the anterodorsal marginal rib. *Semicytherura challengerae* sp. nov. was found apparently living interstitially, within beach sand.

Family XESTOLEBERIDIDAE Sars, 1928
Genus *Xestoleberis* Sars, 1866

Type species: *Xestoleberis aurantia* (Baird, 1838). Combined with *Xestoleberis* by Brady (1868) (see also Athersuch *et al.*, 1989)

Xestoleberis hawaiiensis Hartmann, 1991

(Fig. 3)

1991 *Xestoleberis hawaiiensis* Hartmann: 172-173, Figs. 45-56

Material.–One female specimen (MPK12813) from intertidal beach sand Keawe'ula Bay on the north-western flank of Kohala Volcano, north coast of the Island of Hawaii (Fig. 1).

Description.–Carapace elongate, highest immediately posterior of mid-length and longest below mid-height. Anterior and posterior broadly rounded. Ventral margin straight. Dorsal margin arched. Anterodorsal margin straight to weakly convex. Lateral surface smooth. Normal pores large, widely scattered. Interior not observed.

Dimensions.–

		Length (μm)	Height (μm)	Width (μm)
MPK12813	Carapace	316	167	150

Remarks.–*Xestoleberis hawaiiensis* is represented by only a single female, which had been dead for some time prior to collection judging from absence of soft-parts and the borings on the lateral surface. Hartmann (1991, figures 45 to 56) included only a line drawing of a male valve, which is more elongate and with a deeper ventral concavity compared to the presumed female specimen illustrated herein. *Xestoleberis hawaiiensis* is an interstial species which Hartmann (1991, page 173) found living in coarse sediment in a sheltered embayment on Big Island. *Xestoleberis curta* (Brady, 1865), recorded off Honolulu by Brady (1880), differs in having a long, straight anterodorsal margin and being highest towards the posterior. *Xestoleberis hawaiiensis* resembles *X. nana* Brady 1880 (see Puri & Hulings, 1976), from the Phillipines, but differs in outline, particularly the less acutely rounded anterior margin.

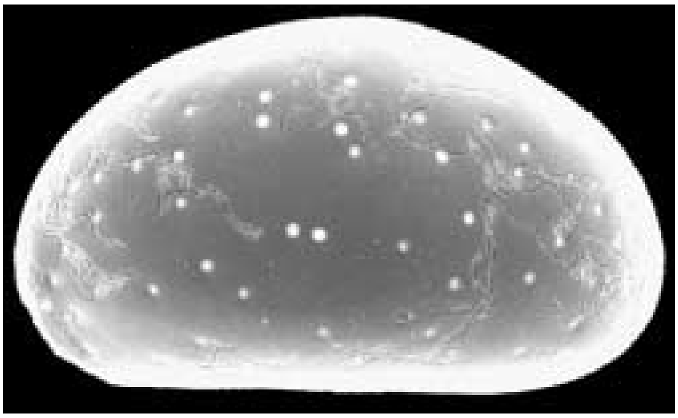

FIGURE 3–*Xestoleberis hawaiiensis* Hartmann, 1991, from intertidal beach deposits at Keawe'ula Bay, on the north-western flank of Kohala Volcano, northern Hawaii. For dimensions, see text. Carapace, right valve, lateral view; MPK 12813.

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REVIEW OF THE *EREMITA* SPECIES-GROUP OF THE GENUS *PSEUDOCANDONA* KAUFMANN (OSTRACODA, CRUSTACEA), WITH THE DESCRIPTION OF A NEW SPECIES

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Abstract

The Recent species belonging to the *eremita* species group of the genus *Pseudocandona* Kaufmann (Ostracoda, Candonidae) are reviewed and some morphological traits of the valves, the limbs as well as the mode of the postembryonic development of the carapace shape analysed in the context of their taxonomic value. Eleven species with living representatives are retained (among them one new species is here described, and two other species are tentatively retained). The features uniting these species within the group refer mainly to the details of valve morphology (triangular shape, narrow inner lamella, faint ornamentation). The apical chaetotaxy of the second antenna and the genital morphology can be also used to characterise this group. Extant species are exclusively stygobionts and most of them apparently display a high degree of geographic endemism. Additionally, *Pseudocandona marmonieri* sp. nov. is described from groundwater in Southern France and as such constitutes the first West European representative of the group. The new species differs from the other members of the *eremita* species group mainly in the carapace shape and the morphology of the hemipenis.

Key words: Recent, Ostracoda, *Pseudocandona*, non-marine, stygobites, southern France, new species.

Resumen

Se revisan las especies actuales pertenecientes al grupo *eremita* del género *Pseudocandona* Kaufmann (Ostracoda, Candonidae) y se analizan algunos rasgos morfológicos de las valvas en el contexto de su valor taxonómico. Entre los representantes del grupo se retienen once especies (entre ellas una nueva especie, y dos especies más sólo incluidas aquí de manera tentativa). Las características que ligan a estas especies dentro del grupo se refieren fundamentalmente a rasgos de su morfología valvar (forma triangular, estrecha lamela interna y ornamentación sutil). La quetotaxia de la región apical de la segunda antena y la morfología genital pueden ser empleadas también para caracterizar este grupo. Las especies actualmente existentes son exclusivamente estigobiontes y muchas de ellas muestran aparentemente un alto grado de endemismo geográfico. Además, *Pseudocandona marmonieri* sp. nov. es descrita de aguas subterráneas del sur de Francia y como tal constituye el primer representante del grupo en el occidente europeo. La nueva especie difiere de otros miembros del grupo *eremita* fundamentalmente por la forma del caparazón y la morfología del hemipene.

Palabras clave: Reciente, Ostracoda, *Pseudocandona*, estigobiontes, no-marinos, sur de Francia, nueva especie.

INTRODUCTION

The subfamily Candoninae Kaufmann is one of the most diversified and species-rich lineages of non-marine ostracods. Recent representatives of Candoninae lack the natatory setae on the second antennae and are therefore benthic dwellers. They inhabit almost every epigean fresh-water habitats and are well represented in subterranean waters. Some species are found in weakly brackish-waters, others even occur in humid terrestrial environments. The subfamily comprises more than 250 Recent species (Krstić & Shao-zeng, 2000) distributed mostly in the Holarctic Region. The results of investigations of the subtropical and tropical regions have extended the distribution range of the subfamily to being nearly cosmopolitan. There are much more fossil species referred to the Candoninae, especially Tertiary ones. Swain (1999) and Krstić & Shao-zeng (2000) consider that the fossil records of representatives of this subfamily extend back to the Carboniferous.

Despite a number of extensive investigations carried out by both zoologists and palaeontologists during the last few decades, which resulted in detailed revisions of some genera, the taxonomy of other generic taxa remains imperfectly known and the systematics of the whole subfamily Candoninae is still subject to a lot of discussion. The optimal taxonomic solution for unifying the so far discordant palaeontological and neontological classifications (compare e.g. classification in Meisch, 2000 for living taxa with that of Krstić & Shao-zeng, 2000 encompassing both living and fossil taxa) should provide genera that are recognisable by both carapace and soft-part characters.

Of about 25 Candoninae genera with Recent representatives, 18 are in use and nearly all of them have satisfactory diagnoses with good differential characteristics (Meisch, 1996; Karanovic, 1999a, 2001).

Pseudocandona Kaufmann, 1900 is one of the Candoninae genera with uncertain taxonomic status. Although Meisch (1996) has recently attempted to clarify certain taxonomic aspects of this genus by: (a) introducing a new genus *Schellencandona* Meisch for the species of the *schellenbergi*-group, (b) extracting the Baikal species referred previously to *Pseudocandona*, (c) transferring a number of *Pseudocandona* species without group assignments to the genus *Fabaeformiscandona* Krstić and finally (d) establishing a differential diagnosis of *Pseudocandona* s. str. based also on chaetotaxy of the cleaning leg, the genus seems to be still rather heterogeneous and specific relationships within it remain ambiguous. At the present state of knowledge, the genus *Pseudocandona* sensu Meisch (1996) is best characterised mainly by the following traits: (a) surface of adult valves smooth or pitted and usually bearing long stiff setae, (b) male second antenna with penultimate podomere differentiated or not (when divided than with male bristles), (c) externo-distal seta (γ) on the penultimate podomere of the mandibular palp smooth (not plumose), (d) branchial plate on maxilliped rudimentary and set with 2 setae, (e) protopodite of the cleaning leg bearing 3 setae, penultimate segment lacking the medial seta (f seta) and terminal segment with 2 long and one short setae, (f) Zenker's organ with 7 rosettes of chitinous spikes, (g) hemipenis with flat and weakly sclerotized M-process.

According to Meisch (1996, 2000), 35 living species of *Pseudocandona* distributed throughout the Holarctic are allocated to five species groups: the *caribbeana*-, *compressa*-, *eremita*-, *rostrata*- and *zschokkei*-groups. Recently, Karanovic (1999b) introduced a sixth species group: *prespica*. Diagnoses of the species groups of the genus *Pseudocandona* (after Meisch, 1996, and Karanovic, 1999b) are briefly presented here:

(1) *caribbeana*-group: Carapace trapezoidal with rounded anterior and posterior margins. Setal group on the 2nd podomere of the mandibular palp with 3 setae.

(2) *compressa*-group: Carapace not trapezoidal or triangular in lateral view. Setal group on the 2nd podomere of the mandibular palp with 5 setae.

(3) *eremita*-group: Carapace triangular in lateral view. Left valve overlapping the right one with a dorsal hump. Valves with shallow pits in the central area. Setal group on the 2nd podomere of the mandibular palp with 3 setae.

(4) *prespica*-group: Carapace not trapezoidal or triangular in lateral view. Setal group on the 2nd podomere of the mandibular palp with 4 setae.

(5) *rostrata*-group: Carapace not trapezoidal or triangular in lateral view. Setal group on the 2nd podomere of the mandibular palp with 3 setae.

(6) *zschokkei*-group: Carapace trapezoidal in lateral view. Valves with shallow pits in the central area. Setal group on the 2nd podomere of the mandibular palp with 3 setae.

From the above-presented diagnoses it appears that distinction of these groups relies on (a) the carapace shape, and (b) the number of setae in the setal group situated on the second segment of the mandibular palp. Based solely on the latter character, two groups are best distinguished: *compressa* (with 5 setae) and *prespica* (with 4 setae). After those two groups have been discarded, the shape of the carapace remains the only character allowing distinction of the remaining four groups. Within these groups, the *eremita*-group seems to be reasonably well separated by the triangular carapace shape.

The main aim of this study is to analyse the selected features used for the identification and characterisation of the *eremita*-group. The morphological traits of the valves, the limbs as well as the mode of the developmental trajectory of the carapace shape and ornamentation are critically examined in the context of their taxonomic value. In the first step, after introducing the taxonomic history and providing the series of diagnostic characteristics of the group *eremita* used so far, all species assigned to this group are reviewed in respect of their geographical distribution and ecology. Then morphological traits of the valves of the *eremita*-group are compared with five other groups of *Pseudocandona* and figures of the juvenile valves of some representatives from different groups of *Pseudocandona* are given to trace differences in developmental trajectories. Further on details of chaetotaxy of the second antennae are presented for a number of species from different groups and are checked for the constancy of the scheme within the groups considered. In addition to the results of the examination of specimens, data provided by published descriptions and illustrations were used in this analysis. Subsequently, genital morphology (the shape of the M-process of the hemipenis and the female genital lobe) is considered and included in the study. An emended differential diagnosis of the group *eremita* is given. Finally, *P. marmonieri* sp. nov., a new species of the *eremita*-group is described.

REVIEW OF THE EREMITA SPECIES GROUP

Taxonomic history and diagnostic characteristics used so far

The species group *eremita* was introduced by Danielopol (1978, 1982). As stated by this author (Danielopol, 1982), the following combination of features characterise this group of species: (1) carapace triangular in lateral view, (2) dorsal margin of the left valve with a hump that overlaps the right valve, (3) valves with shallow pits predominantly in the central valve area, (4) carapace of medium length (0.7-1.1 mm), (5) apical chaetotaxy of second antennae sexually dimorphic: females bear 2 large claws G_1 and G_3, one reduced claw G_2 (c. 1/2 x G_1), 3 external z setae and G_m claw equalling 2/3 x the claw G_M; males bear reduced claws G_1 and z_1 (annotated as G_2 and G_3, respectively in Danielopol, 1982) of which z_1 amounts to 1/2 of G_2 (G_1 in Danielopol, 1982), (6) male prehensile palps asymmetrical, the right one larger than the left one, (7) cleaning leg protopodite with 3 setae, 2nd and 3rd endopodial podomeres fused, subterminal podomere bearing a long distal seta and terminal podomere with a short seta being larger than 1/2 of the length of this segment, (8) furca (caudal ramus) with a long posterior seta and with distal claws bearing on their posterior margins two groups of fine spinules, (9) Zenker's organ with 7 rings of spines (the distal one is funnel-shaped), (10) female genital lobe flat in the region of the genital opening and posteriorly with a finger-like expansion, (11) hemipenis with a well developed inner lobe and a cornet-shaped bursa copulatrix.

Type species and other Recent species

According to Danielopol & Hartmann (1986), the group *eremita* includes eight species: the type species *Pseudocandona eremita* (Vejdovský, 1882), *P. cavicola* (Klie, 1935), *P. dispar* (Hartmann, 1964), *P. pretneri* Danielopol, 1978, *P. puteana* (Klie, 1931), *P. serbani* Danielopol, 1982, *P. trigonella* (Klie, 1931) and *P. szoecsi* (Farkas, 1958) with two subspecies *P. s. szoecsi* (Farkas, 1958) and *P. s. pannonicola* (Löffler, 1960a). However, as the morphology of the appendages of these two subspecies (originally described as two species) is not known in detail, the specific division is only provisionally maintained in the present paper.

Recently, two other living species have been discovered to complement our knowledge of the soft part morphology of this group. The first of these, *P. sywulai* Namiotko *et al.*, 2004, has been collected in Croatia (Namiotko *et al.*, 2004). The second one, *P. marmonieri* sp. nov., is described below.

Geographical distribution and ecology

Extant species of the group *eremita* are exclusively stygobionts and most of them display a high degree of local endemism (Fig. 1).

The type species of the group, *P. eremita,* was originally collected in wells at Prague, Czech Republic (Vejdovský, 1882). To judge from the published data, *P. eremita* is a widely distributed species. Living specimens were recorded in the ground waters of 14 countries in Central and South-Eastern Europe: Austria, Bulgaria, Croatia, Czech Republic, Germany, Hungary, Macedonia, Poland, Romania, Slovakia, Slovenia, Turkey (European part), Ukraine and Yugoslavia (Fig. 1). Wolf's (1920) record of the species in Switzerland is dubious (discussion in Klie,

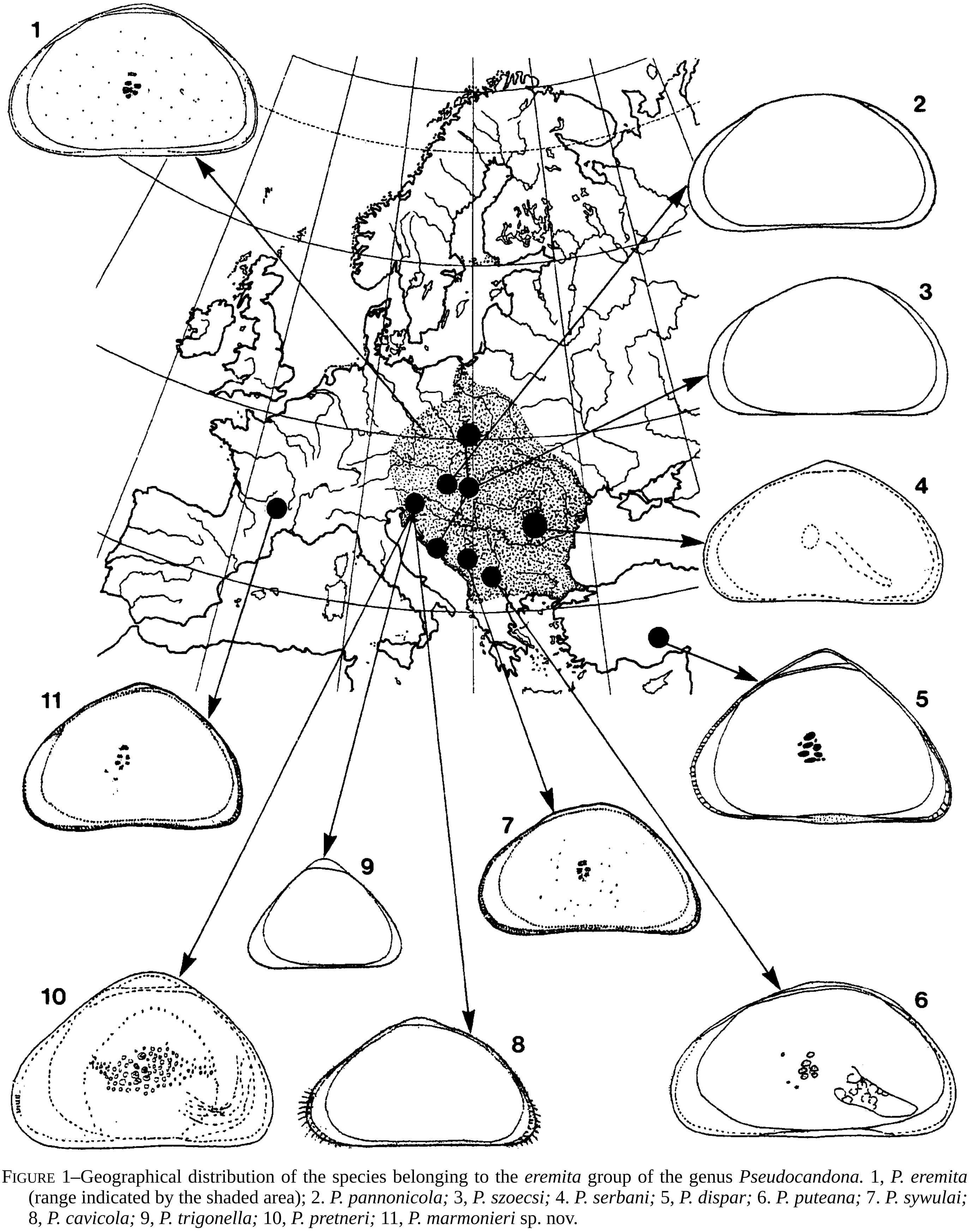

FIGURE 1–Geographical distribution of the species belonging to the *eremita* group of the genus *Pseudocandona*. 1, *P. eremita* (range indicated by the shaded area); 2. *P. pannonicola;* 3, *P. szoecsi;* 4. *P. serbani;* 5, *P. dispar;* 6. *P. puteana;* 7. *P. sywulai;* 8, *P. cavicola;* 9, *P. trigonella;* 10, *P. pretneri;* 11, *P. marmonieri* sp. nov.

1940, and Meisch, 2000). For the review of the distribution of this species see Meisch (2000) with supplementary data by Jaworowski (1893), Gülen (1985), Kovalenko (1988) and Gidó & Lakatos (2001). However, it is not unlikely that at least some of these reports are uncertain as only a few of them provide indications on carapace and/or limb morphology. Therefore, the accurate description of the geographical range of *P. eremita* is problematic at this moment.

Seven species of this group (*Pseudocandona cavicola*, *P. dispar*, *P. pretneri*, *P. puteana*, *P. sywulai*, *P. trigonella* and *P. marmonieri* sp. nov. described below from Southern France) are so far only known from their type localities (Fig. 1). *P. cavicola* is possibly endemic in the Krška cave (Klie, 1935) and *P. trigonella* – in the Postojna cave, both in Slovenia (Klie, 1931). *P. pretneri* was found in a karstic spring at Rak also in Slovenia (Danielopol, 1982), close to the type localities of *P. cavicola* and *P. trigonella*. *Pseudocandona dispar* was originally described from the Erekli cave in Turkey (Hartmann 1964). The largest and the most elongated species in the group, *P. puteana*, is only known from wells at Skopje in Macedonia (Klie, 1931; Petkovski, 1969; Danielopol, 1982). *P. sywulai* was found in the cave Đuderina Jama near Split in Croatia (Namiotko *et al*., 2004).

The three remaining species of the group, which are very similar to *P. eremita*, are known from various alluvial aquifers accessed mainly through wells: *P. pannonicola* was collected in Burgenland, Austria (Löffler (1960a, 1960b, 1964); *P. serbani*, in Southern and Central Romania (Danielopol, 1982), while *P. szoecsi*, originally described from a well in surroundings of Budapest (Farkas, 1958), was later recorded by Petkovski (1969) in Croatia and by Sywula (1981) and Skalski (1982), as *P. eremita* f. *szoecsi*, in Poland (Fig. 1).

Males are known for: *P. eremita* (single sites), *P. dispar*, *P. puteana*, *P. pretneri*, *P. serbani*, *P. sywulai*, *P. szoesci* (two wells in Croatia – these records are doubtful) and for *P. marmonieri* sp. nov.

A small number of fossil forms were assigned to *P. eremita* sensu lato (some of them as *P*. aff. *eremita* or *P.* cf. *eremita*). They were mostly recorded from Quaternary sediments in Croatia, the Czech Republic, Germany, the United Kingdom and Yugoslavia (for the review of the Quaternary distribution see Griffiths, 1995) but also from older deposits, so for instance from the Pliocene in Turkey (Freels, 1980) and from the Late Miocene in Slovakia (Pipik, 2000, 2001). It is questionable, however, if all fossil records are valid and really represent *P. eremita*. A reappraisal of the taxonomic allocation of these valves is required by the direct comparison with the valves of individuals determined on the base of their soft parts.

Morphological traits of valves

Table 1 shows the comparison of some valve morphological traits of six species groups of the genus *Pseudocandona*. From this table, it can be seen that the triangular carapace shape is a good diagnostic character of the *eremita*-group. Valves of these species are relatively high (height to length ratio usually exceeds 0.55, except *P. pannonicola* and *P. puteana*) and the greatest height is situated at mid-length or just behind mid-length. In the other groups the greatest height is either distinctly behind or in front of mid-length. Because species of the *caribbeana*-group have almost straight dorsal valve margin, the greatest height is seen at 1/3 to 2/3 of the valve length. The attention should also be drawn to the development of the calcified inner lamella. In the *eremita*-group it is narrow, anteriorly extending typically over not more than 10% of the valve length and usually being less than twice as wide as in the posterior part. It is quite unlike as in the other groups except the *zschokkei*-group.

Postembryonic development of the carapace shape and ornamentation

Figure 2 presents illustrations of the juvenile valves of some representatives of different groups of *Pseudocandona* in order to trace differences in the carapace shape throughout the postembryonic development. As can be seen, the shape of the valves and the relative width of the inner lamella remain almost constant throughout at least the last 4 juvenile stages in representatives of the *eremita*-group. One can conclude that adults retain a juvenile character. In the other groups, juveniles differ in shape from those of the *eremita*-group and the inner lamella significantly increases at the last moult, hence the adults usually have a significantly wider lamella than the juveniles. It should be added that the neotenic nature of the representatives of the *eremita*-group is also visible in the ornamentation of the valves, which are invariably faintly pitted (mostly in the central area) in both the last juvenile stages and the adults. Conversely, juvenile valves of the *compressa* and *rostrata* groups are always more markedly ornamented (over the whole surface) and this ornamentation usually disappears during the last moult, hence adult valves are normally smooth (only rarely covered with shallow pits and when pitted than over the entire valve).

Character	*eremita*	*caribbeana*	*rostrata*	*zschokkei*	*prespica*	*compressa*
Carapace shape seen laterally	triangular	elongated, somewhat trapezoidal	usually stout, not triangular or trapezoidal	trapezoidal	not triangular or trapezoidal	stout, not triangular or trapezoidal
Location of the greatest height of the ♀ left valve	at mid-length or just behind mid-length: at 50-60% of the length	at 1/3-2/3 of the length	distinctly behind mid-length: at > 60% of the length	in front of the mid-length: at > 50% of the length	distinctly behind mid-length: at > 60% of the length	distinctly behind mid-length: at < 60% of the length except *P. lobipes*)
Width of the inner lamella of ♀ left valve anteriorly	≤ 10% of the length (except *P. pretneri*)	9-13% of the length	usually > 10% of the length	≥ 10% of the length	≥ 10% of the length	usually > 10% of the length
Width of the inner lamella anteriorly / posteriorly	≤ 2 (except *P. pretneri* and *P. puteana*)	≥ 2	≥ 2	< 2	> 2	≥ 2

TABLE 1– Comparison of the valve morphological traits of six species groups of the genus *Pseudocandona*.

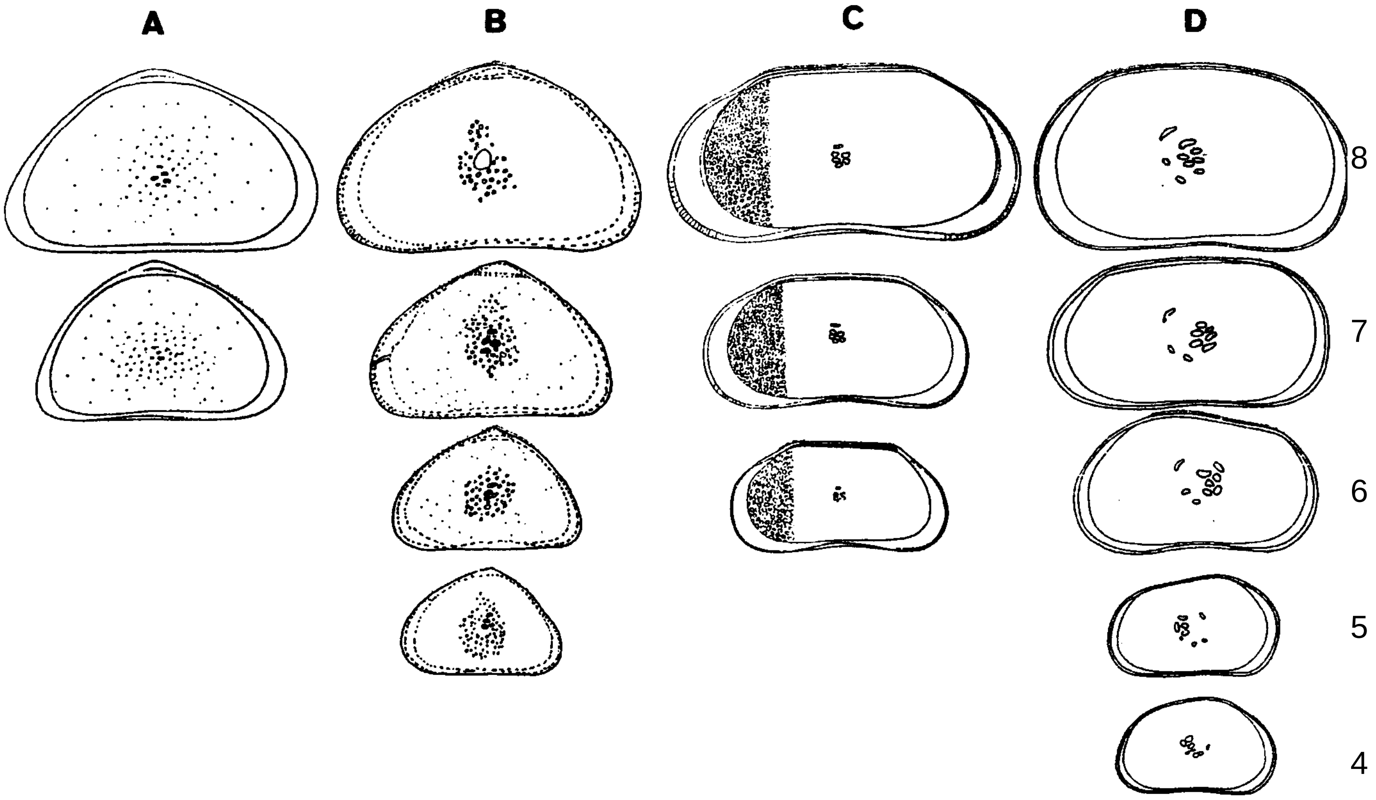

FIGURE 2–Developmental trajectories of the carapace shape and ornamentation in some representatives of the genus *Pseudocandona.* A, *P. eremita* (after Absolon, 1978); B, *P. serbani* (after Danielopol, 1982); C, *P. sarsi* from the *rostrata*-group (after Absolon, 1978); D, *P. albicans* from the *compressa*-group (after Kovalenko, 1983). *Numbers in the right column indicate juvenile stages.* Not to scale.

Although the distinction of the group-*eremita* based on the morphology of valves and the developmental trajectory of the carapace shape and ornamentation may be justifiable, there are already several known cases of homeomorphy in the Candoninae, as was pointed out by many authors (e.g. Danielopol, 1982). The triangular carapace could evolve convergently in relation with the colonisation of the hypogean habitat. Therefore, in the next step, features based on the soft parts were analysed in the context of their taxonomic significance.

Apical chaetotaxy of the second antenna

The antennae of the Candoninae are usually sexually dimorphic in structure and chaetotaxy. According to the model proposed by Broodbakker & Danielopol (1982) as revised by Martens (1987), in the adult female 3 long apical claws are usually present: G_1, G_3 and G_M. The modifications observed in adult males affect mainly the claw G_3, which is reduced into a seta, and the female z_1 seta, which in males is transformed into a claw. Therefore, the 3 long claws seen in the males are G_2, z_1 and G_M (Fig. 4B). Additionally, the 2nd and 3rd endopodial A2 podomeres in the males are usually not fused and bear the so-called male bristles.

Table 2 summarises measurements of the relative lengths of apical claws in a number of species from different groups of the genus *Pseudocandona*. As seen in this table, females of the *eremita*-group have relatively long apical claws in comparison to those of species of the other groups, especially of the group *compressa*. The long claws can be observed also in the group *zschokkei* and to a lesser extent in the group *prespica*. In the species of the group *rostrata*, for which the data are available, only *P. slavei* Petkovski, 1969 has an atypically large claw G_1 (2.5 times the length of the penultimate endopodial podomere). Interestingly, *P. slavei* has a triangular carapace shape, with the greatest high of the left valve situated just behind mid-length (at 58% of the length in the female

Species	♀ claw G_1 / EII+III	♀ claw G_M / EII+III	♂ claw G_2 / EII+III	♂ claw G_M / EII+III	♂ claw z_1
eremita-group					
P. eremita (U, *)	2.5-2.7	2.0	2.2	1.8	short
P. cavicola (K)	4.5	?	–	–	–
P. dispar (F)	2.4	2.1	2.3	2.0	short
P. marmonieri sp. nov. (*)	–	–	2.4	2.2	short
P. pannonicola (M)	2.3-2-6	2.0		–	–
P. pretneri (D)	–	–	4.1	3.6	short
P. puteana (D, J, *)	2.2	1.8	1.5-1.7	1.2-1.4	long
P. serbani (D)	2.5	2.2	2.0-2.8	1.6	short
P. sywulai (R)	3.0-3.1	2.5-2.7	2.5	2.2	short
P. szoecsi (E)	2.2	2.0	?	?	?
P. trigonella (C, J)	2.4-2.7	1.9	–	–	–
RANGE	2.2-4.5	1.8-2.7	1.5-4.1	1.2-3.6	short(-long)
caribbeana-group					
P. caribbeana (B)	1.9	1.4	–	–	–
P. cubensis (B)	1.6	1.5	–	–	–
P. marengoensis (C)	1.8	1.5	–	–	–
RANGE	1.6-1.9	1.4.1.5	–	–	–
compressa-group					
P. compressa (I, O, *)	1.2-1.4	0.9-1.0	1.2	0.9	long
P. albicans (L, M, *)	1.4-1.7	1.1-1.3	?	?	?
P. insculpta (A, P)	1.3-1.5	0.9-1.1	?	?	?
P. pratensis (O, P, *)	1.3-1.6	1.0-1.2	1.1-1.4	0.8-1.0	long
P. regisnikolai (H)	?	?	?	?	long
P. sucki (O)	1.2	0.9	?	?	?
RANGE	1.2-1.7	0.9-1.3	1.1-1.4	0.8-1.0	long
prespica-group					
P. prespica (G)	2.2	1.8	1.8	1.6	long
rostrata-group					
P. rostrata (O, T)	1.3-1.6	0.9-1.2	1.0-1.1	0.8	long
P. antilliana (B)	1.6	1.3	1.5	1.2	long
P. geratsi (B)	1.7	1.3	?	?	?
P. lobipes (*)	?	?	2.6-2.9	2.2	long
P. marchica (I, *)	1.5-1.6	1.2	1.3-1.5	1.1	long
P. sarsi (I, T)	?	?	1.2-1.7	0.8-1.4	long
P. slavei (S)	c. 2.5	?	?	?	?
RANGE	1.3-2.5	0.9-1.3	1.0-2.9	0.8-2.2	long
zschokkei-group					
P. zschokkei (N)	3.2	2.9	2.7	2.4	short
P. delamarei (C, *)	3.0	2.7	2.9	2.1	long
P. rouchi (*)	3.0	2.7	2.7	2.3	long
RANGE	3.0-3.2	2.7-2.9	2.7-2.9	2.1-2.4	short-long

TABLE 2–Comparison of the relative lengths of the selected apical claws on the second antenna (referred to the length of the anterior margin of 2nd and 3rd endopodial podomeres combined) in six species groups of the genus *Pseudocandona*. Data from: A, Bronstein (1947); B, Broodbakker (1983); C, Danielopol (1973); D, Danielopol (1982); E, Farkas (1958); F, Hartmann (1964); G, Karanovic (1999a); H, Karanovic & Petkovski (1999), I, Kaufmann (1900); J, Klie (1931); K, Klie (1935); L, Kovalenko (1983); M, Löffler (1960a, 1964); N, Marmonier (1988); O, Meisch (2000); P, Müller (1900); R, Namiotko *et al.* (2004); S, Petkovski (1969); T, Sars (1925); U, Vávra (1891); *, present paper.

and at 55% in the male), and with a narrow inner lamella (width ≤ 10% of valve length) (Petkovski, 1969). This description perfectly fits the diagnosis characters of the *eremita*-group as presented above (Table 1). Further investigations are needed, however, to support the transfer of this species from the *rostrata* into the *eremita* group. *Pseudocandona slavei* is possibly endemic to the lake Ohrid, where it was collected in the littoral zone (Petkovski, 1969).

In the males of the *eremita*-group the apical claws are also relatively long (except *P. puteana*), a character shared with species of the group-*zschokkei* (Table 2). Additionally, the z_1 claw in the *eremita*-group is reduced (except *P. puteana*), distinctly shorter than G_2 and G_M (not exceeding 3/4 of the length of the G_2 claw and referred to as short in Table 2). In contrast, the males of the species belonging to the groups *compressa*, *prespica* and *rostrata* have a fully developed z_1 claw, which is subequal to G_2 and referred to as long in Table 2. Of the species of the group *rostrata* considered here, only *P. lobipes* (Hartwig) has relatively large apical claws G_2 and G_M; its z_1 claw is fully developed. Development of the z_1 claw in the species of the group *zschokkei* varies considerably; in *P. zschokkei* it is reduced, whereas in two other species – it is fully developed.

From these data it may be concluded that the length of the apical claws on the second antenna is more or less constant within the groups considered here and may be an additional to the carapace traits important diagnostic feature of the *eremita*-species group.

Genital morphology

The female genital lobes of *P. cavicola*, *P. dispar*, *P. eremita*, *P. puteana*, *P. serbani*, *P. sywulai* and *P. szoecsi* are known to be weakly developed, anteriorly usually with undulated wrinkles (or fine folds) and posteriorly displaying a remarkable (usually finger-shaped) extension of variable length and orientation (see Klie, 1935, 1940; Petkovski, 1969; Danielopol, 1982; Namiotko *et al*., 2004). Anterior folds and finger-like extension in some of these species are separated by a flat depression (Danielopol, 1982). The genital lobe of *P. eremita* observed by the present authors before smashing by a cover glass shows two indistinct, fine and somewhat laterally oriented, rounded folds (posterior one more developed and finger-like) separated by a small depression with a well sclerotized margin. When compressed under the cover glass, the folds sometimes do not protrude distinctly beyond the margin of the central depression and then the genital lobe gives the impression of being flat or only slightly and evenly rounded with the wrinkled margin. Therefore, the shape of the genital lobe ought to be observed before making a permanent slide, on the entire female. The above-presented structure of the genital lobe may be diagnostic of the species of the group *eremita*. In the other groups of *Pseudocandona*, the genital lobe is either evenly rounded (slightly or distinctly protruding) or flat and without any distinct extensions (except *P. antilliana* Broodbakker, *P cubensis* Broodbakker, *P. stagnalis* (Sars) and *P. sucki* (Hartwig)).

As only a few papers provide data on the detailed internal morphology of the hemipenis of the representatives of the genus *Pseudocandona* (e.g. Danielopol, 1969) and so far particular studies devoted to variability of this organ have not been undertaken, the precise assessment of the taxonomic usefulness of the hemipenis features within *Pseudocandona* is difficult at the moment. However, some traits may be diagnostic of the *eremita* species group. In *P. eremita*, *P. puteana*, *P. serbani*, *P. sywulai* and *P. marmonieri* sp. nov. the bursa copulatrix is distinctly cornet-shaped (Fig. 6A-B). The weak sclerotization of the distal part of the M-process commonly seen in *Pseudocandona* hampers detailed comparison of the shape of this part between different species. It has to be pointed out, however, that at least in *P. eremita*, *P. serbani* and *P. sywulai*, the distal part of the M-process bears a conspicuously crenulated appendix, despite its different shape and orientation in these species. It is not unlikely that this character is a common and unique one of the species of the group *eremita*, but this needs further study.

Emended diagnosis

Type species: *Cypris eremita* Vejdovský, 1880.

Carapace of medium length (inferior to 1.1 mm), approximately triangular in lateral view, with the greatest height at mid-length or just behind mid-length (at 50-60% of the length). Height to length ratio above 50%. Left valve with a dorsal hump, larger and higher than the right one, and overlapping the right valve at both ends. Valves thin with a fine ornamentation consisting of shallow pits mostly located in the central area. Calcified inner lamella very narrow, anteriorly representing not more than 10% of the valve length and usually being less than twice as wide as in the posterior part. Inner and outer margins more or less parallel. The shape and ornamentation of the valves as well as the relative width of the inner lamella remain almost unchanged throughout the last four stages of the postembryonic development; hence, the adults retain juvenile characters. Sexual dimorphism in size and shape of the carapace weakly expressed; male carapace slightly larger than that of the female.

Female second antenna with long terminal claws G_1 and G_M (≥ 2.2x and ≥ 1.8x the length of the penultimate segment, respectively).

Male second antenna: 2nd and 3rd endopodial podomeres fused or not (when fused then with male bristles); G_2 and G_M claws relatively long (generally ≥ 2.0x and ≥ 1.6x the length of the 3rd and 4th endopodial segments combined, respectively); z_1 claw relatively short (not fully developed), usually not exceeding 3/4 of G_2 (except *P. puteana*).

Mandibular palp bearing 3 setae in the setal group situated on the 2nd segment.

Cleaning leg: distal seta of the subterminal segment (seta g) long; apical segment with two long (h2 and h3) and one short seta (h1).

Female genital lobe with two fine folds (the posterior one markedly more developed) separated by a flat depression or weakly developed and evenly rounded.

Hemipenis: three lobes (a, b, h) well developed; M-process with a broad proximal plate, central part contracted and distal part weakly sclerotized, variously shaped, and often crenulated; bursa copulatrix cornet-shaped.

The group includes 11 nominal species: *Pseudocandona cavicola* (Klie, 1935), *P. dispar* (Hartmann, 1964), *P. eremita* (Vejdovský, 1882), *P. marmonieri* sp. nov., *P. pannonicola* (Löffler, 1960a), *P. pretneri* Danielopol, 1978, *P. puteana* (Klie, 1931), *P. serbani* Danielopol, 1982, *P. sywulai* Namiotko *et al.*, 2004, *P. szoecsi* (Farkas, 1958) and *P. trigonella* (Klie, 1931). It has to be emphasised that the chaetotaxy of the cleaning leg of *P. pretneri* and *P. trigonella* is not known, therefore these two species are only provisionally retained in the *eremita*-group. Furthermore, the gradational nature of the characters used for distinguishing *P. pannonicola*, *P. szoecsi* and *P. serbani* from *P. eremita* makes it highly likely that the different name-bearing types of these nominal taxa actually belong to *P. eremita*. Although these names could be subjective synonyms at the rank of species, they do not need to be synonyms at a subspecies or infrasubspecific rank, as already suggested by Löffler (1964) who considered *P. pannonicola* a subspecies of *P. eremita*, and Sywula (1981) who deemed *P. szoecsi* a form of *P. eremita*. As the taxonomic relationships between these species require clarification, forthcoming studies will be devoted to inter- and intrapopulational variability of these taxa.

Final remarks

From the above-presented data it may be concluded that the studied morphological characters appear constant within the group *eremita*. The differences between this group and five other species groups of *Pseudocandona* allow fairly easy distinction of the species belonging to the group *eremita*. However, there are a number of non *eremita*-group species in *Pseudocandona*, which share some characters with the species of that group. Furthermore, many of the characters presented in the emended diagnosis of the group *eremita* display continuous variability and it is possible that the evolution of these traits was gradual and liable to convergence. It seems that species of this group are neotenic with respect to some features of the carapace and the underdevelopment of the male z_1 claw of the second antenna, which would be a developmental strategy for adapting to the groundwater habitat or, alternatively, a result of the life in the energetically poor groundwater system. It has also to be emphasised, that not all species of *Pseudocandona* have been yet thoroughly examined regarding the traits considered here and still intraspecific variability of various traits is hardly known. For this reasons, it is difficult to establish the generic rank of the traits mentioned above. On the other hand, the group *eremita* is the only one in the genus *Pseudocandona* sensu Meisch (2000) that has been separated and used commonly by palaeontologists, either as a subgenus, *Candona (Typhlocypris)* Vejdovský (e.g. Triebel, 1963; Krstić, 1993), or as a separate genus, *Typhlocypris* Vejdovský (e.g. Sokač, 1978), whereas the species of the groups *compressa* and *rostrata* (as defined above) have been generally assigned to the genus *Pseudocandona* by palaeontologists. However, the palaeontological concept of *Typhlocypris* has been so broad as to encompass also other triangular Candoninae species, which in the opinion of neontologists belong to separate genera according to characters of either the soft parts or the carapace, so for instance *Fabaeformiscandona aemonae* (Klie) or *Schellencandona triquetra* (Klie) (Meisch, 2000). The name *Typhlocypris* at the rank of a subgenus or genus has been used by a few neontologists too (e.g. Sywula, 1974; Kovalenko, 1988), although most of the modern zoologists consider *Typhlocypris* an older but unused synonym of *Pseudocandona* (Meisch, 2000). This view was adopted also in the present paper because of a better characterisation of the type species of the latter genus, i.e. the presence of generic traits also for the male, which is not true for the type species of the genus *Typhlocypris*, i.e. *T. eremita*.

As at present we cannot provide reliable diagnostic characters based on soft parts for assigning the group *eremita* the rank of a genus, in order to avoid confusion as well as for stability of the nomenclature we decided, in contrast to our earlier presentation at the 5th European Ostracodologists Meeting in Cuenca, Spain (Namiotko & Danielopol, 2003), to maintain the *eremita*-group (as defined above) within the genus *Pseudocandona* sensu Meisch (2000). Future studies based on both the carapace and limbs (possibly on molecular descriptors too) should focus on inter- and intraspecific variation to verify if this lineage deserves a separate generic status. If so, then the name *Typhlocypris* Vejdovský, 1882, should be reassessed and restricted to the species of the group *eremita* as discussed above.

SYSTEMATIC DESCRIPTIONS

In the systematic part of this paper the chaetotaxy of the limbs was coded according to the model proposed by Broodbakker & Danielopol (1982), as revised for the second antenna by Martens (1987), and extended to the thoracopods by Meisch (1996). Names for the limbs were used according to Meisch (2000). The nomenclature of Danielopol (1969), as reviewed by Meisch (2000), was used for the morphology of the hemipenis.

Class Ostracoda Latreille, 1806
Order Podocopida Sars, 1866
Suborder Podocopina Sars, 1866
Infraorder Cypridocopina Jones, 1901
Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Candoninae Kaufmann, 1900
Genus *Pseudocandona* Kaufmann, 1900
Pseudocandona marmonieri sp. nov.
(Figs. 3-6)

Derivatio nominis.–The new species is named in honour of Dr Pierre Marmonier (Biological Station at Paimpont, University of Rennes I, France) for his outstanding contribution to the knowledge of the stygobitic ostracods. The name is a noun in the genitive case.

Type material.–Holotype: a male with limbs dissected in glycerine and mounted on a permanent slide; left valve stored dry in a micropalaeontological cell. Paratypes: three males dissected and stored as the holotype (nos. 1-3) and one not dissected male with the broken carapace preserved on ethanol tube (no. 4). Deposition: the holotype and three paratypes (nos. 1-2, 4) are housed at the Limnological Institute of the Austrian Academy of Sciences (Mondsee). One dissected paratype (no. 3) mounted on a slide is lodged at the University of Gdańsk (the collection of the first author).

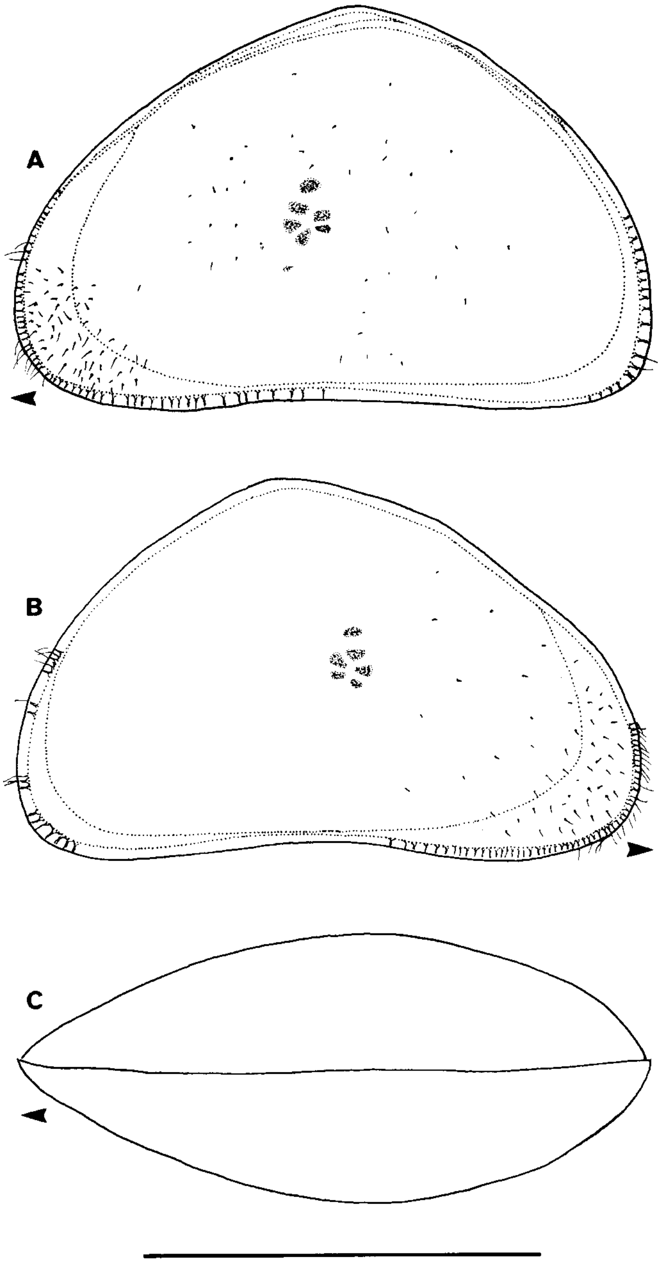

Figure 3–A-C, *Pseudocandona marmonieri* sp. nov. *A*, paratype no 1, left valve viewed laterally; *B*, paratype no 3, right valve viewed laterally; *C*, paratype no 3, carapace in dorsal view. Scale: 0.5 mm.

Type locality.–The site is situated in southern France within the karstic area of the Plateau d'Anglars-Amiel, Massif des Causses (Departement du Tarn, Commune de Penne). The material was collected in 1984 by Claude Bou (Albi) within the cave Amiel at the site LM0 (figure 5 in Bou, 1999).

Diagnosis.–Small representative of the *eremita*-species group of the genus *Pseudocandona* with a relatively high carapace (H/L = 0.62-0.64). Dorsal margin of the LV roundly arched with a hump that overlaps the RV. Greatest H of LV located just behind mid-length, at c. 54% of valve L. Calcified inner lamella at the anterior end of the LV amounting to c. 9% of L. 2nd and 3rd endopodial podomeres of A2 in males separa-

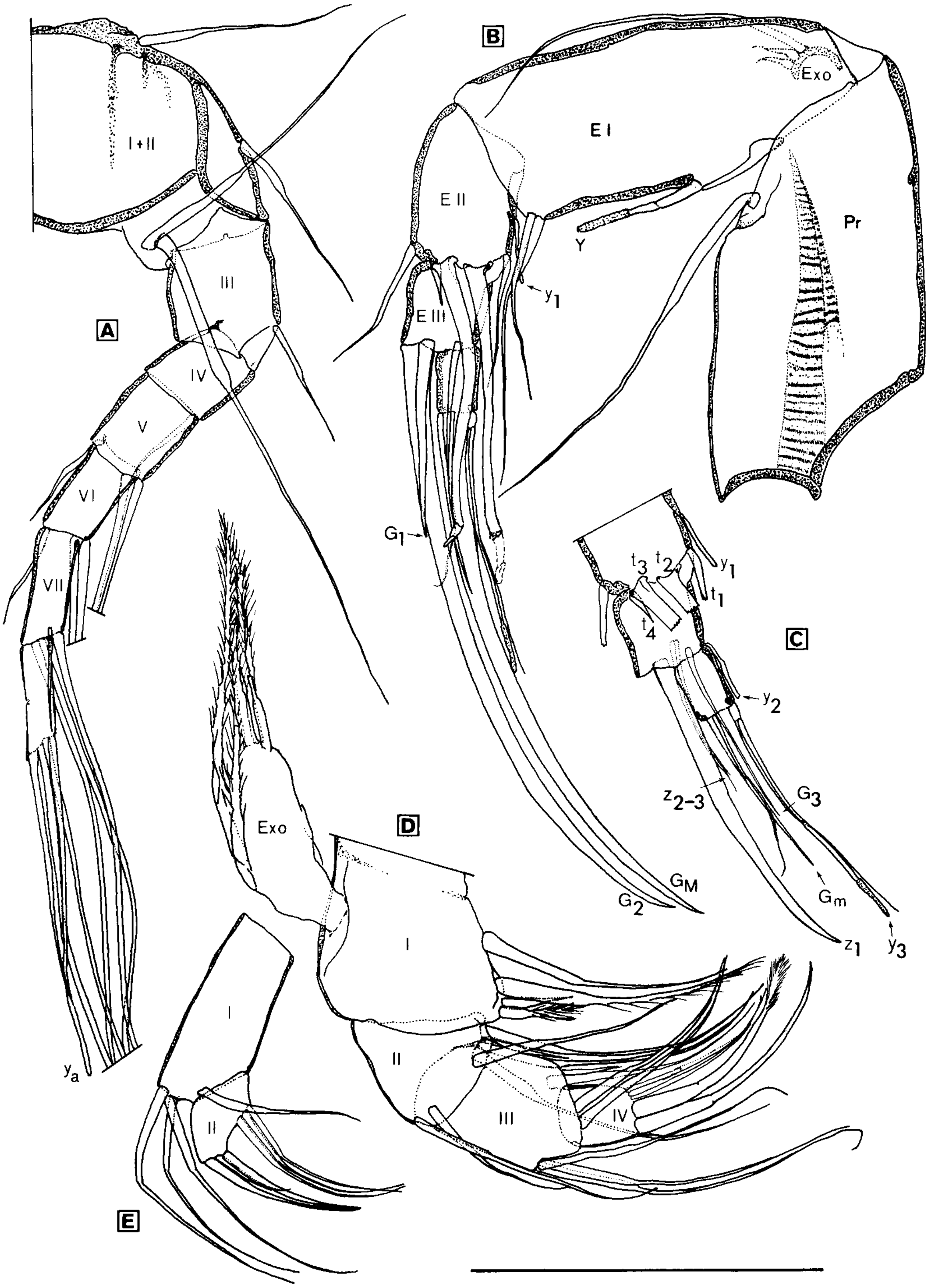

FIGURE 4–*A-E, Pseudocandona marmonieri* sp. nov., holotype. *A,* antennule; *B,* right antenna in internal view; *C,* details of apical chaetotaxy of the right antenna; *D,* mandibular palp; *E,* maxillular palp. Scale: 100 µm.

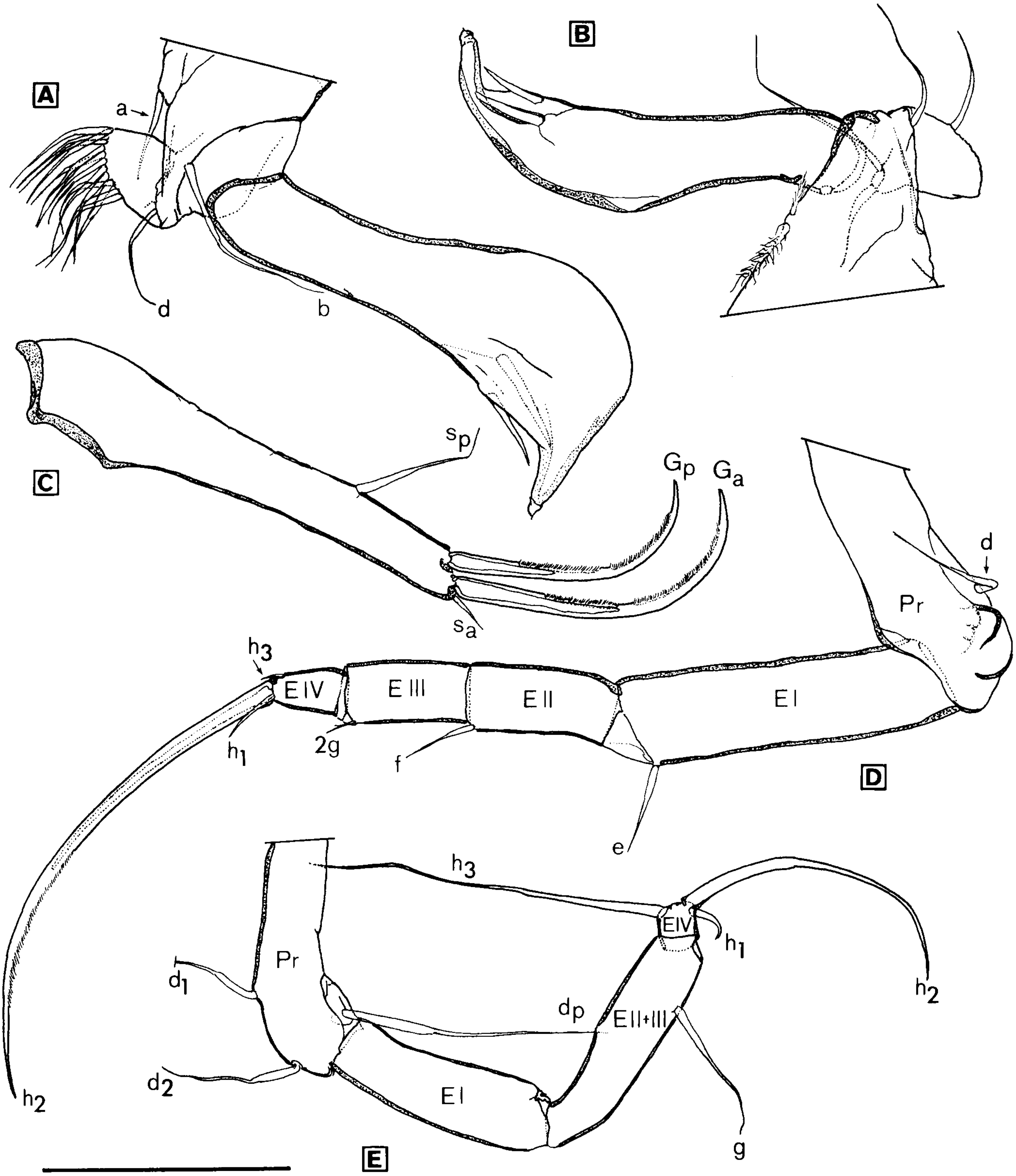

FIGURE 5–*A-E, Pseudocandona marmonieri* sp. nov., holotype. *A,* right maxilliped; *B,* left maxilliped (setal group of the distal part of endite not shown); *C,* caudal ramus; *D,* walking leg; *E,* cleaning leg. Scale: 100 µm.

ted and with male bristles; the largest claw (G_2) of EIII of this limb equalling 3.8-3.9x, and the major claw (G_M) of the terminal podomere c. 3.5x the length of the anterior margin of EII. Posterior seta on Pr of A2 lar-

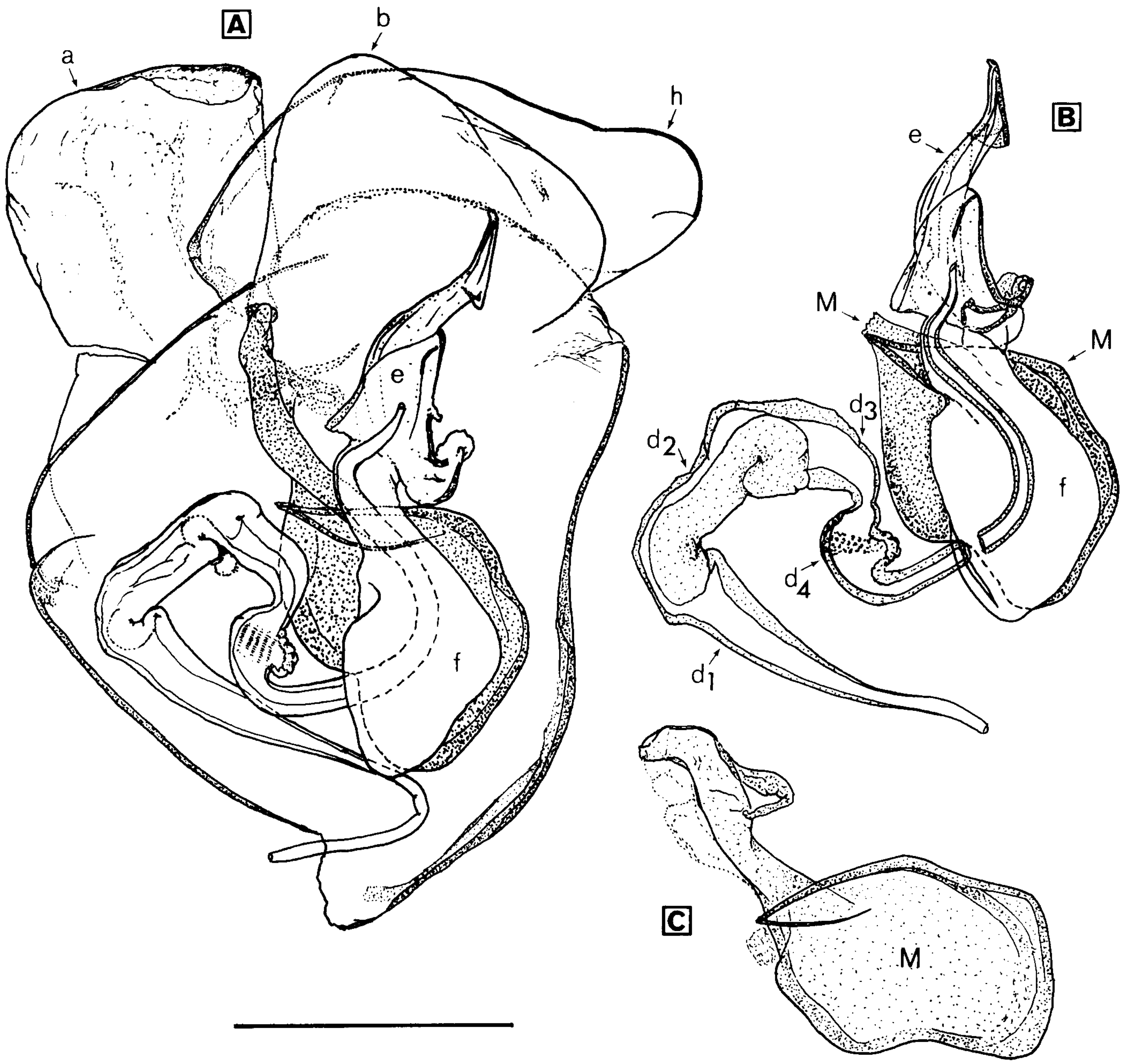

FIGURE 6–*A-C*, *Pseudocandona marmonieri* sp. nov. *A*, holotype, right hemipenis, internal view; *B*, paratype no 2, internal details of right hemipenis viewed internally: spermiduct (d1-d4), bursa copulatrix (e), muff (f) and proximal part of M-process (distal part broken); *C*, paratype no 3, M-process of right hemipenis, internal view. Scale: 100 µm.

ger than the anterior margin of EI. Cleaning leg 4-segmented, EII and EIII fused, short terminal seta (h_1) hook-like and recurved basally. Medial lobe (h) of hemipenis with a distinct rounded expansion oriented to the postero-ventral end of the body.

Male.

Carapace viewed dorsally (Fig. 3C) moderately compressed, sub-obese, with greatest W inferior to 1/2 L (c. 43% of L), and situated just behind mid-length (56-57% of L). Anterior end weakly pointed, posterior end moderately rounded; LV overlaps RV at both extremities. LV (Fig. 3A) relatively high (H/L = 0.62-0.64) and triangular in lateral view with greatest H located just behind mid-length (54% of valve L). Dorsal margin roundly arched with a hump that overlaps the RV. Ventral margin slightly concave. Calcified part of the inner lamella narrow, on the anterior end amounting to 9% and on the posterior end to 4-5% of L. RV (Fig. 3B) similar in outline to the LV but smaller and lower (see measurements below), with the greatest H situated at 58% of L and with almost straight and then slightly concave antero-dorsal margin. Fused marginal valve zone narrow, with straight, short and dense radial pore canals. Valves whitish, with mostly smooth surface (rare shallow pits can be found only in the central area) and covered with setae located mainly on the anterior and posterior areas. Central muscle scar arrangement typical of the tribe Candonini.

Dimensions.–Holotype LV: L = 0.81 mm, H = 0.52 mm, H/L = 0.64. Paratypes LV: L = 0.77-0.80 mm (n = 4), H = 0.48-0.50 mm (n = 3), H/L = 0.62-0.63 (n = 3); RV: L = 0.76-0.78 mm (n = 2), H = 0.47 mm (n = 1), H/L = 0.60 (n = 1).

Antennule, A1 (Fig. 4A). I+II: A-2*l*, P-2*l* / III: A-1*m* / IV: A-1*m* / V: A-2*l*, P-1*m* / VI: A-2*l*, P-1*m* / VII: A-1*m*-2*l*, P-1*l* / VIII: D-y_a-1*l*(cs)- 2*l*. The largest anterior setae on the penultimate podomere c. 2.7-2.9x the L of the ramus (the last five podomeres combined). Aesthetasc y_a 2.9-3.2 times as long as the terminal podomere. Relative lengths of the posterior margins of the last 5 distal podomeres (IV-VIII) as: 1.0 : 1.1-1.2 : 1.3 : 1.5 : 1.4, L/W of these podomeres, from proximal onwards as: 1.0, 1.2, 1.9, 2.9-3.1, 4.1-4.3.

Antenna, A2 (Fig. 4B-C). Pr: P-1*l* / Exo: D(Ex)-2*s*-1*l* / EI: P-Y, P(D)-2*m* / EII: A(D)-1*s*, P-y_1, D(In)-2*s*(t_1,t_4)-2*m*(t_2,t_3) / EIII: D(P)-y_2, D(A)-1*l*(G_2), D(Ex)-2*s*(z_2,z_3)-1*m*(z_1:G), D(In)-1*m*(G_3)-1*m*(G_1) / EIV: D(A)-1*l*(G_M), D(P)-y_3+1*m*, D(In)-1*m*(G_m), D(In)-1*m*. Endopod 4-segmented, and the relative L of the anterior margin of EI : EII : EIII : EIV as: 1.0 : 0.40 : 0.25 : 0.18. Aesthetasc Y equalling c. 0.4 of EI (the sensory part of this organ represents 41-42% of its L). Setae t_2 and t_3 transformed into sub-equal male bristles (t_2 slightly larger than t_3) and their lengths represent c. 0.8 of the length of EI; t_1 short (0.4), t_4 rudimentary (0.1). Relative lengths of claws, some setae and the remaining aesthetascs compared with the L of EI as: G_1 (claw) = 0.5, G_2 (claw) = 1.7, G_3 (seta) = 0.5, z_1 (claw) = 0.9-1.0, z_2 and z_3 (setae) = c. 0.45, G_M (claw) = 1.5, G_m (claw) = 0.5-0.6, y_1 = 0.2, y_2 = 0.2, y_3 = 0.7-0.8 (sensory part 16-19% of its L).

The mandible, Md (Fig. 4D) consists of the coxal plate and a 4-segmented palp (Mdp). Coxa typically elongated and heavily chitinized with the masticatory part bearing one plumed seta, seven strong teeth interspaced with sets of diverse setae and one lateral seta. Mdp: I: In-1*s*(α)-1*s*(S_2)-1*m*-1*m*(S_1) / II: Ex-2*m*, In-1*s*(β)-4*m* / III: Ex-1*m*-2*l*, In-1*s*-1*m*, D-1*m*(γ)-1*m* / IV: D-1?-2*m*-2*m*(G). First podomere externally with the exopodite plate. Setal group on the 2nd podomere with 3 setae. Externo-distal **δ** seta on 3rd podomere smooth. Anterior claw of the terminal podomere amounting to 1.6 and posterior to 1.4 of the L of the 3rd palp podomere. The relative L of one distal seta on the 4th palp podomere could not be determined.

Maxillule, Mx1 (Fig. 4E) with a branchial plate, 3 masticatory processes, and a 2-segmented palp: I: Ex-1*m*-3*l* / II: D-3*m*-1?-2*m*(cs). The relative L of one distal seta on the 2nd palp podomere could not be determined.

Maxilliped, L5 (Fig. 5A-B). Pr bearing one anterior ‘d’ seta and two exterior setae ‘b’ and ‘d’. Masticatory process (endite) apically with a group of 14 setae. Exo plate bearing two filaments, one longer and flexible and one shorter and stiff. E developed into asymmetrical, prehensile palps. Right palp (Fig. 5A) more developed, distally helmet-shaped; left one (Fig. 5B) slender.

Walking leg, L6 (Fig. 5D). Pr: A(D)-1*s*(d) / EI: A(D)-1*s*(e) / EII: A(D)-1*s*(f) / EIII: A(D)-2*s*(g) / EIV: P-1*s*(h_3), D-1*s*(h_1)-1*l*(h_2: G). Terminal claw (h_2) serrated and equalling 3.1 of the length of EII.

Cleaning leg, L7 (Fig. 5E). Pr: Ex-2*m*(d_1,d_2), In-1*l*(d_p) / EII+III: P-1*m*(g) / EIV: D-1*s*(h_1)-1*l*(h_2)-1*l*(h_3). Cleaning leg 4-segmented, EII and EIII fused. Relative lengths of three apical setae as: h_1 = 0.1-0.2, h_2 = 1.1, h_3 = 1.6. Seta h_1 hook-like and recurved downwards.

Caudal ramus, CR (Fig. 5C). Ratio of lengths of anterior margin, s_a, G_a, G_p, s_p and the distance between insertion points of s_p and G_p as: 100 : 12-13 : 77-79 : 65-68 : 38-39 : 28-29. Distal claws serrated and strongly curved.

Zenker’s organ with 7 internal rings of spines, its length represents c. 30% of the carapace L.

Hemipenis (Fig. 6A-C). Outer lobe (a) sub-rectangular. Inner, shortest lobe (b) wide, distally flat and postero-dorsally slightly reaching beyond the medial lobe. Medial lobe (h) well developed, distally broadly rounded, with a distinct, rounded and weakly slanted expansion oriented to the postero-ventral end of the body. M-process with a broad proximal plate, a contracted central part, and a weakly sclerotized and elongated distal part (Fig. 6A, C). Bursa copulatrix elongated and cornet-shaped (Fig. 6A-B).

Female.–Not found.

Distribution and ecology.–The new species is known only from the type locality, where it was collected in the cave Amiel at the site LM0 (Bou, 1999). The site is a subterranean spring (“griffon”) discharging water from the surrounding karst system. The spring remains active during periods of low water stands when the gallery is accessible for exploration.

Ostracods were caught by the long-term (several days) permanent filtering of the LM0 exurgency. Along this stygobitic ostracod species, during the same period of sampling, a very diverse amphipod fauna was also collected at the site (C. Bou pers. comm. to D. L. D.).

Remarks.–Pseudocandona marmonieri sp. nov. differs from its congeners belonging to the *eremita* species group by the morphology of the hemipenis, mainly by the presence of the characteristic postero-ventral expansion of the medial lobe (Fig. 6A). The conspicuously triangular shape of the carapace viewed laterally (H/L = 0.62-0.64) makes *P. marmonieri* sp. nov. similar to *P. dispar*, *P. pretneri* and *P. trigonella* (H/L ratio in those species is in the range of 0.62-0.67). However, *P. dispar* is a larger species (L of males = 0.95-0.97 mm; Hartmann, 1964), and *P. pretneri* lacks male bristles and separation of EII and EIII of A2 (Danielopol, 1982). Since *P. trigonella* was described from only one female (Klie, 1931), this precludes a comparison of the genital morphology of that species and the new one. *P. trigonella* is a remarkably small species (L = 0.55 mm), having an extremely large claw (h_2) on EIV of L6 and a reasonably long and straight (not hook-like) seta h_1 on EIV of L7 (Klie, 1931). The new species cannot be confused also with the remaining species of the *eremita* group, for which the H/L ratio of the carapace is ≤ 0.6. Males of *P. eremita*, *P. puteana*, *P. serbani*, *P. sywulai* and *P. szoecsi* have a hemipenis with a differently shaped medial lobe (Klie, 1931, 1940; Petkovski, 1969; Danielopol, 1982; Namiotko *et al*., 2004). The males of *P. cavicola* and *P. pannonicola* remain unknown; however the females of the first species have separated EII and EIII of L7 and a gently arched (not hook-like) seta h_1 of this limb (Klie, 1935), whereas females of the second one are larger (L = 0.86-0.90 mm) than *P. marmonieri* sp. nov. and, seen laterally, have a more rounded dorsal and dorso-posterior margin on both valves (Löffler, 1960a, 1964).

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LIVING FRESHWATER OSTRACODA (CRUSTACEA) OF A FLOODPLAIN RELICT OAK FOREST (POLESYE, BELARUS)

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Abstract

The oak forest of Polesye is an example of the deciduous wood areas of Western Europe, which covered large parts in many European countries and were transformed due to industrial and agricultural use during past centuries. Vast expanses of the relict oak forest in the floodplain of the Pripyat River (National Park “Pripyatski”) are pristine and uninhabited and human influence is negligible. The area maintains many diverse water ecosystems (temporary pools, brooks, ponds, bogs, oxbow lakes). The main sources of natural disturbance are flooding and droughts in some years. This investigation of 23 reservoirs in the extremely dry year of 2002 showed their rich and diverse flora (>200 species) and fauna (>420 species). Hydrochemical parameters of the investigated pools were measured in situ during the sampling and demonstrated considerable variability, for example in pH (6.1-8.8), conductivity (41.1-410 µS/cm), temperature (9.6-28.4ºC), oxygen (0.38-14.1mg/l), hardness total and carbonate (0.4-3.6 mmol/l), NH_4^+ – (0-0.6 mg/l), NO_2^- – (0-0.01 mg/l), NO_3^- – (0-5 mg/l), PO_4^{3-} (0-0.75 mg/l). The species richness of Ostracoda in the reservoirs investigated totaled 27 species (6.3% of the total fauna community composition). The Ostracoda assemblages consisted of 2-6 (temporary pools, bogs), 6-12 (brooks), 7-10 (ponds), 17-19 (oxbow lakes) species. Species number correlated primarily with the chemical composition of the pools (hardness, conductivity and so on). The total species number in the reservoirs in the relict oak forest is 64% of the total Ostracoda list for the Pripyat floodplain area.

Key words: National Park “Pripyatski”, Belarus, landscape, diversity, species richness, environmental factors, freshwater ostracods assemblages.

Resumen

El bosque de robles de Polesye es un ejemplo de áreas de madera caducifolia de Europa occidental, que cubre amplias áreas de muchos países europeos y que fueron transformados debido al uso industrial y agropecuario durante los siglos pasados. Vastas áreas del bosque relicto de robles de la llanura de inundación del río Pripyat (Parque Nacional “Pripyatski”) permanecen prístinas e inhabitadas y la influencia humana en ellas es inapreciable. El área mantiene diversos ecosistemas acuáticos (charcas temporales, arroyos, pantanos, turberas y lagos *oxbow*). La mayor fuente de alteración natural son las inundaciones y sequías de algunos años. Esta investigación de 23 reservorios en el año extremamente seco de 2002 muestra su rica y diversa flora (>200 especies) y fauna (>420 especies). Los parámetros hidroquímicos de los cuerpos acuosos investigados fueron medidos *in situ* durante el muestreo y ofrecieron una variabilidad considerable. Así, por ejemplo, en el pH (6.1-8.8), la conductividad (41.1-410 µS/cm), temperatura (9.6-28.4ºC), oxígeno (0.38-14.1mg/l), dureza total y carbonato (0.4-3.6 mmol/l), NH_4^+ (0-0.6 mg/l), NO_2^- (0-0.01 mg/l), NO_3^- (0-5 mg/l), PO_4^{3-} (0-0.75 mg/l). La riqueza específica de los Ostracoda en los reservorios investigados totalizan 27 especies (6,3% del total de la composición faunística de la comunidad). Las asociaciones de Ostracoda consisten en 2-6 especies de charcas temporales y turberas, 6-12 de arroyos, 7-10 de pantanos y 17-19 especies de lagos *oxbow*. El número de especies se correlaciona principalmente con la composición química de las aguas (dureza, conductividad y otros). El número total de especies en los reservorios del bosque relicto de robles constituye el 64% del total de los ostrácodos referidos en el área de la llanura de inundación del río Pripyat.

Palabras clave: Parque Nacional “Pripyatski”, Bielorrusia, diversidad, riqueza específica, factores ambientales, ostrácodos de agua dulce.

INTRODUCTION

The interest in flora and fauna of the natural undisturbed riverine zones and river floodplains is due to social, political and economical strategy in many countries, which try to protect global biodiversity, to reconstruct some disturbed areas (Fittkau & Reiss, 1983; Buijse *et al.*, 2002), and to support water quality (Gilliam, 1994). Some of the very natural components of the floodplain landscape are the Belarussian relict oak forests in the South of country (Polesye region). The oak forests of Polesye are remainders of the deciduous wood area of Europe, which covered huge territories of many European countries many centuries ago (Yurkevich *et al.*, 1977).

In spite of the fact that the Polesye’ floodplain relict oak forests cover a relatively small part of the Polesye area, they are of great importance to water quality and protection of the soil. Oak forests are also of significant recreational importance thanks to their ability to clean air of dust and to produce oxygen: oak leaves have the highest value of phytoncyde activity of all wood species (Novoseltsev & Bugaev, 1985). The oak forests regulate the hydrological regime, reducing the surface drainage and shifting it to underground drainage. There is no doubt that the oak forests are very important as a biosphere element of the huge Polesye area.

The Polesye area is particularly scientifically interesting since it contains species from various climatic regions (western and eastern Europe, southern steppes and northern coniferous forests), and natural lowland ecosystems are very rare in Europe.

There are various types of water ecosystem in the Pripyat River floodplain (oxbows, lakes, springs, ponds, brooks, temporary water bodies, bogs and wetlands), which are fed by precipitation (rain and snow), soil and underground waters and flooding waters as well as overland flow from neighbouring forests and upland bogs. It seems that both the water sources and the soil character as well as hydrochemical characteristics determine the species composition and fauna richness of the pools (Nagorskaya & de Jonge, 2002; Nagorskaya *et al.*, 2002; Nagorskaya & Keyser, 2004).

Floodplain relict oak forests include all types of the water bodies named above and are an important element of the floodplain landscape structure (Yurkevich *et al.*, 1977). However, there was no information on the aquatic invertebrates, including Ostracods, inhabiting their reservoirs.

The goals of the present investigation were:

- to give insights into the morphological, hydrochemical and biotic characteristics of the various types of water bodies in the floodplain relict oak forest.
- to characterise their Ostracod assemblages.

AREA OF INVESTIGATION

The Polesye lowland is situated in the north-west Ukraine, the south of Belarus and the western area of the Bryansk region, Russia. It has an altitude of 100 - 200 m. The lowland developed on an ancient Paleozoic tectonic basin, filled in by more recent deposits of different geological eras. The modern surface of the lowland was formed by the deposition of sandy and sandy clay of both fluvio-glacial and alluvial origin with occasional moraine inputs such as clay sands and loam (Vozniyachuk *et al.*, 1972).

During the Paleozoic period, the Polesye lowland underwent many movements. It was a bottom of a marine basin during foundering periods, while during upheaval periods it was lowland. The maximal sea extension was during the Oligocene and by the end of that era (20-25 million years ago) sea retreated. Both erosive and accumulative processes prevailed during the Neogene. Finally, the glacial Quaternary period superimposed the line of gradual changes of the landscape during four advances and retreats of glaciers (Machnach *et al.*, 1975). The outlet of the ancient lakes was via streams directly to the Pripyat River (Dementiev, 1956). The inflow rivers to the ancient lakes continued to flow during the Riss-Würm interglacial, diminishing in flow rate by natural drainage. Therefore the connection between the river basins of Middle and Southern Europe is very ancient and was of one of the reasons for exchange of aquatic water fauna and flora.

The Pripyat Polesye is located within the region delimited by the basin of the Wisla River from the West, the Dnyepr River from the East and the Mozyr - Volyn area from the South. The northern part of the Polesye lowland is named the Belarussian Polesye and covers 58,000 sq. km. The area is a uniform plain with only a 20-meter slope along the Pripyat River flow over a distance of 300 km, from the Dnyepr-Bug channel to the Mozyr area. The interfluvial territories are heterogeneous and range from dry sand lowlands with forests and bushes to peatlands and lowland bogs. These lands are characterised by a high ground water levels and are covered with wet alder-birch forests and alder-osier bushes. The oak forests are 10% of the total forests of the area. At the same time, this area comprises 64% of the total floodplain oak forest of Belarus (Yurkevich *et al.*, 1977).

DESCRIPTION OF SAMPLING SITES

Samples were taken from 16 different types of water body in the Gomel area of Belarus during 3 months of 2002 (Table 1, Fig. 1). In total 25 biotopes were investigated. The study area was located 5-15 km E from the village Hlupin (28°10’E-51°59’N) and 35 km E of the town Turov (Fig. 1). Human influence in the region is slight. Drainage is natural, resulting in a very high water table. The floodplain is used only for the grazing of cattle. Vast expanses of marsh and forest in the watershed are pristine and uninhabited.

MATERIALS AND METHODS

34 samples were collected in May, July and September 2002. Qualitative samples were taken for total benthos, where ostracods were a constituent part of the community. Benthos was sampled with a 180 µm mesh hand dredge net, which was dragged over the bottom surface to a depth of 3-5 cm. The total sample

NN of pool	Legend for Fig.1	The type of pool
1	PIT1	Pit
3	BR3	Brook temporary
4	PO4	Pond
5	TP5	Temporary pool in the oak forest
6	TP6	Temporary pool in the oak forest
8	TP8	Temporary pool in the oak forest
9	TP9	Temporary pool in the oak forest
10 (1)	BR101	Brook (drift)
10 (2)	BR102	Brook (peaty zone)
10 (3)	BR103	Brook (pond zone)
11 (1)	LLB111	Liuben Lake, st.1, S shore
11 (2)	LLB112	Liuben Lake, st.2, N shore
14	LCR14	Carasino Lake, S shore
15	BOG15	Boggy land S from Carasino Lake
16	LCR16	Carasino Lake, W edge of the lake
17 (1)	OX171	Oxbow, st.1
17 (2)	OX172	Oxbow, st. 2
18	OX18	Oxbow
19	BOG19	Boggy lands near a canal
20	PO20	Pond in the forest
21	TP21	Temporary pool in the oak forest

TABLE 1–The sample sites in the area of investigations.

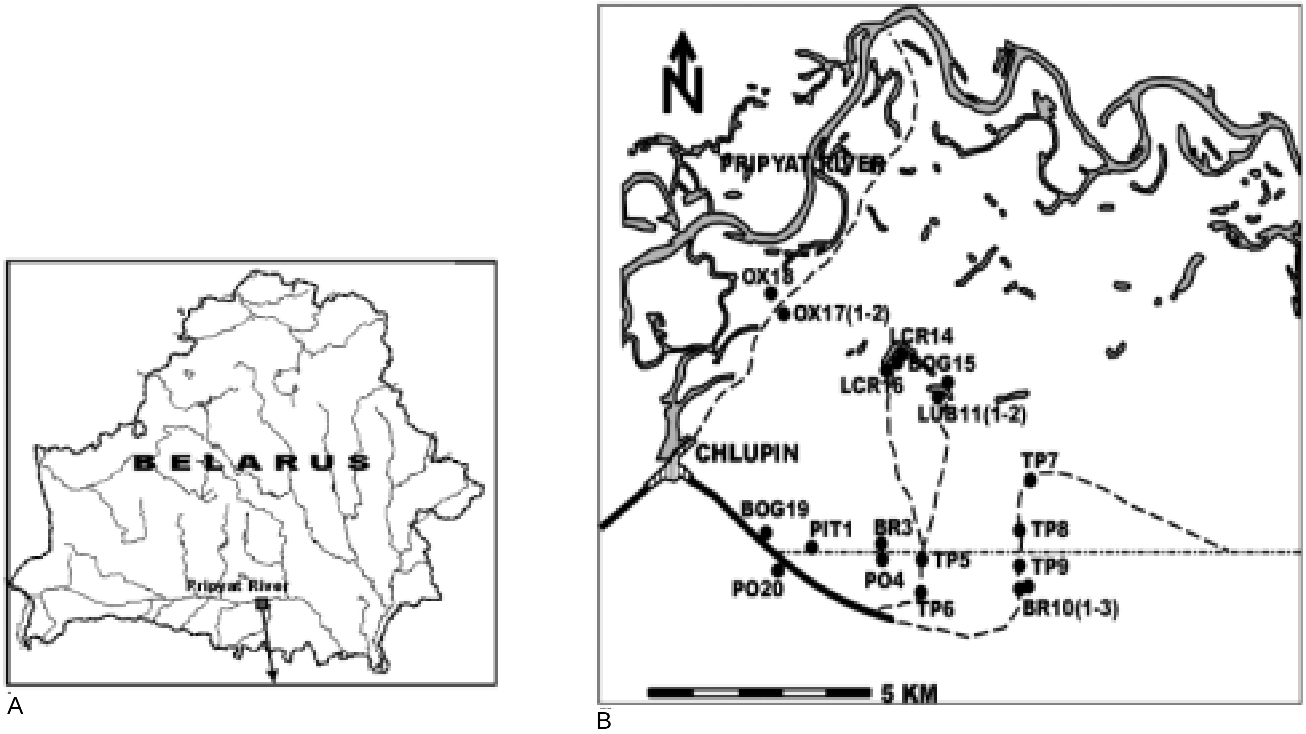

FIGURE 1–*A*, the map of Belarus; *B*, the schema of sampling sites in a vicinity of the Hlupin village (legends of sampling sites, see Table 1).

Variables	**Valid N**	**Mean**	**Minimum**	**Maximum**	**Std. Dev.**	**Std. Error**
pH	32	6.91	5.04	8.78	0.61	0.11
T , °C	32	18.4	9.6	28.4	3.8	0.7
CONDUCT, μS/cm	32	220.4	41.1	410	102.1	18.1
TDS, mg/l	32	111.0	20.6	216	52.0	9.2
O_2, %	32	58	0	147	35.7	6.3
O_2, mg/l	32	5.1	0.38	14.1	3.2	0.57
HARTOTD, °dH	32	7.1	2.1	12	2.62	0.46
HARTOTM, mmol/l	32	1.3	0.4	2.2	0.48	0.08
HARCARD, °dH	32	5.8	0.9	10.2	2.85	0.50
HARCARM, mmol/l	32	2.1	0.4	3.6	1.01	0.18
NO_2^-, mg/l	32	0.00	0	0.013	0.00	0.00
NO_3^-, mg/l	32	0.9	0	5	1.98	0.35
PO_4^{3-}, mg/l	32	0.2	0	1.5	0.34	0.06
NH_4^+, mg/l	32	0.04	0	0.6	0.15	0.03

TABLE 2–Descriptive statistics of the hydrochemical variables.

including all replicates (from 1 to 6 replicates, depending on the sediment type) was washed through a set of sieves of mesh size 1.0, 0.5 and 0.25 mm. Separate taxa were fixed with 70% alcohol in tubes. In the laboratory we divided taxa, identified species and estimated the species number and their relative abundance.

Morphology of pools, vegetation type and the characteristics of the bottom sediments were also described for every sample site.

Measurement of hydrochemical parameters was performed in situ during the sampling with the Hydrochemical express laboratory (Merck^R) (O_2, hardness total and carbonate, NH_4^+, NO_2^-, NO_3^-, PO_4^{3-}), and Corning^R Checkmate System (pH, temperature, oxygen saturation and conductivity). Correlations of hydrochemical parameters, water body type and species number were carried out.

Habitat-based methods were used. These are species inventory and evaluation (ostracods species/rank/abundance), habitat variables analyses and evaluation.

All data were combined in a matrix and were analyzed in Excel spreadsheet format. The data analysis was carried out using the STATISTICA 5.5 software package for Windows.

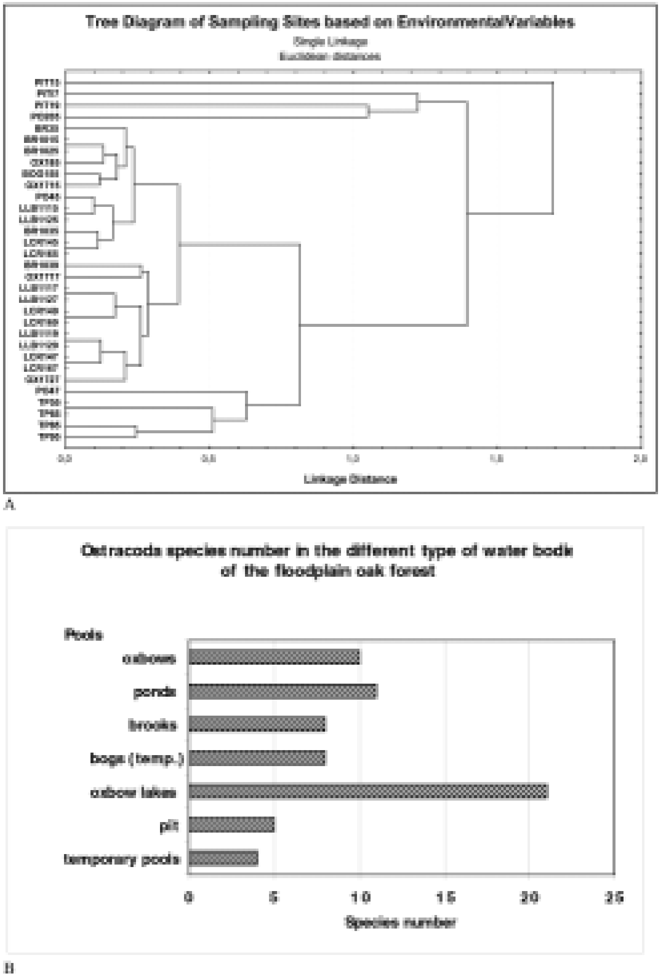

FIGURE 2–*A*, the cluster tree of different sampling sites based on a set of environmental factors: hydrochemical variables, characteristics of water bodies (permanent or temporary; lotic or lentic); *B*, the species number in the different type of pools.

RESULTS

The hydrochemical parameters (Table 2) varied in a wide range from very soft (temporary pools and a pit) to moderately mineralized (lakes) water bodies. The cluster analyses (Fig. 2A) based on hydrochemical variables and morphological-physical characteristics allow us to divide all sampling sites in 4 groups:

Cluster 1 consisted of spring sampled water bodies of various types, not including the pit and temporary pools;

Cluster 2 joined temporary pools;

Cluster 3 described three months’ samplings of the pit;

Cluster 4 were mainly lakes sampled during the drought (in July and September).

The number of ostracod species varied in the different types of pool, from 4 (temporary pools) to 21 (lakes) species (Fig. 2B). There is no doubt that the species number in these water bodies was determined by the duration of the water phase. Temporary water bodies began to dry in the middle of May, while lakes and oxbows, in spite of the sudden water level reduction at the end of summer, had a depth of 0.3-0.5 metres from the water surface to sediments.

The investigation of 16 reservoirs in the extremely dry year 2002 displayed their rich and diverse flora (>200 species) and fauna (>420 species). The species richness of Ostracoda in the reservoirs investigated came to 27 species (6.3% of the total fauna composition) (Fig. 3). At the same time the character of the community structure was similar to that of other floodplain pools (Nagorskaya *et al*., 2002).

The total number of ostracod species in water bodies of the relict oak forest form 64% of the total Ostracoda list for the Pripyat floodplain area (Nagorskaya & de Jonge, 2002) (Table 3). The reason that not many species were found could be due to both the drought (and loss of biotopes) and the specific characteristics of the sediment substances.

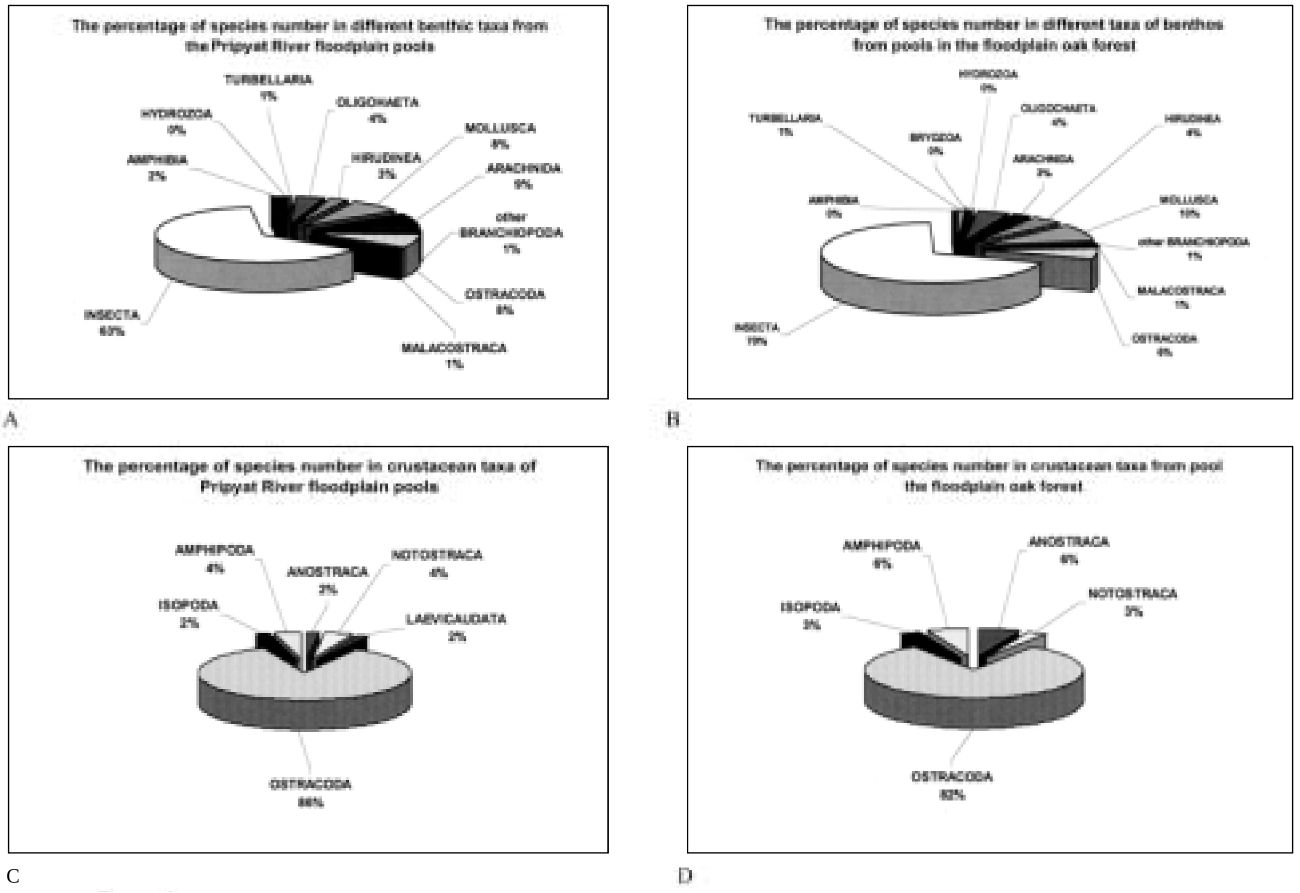

FIGURE 3–The percentage of species number in different taxa: (*A, B,* benthos; *C, D,* crustaceans) from A, C- the Pripyat River floodplain, B, D- the relict oak forest.

The total ostracods species number in every sampling site significantly correlated mainly with the characteristics of the water chemistry of the pools (conductivity, hardness) and with the pool type (Table 4). It appears to be an indirect correlation through the duration of the water phase in the pool, which influences the species life cycles and the water layer depth, and thereby the water temperature regime.

The Ostracoda assemblages (Table 5) consisted of 2-6 (temporary pools, bogs), 6-12 (brooks), 7-10 (ponds), 17-19 (oxbow and lakes) species. Together with common species, which were found in more than 50% of pools, some ostracods were more rare for this area and were found in only one or two of the pools studied (Table 3), for example, *Fabaeformiscandona acuminata* (the Liuben Lake LLB 112), *F. balatonica* (brook BR101), *F. protzi* (the Liuben Lake LLB111), *Limnocythere stationis* (PIT1), *Pseudocandona marchica* (the Liuben Lake LLB112) and *Ps. rostrata* (the Carasino Lake LCR14), *Metacypris cordata* (the Carasino Lake LCR14), *Eucypris pigra* (only in brooks BR3 and BR101). It is remarkable that a few common species were found only in two sampling sites, as *Cyclocypris ovum* (temporary pool TP9 and pond PO4), *Cypria exsculpta* (the Carasino Lake LCR16 and a boggy part of brook BR103) as well as *F. fabaeformis* (brook BR3 and Liuben Lake LLB112).

Despite a relatively low ostracod occurrence in some local patches, the area of the floodplain relict oak forest exhibited much higher species richness than we expected for such an unusually dry year and concomitant unfavorable conditions in the water bodies of the area.

DISCUSSION

Research into biota of aquatic systems is of interest to the study of the function of unstable ecosystems

Species	**Pfl**	**OF (species occurrence in the area)**		
			number of pools	**% of pools**
Family CANDONIDAE KAUFMANN, 1900				
Candona candida (O. F. MÜLLER, 1776)	X	X	2	12.5
Candona lindneri PETKOWSKI, 1969	X			
Candona neglecta SARS, 1887	X	X	3	18.75
Candona weltneri HARTWIG, 1899	X	X	5	31.25
Candona juv.	X	X	7	43.75
Fabaeformiscandona acuminata (FISCHER, 1851)	X	X	1	6.25
Fabaeformiscandona balatonica (DADEY, 1894,)		X	1	6.25
Fabaeformiscandona fabaeformis (FISCHER, 1851)	X	X	2	12.5
Fabaeformiscandona fragilis (HARTWIG, 1898)	X	X	3	18.75
Fabaeformiscandona holzkampfi (HARTWIG, 1900)	X			
Fabaeformiscandona protzi (HARTWIG, 1898)	X	X	1	6.25
Fabaeformiscandona juv.	X	X	3	18.75
Pseudocandona compressa (KOCH, 1838)	X	X	7	43.75
Pseudocandona hartwigi (G. W. MÜLLER, 1900)	X	X	5	31.25
Pseudocandona insculpta (G. W. MÜLLER, 1900)	X	X	7	43.75
Pseudocandona marchica (HARTWIG, 1899)	X	X	1	6.25
Pseudocandona pratensis (HARTWIG, 11901)	X			
Pseudocandona rostrata (BRADY & NORMAN, 1889)	X	X	1	6.25
Pseudocandona semicognita (SCHÄFER, 1934)	X	X		
Pseudocandona juv.	X		2	12.5
Candonopsis kingsleii (BRADY & ROBERTSON, 1870)	X	X	4	25
Candonopsis scourfieldi BRADY, 1910	X			
Cypria exsculpta (FISCHER, 1855)	X	X	2	12.5
Cypria lata (SYWULA)	X			
Cypria ophtalmica (JURINE, 1820)	X	X	13	81.25
Bentocypria curvifurcata (KLIE, 1923I)	X			
Physocypria kraepelini G. W. MÜLLER, 1903	X	X	4	25
Cyclocypris laevis (O. F. MÜLLER, 1776)	X	X	9	56.25
Cyclocypris ovum (JURINE, 1820)	X	X	2	12.5
Family ILYOCYPRIDIDAE KAUFMANN, 1900				
Ilyocypris decipiens MASI, 1905	X			
Ilyocypris gibba (RAMDOHR, 1808)	X			
Family NOTODROMADIDAE KAUFMANN, 1900				
Notodromas monacha (O. F. MÜLLER)	X	X	4	25
Family CYPRIDIDAE BAIRD, 1845				
Cypris pubera O. F. MÜLLER ,1776	X	X	9	56.25
Trajancypris clavata (BAIRD, 1838)	X			
Eucypris crassa (O. F. MÜLLER, 1785)		X	4	25
Eucypris pigra (FISHER, 1851)		X	2	12.5
Bradleystrandesia reticulata (ZADDACH, 1844)	X	X	16	100
Heterocypris incongruens (RAMDOHR, 1808)	X			
Dolerocypris fasciata (O. F. MÜLLER, 1776)	X			
Cypridopsis elongata (KAUFMANN, 1900)	X			
Cypridopsis parva G. W. MÜLLER, 1900	X			
Cypridopsis vidua (O. F. MÜLLER, 1776)	X	X	16	100
Plesiocypridopsis newtoni (BRADY & ROBERTSON, 1870)	X			
Family LIMNOCYTHERIDAE KLIE, 1938				
Limnocythere inopinata (BAIRD, 1843)	X			
Limnocythere stationis VÁVRA, 1891		X	1	6.25
Paralimnocythere relicta (LILLJEBORG, 1863)	X			
Metacypris cordata BRADY & ROBERTSON, 1870	X	X	2	12.5
The total species number	42	27		

TABLE 3–The ostracods occurrence in different reservoirs of the Polesye area (The Pripyat River floodplain) (Pfl) (n=12) (Nagorskaya &, de Jonge, 2002) and in the pools of the floodplain relict oak forest (OF) (n=16).

Marked correlations are significant at $p < .05$

N=32 (Casewise deletion of missing data)

Value	COND	TDS	HARTOTD	HARTOTM	HARCARD	HARCARM	PERM	TEMP	spN
COND	1	1.00	0.95	0.94	0.97	0.95	0.03	-0.03	0.53
TDS	1.00	1	0.95	0.94	0.97	0.95	0.04	-0.04	0.53
HARTOTD	0.95	0.95	1	1.00	0.94	0.95	0.11	-0.11	0.53
HARTOTM	0.94	0.94	1.00	1	0.94	0.95	0.09	-0.09	0.53
HARCARD	0.97	0.97	0.94	0.94	1	0.99	0.10	-0.10	0.60
HARCARM	0.95	0.95	0.95	0.95	0.99	1	0.13	-0.13	0.60
PERM	0.03	0.04	0.11	0.09	0.10	0.13	1	-1.00	0.74
TEMP	-0.03	-0.04	-0.11	-0.09	-0.10	-0.13	-1.00	1	-0.74
spN	0.53	0.53	0.53	0.53	0.60	0.60	0.74	-0.74	1

TABLE 4–The correlation matrix for some hydrochemical variables, the pool type (permanent/temporary) and species number (spN).

(White, 1985; Williams, 1987). Aquatic invertebrates play a multifunctional role in the ecosystem of the *Quercetum fluvialis* forest (sedimentation and transformation of suspension matter, food for birds and amphibians and so on).

A number of works on terrestrial invertebrates of the floodplain oak forest demonstrated that the average species richness (70 species) was 2.5-2 times less than in a pine forests (242 species) and in fields (143 species) (Khotko, 1993). That number could be effected by both flooding (which would be fatal for some terrestrial species) and specific conditions of the area (Kagan & Gelfer, 1956). The decay of oak leaves is effected more by soil fungi than bacterial degradation, and it could result in the production of some specific chemical agents. We expected that the hydrobiontic species number should be less than in other floodplain pools as well. However, neither a depleted fauna (Table 3) nor a specific community composition (Fig. 3) was observed.

The species richness of ostracods was dependent upon the mineralization of water in the different pools and the water phase duration (Table 4). It is well known that species life cycles depend on the water regime situation and the water source (Wiggins *et al.*, 1980; Williams, 1987; Schneider & Frost, 1996; Heino, 2000; Smith, 1993; Therriault & Kolasa, 1999).

Species assemblages in different water bodies of the floodplain oak forest did not demonstrate any special specificity, however *Eucypris pigra* inhabited running brooks solely and some ostracods from Family CANDONIDAE were found in permanent water ecosystems (lakes) (Table 5). The water bodies in which they were found were determined by their life cycles.

Instability of some ecosystems leads to development of special strategies to avoid species disappearance (Thiery, 1982), such as a high speed of development, dormant stages, r – reproduction strategy. Due to the fact that ostracods have diapause stages, they survive the difficult environment (a drought or some other events) (Horne & Martens, 1998) and could re-colonize new ecotopes in the same way as other water crustaceans (Havel *et al.*, 2000).

The dispersal of ostracods species in the floodplain area could be by passive transfer with wind, flooding, birds and animals (Williams, 1987; Neckles *et al.*, 1990; Oertli, 1995). The connection between different pools during a flooding promotes the exchange of species and supports species richness (Amoros & Roux, 1988; Schwartz & Jenkins, 2000).

Landscape diversity is an essential and characteristic feature of whole floodplain, which influences the biodiversity of a region (Caley & Schluter, 1999; Pickett & Cadenasso, 1995; Ward & Stanford, 1995; Shiel *et al.*, 1998). The relations between different floodplain water bodies and their fauna are still subject for further investigations.

The water bodies	**Vegetation (dominant species)**	**Bottom**	**Ostracods assemblages**
Pit (May, July, September)	*Alisma plantago-aquatica* L. *Callitriche palustris* L. *Eleocharis palustris* (L.) Roem. et Schult. *Glyceria fluitans* (L.) R. Br. *Hydrocharis morsus-ranae* L. *Oenanthe aquatica* (L.) Poir. *Phragmites australis* (Cav.) Trin. Ex Steud. *Ranunculus flammula* L. *Typha latifolia* L.	Sand, clay	*Bradleystrandesia reticulata* *Candona neglecta* *Cypria ophtalmica* *Cypridopsis vidua* *Limnocythere stationis*
Lakes, brooks, ponds, bogs, oxbows (May)	*Agrostis stolonifera* L. *Alisma plantago-aquatica* L. *Comarum palustre* L *Equisetum fluviatile* L. *Glyceria fluitans* (L.) R. Br. *Glyceria maxima* (Hartm.) Holmb. *Hottonia palustris* L. *Nymphar lutea* (L.) Smith *Phragmites australis* (Cav.) Trin. Ex Steud.	Sand, fine and coarse detritus, peat, decayed leaves	*Bradleystrandesia reticulata* *Candona candida* *Candona weltneri* *Candonopsis kingsleii* *Cyclocypris laevis* *Cyclocypris ovum* *Cypria ophtalmica* *Cypridopsis vidua* *Cypris pubera* *Eucypris crassa* *Eucypris pigra* *Fabaeformiscandona acuminata* *Fabaeformiscandona balatonica* *Fabaeformiscandona fabaeformis* *Metacypris cordata* *Notodromas monacha* *Pseudocandona compressa* *Pseudocandona hartwigi* *Pseudocandona insculpta* *Pseudocandona marchica* *Pseudocandona rostrata*
Lakes, brooks ponds, bogs, oxbows (July, September)	*Agrostis stolonifera* L. *Alisma plantago-aquatica* L. *Callitriche palustris* L. *Equisetum fluviatile* L. *Glyceria maxima* (Hartm.) Holmb. *Hottonia palustris* L. *Hydrocharis morsus-ranae* L. *Lemna minor* L. *Lemna trisulca* L. *Nymphaea alba* L. *Nymphar lutea* (L.) Smith *Phragmites australis* (Cav.) Trin. Ex Steud. *Ranunculus lingua* L. *Sagittaria sagittifolia* L. *Salvinia natans* L. *Spirodella polyrhiza* (L.) Schleid. *Stratioides aloides* L. *Utricularia vulgaris* L.	Sand, fine detritus, peat	*Candona candida* *Candona neglecta* *Candona weltneri* *Candonopsis kingsleii* *Cyclocypris laevis* *Cypria exsculpta* *Cypria ophtalmica* *Cypridopsis vidua* *Fabaeformiscandona fragilis* *Fabaeformiscandona protzi* *Metacypris cordata* *Physocypria kraepelini* *Pseudocandona compressa* *Pseudocandona insculpta*
Temporary pools (May)	*Alisma plantago-aquatica* L. *Glyceria fluitans* (L.) R. Br. *Ranunculus flammula* L.	Sand, clay, coarse detritus, leaves	*Bradleystrandesia reticulata* *Cyclocypris ovum* *Cypridopsis vidua* *Eucypris crassa*

TABLE 5–Ostracod assemblages in different reservoirs of the floodplain oak forest.

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FIELD AND LABORATORY OBSERVATIONS ON THE MICROHABITAT AND FOOD SELECTION AS WELL AS PREDATOR AVOIDANCE OF *NOTODROMAS MONACHA* (CRUSTACEA: OSTRACODA)

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Abstract

The effect of habitat structure, food abundance and predation risk on the ostracod *Notodromas monacha* (Mueller, 1776) was examined on the basis of 3 years field-work and laboratory observations. The field-work was carried out in different habitats (open water, *Najas marina*, edge of the littoral zone, *Lemno-Utricularietum, Phragmites australis, Typha angustifolia*) of the shallow Lake Fehér (47º 41' N, 17º 21'E, Fertő-Hanság National Park, Hungary). Representatives of this species were recorded only from the reed-belt, supposedly because of the strong wind effect in the lake. Individuals were collected from April to October and the maximum was 32 ind./ L. The number of individuals was significantly higher in the *Lemno-Utricularietum* association than in the dense *Typha* and *Phragmites* beds, indicating that *Notodromas* prefers the small patches and channels in the reed-belt covered by submerged macrophytes to the zone of dense, emergent macrophytes. Laboratory experiments, consisting of eight different treatments, were performed to test how *Notodromas monacha* respond to fluctuations in plant structure, food abundance and predation risk. The position of the ostracods were recorded with respect to three vertical zones of the aquaria (lower, middle and upper zone) and the selection of three different microhabitats (ground, plant, open water). In the absence of fish chemical cues and predators, 93% of the individuals inhabited the upper zone of the aquaria. In the presence of predator chemical signals and fish, *Notodromas* showed distinct antipredator behaviour and an average of 17.26 percent of the animals preferred the lower zone and 68 percent the vegetated half of the aquaria. In the food preference experiments *Notodromas* clearly preferred neustonic food to the periphyton rich *Ceratophyllum* stems, indicating that *Notodromas* is primarily a neuston feeder.

Key words: Ostracoda, *Notodromas monacha*, food preference, habitat selection, predator avoidance.

Resumen

El efecto de la estructura del hábitat, la disponibilidad de alimento y el riesgo de depredación ha sido estudiado en *Notodromas monacha* (Mueller, 1776) basándose en tres años de trabajos de campo y de laboratorio. El trabajo de campo fue realizado en diferentes hábitats (agua abierta, *Najas marina*, borde de la zona litoral, *Lemno-Utricularietum, Phragmites australis, Typha angustifolia*) en el Lago Fehér (47º 41' N, 17º 21'E, Parque Nacional de Fertő-Hanság, Hungría). Representantes de esta especie fueron recogidos solamente en la orla de juncos, supuestamente debido al efecto del fuerte viento en el lago. Se obtuvieron ejemplares desde abril hasta octubre, con un máximo de 32 ind./L. El número de ejemplares fue significativamente mayor en la asociación *Lemno-Utricularietum* que en los lechos densos de *Typha* y *Phragmites,* indicando que *Notodromas* prefiere los pequeños "patches" y canales de la orla de juncos cubiertas por macrofitas sumergidas, a la densa zona con macrofitas emergentes. Los experimentos de laboratorio, consistentes en ocho tratamientos diferentes, fueron realizados para comprobar cómo *Notodromas monacha* responde a las fluctuaciones en la estructura vegetal, disponibilidad de alimento y riesgo depredativo. La posición de los ostrácodos fue registrada respecto a tres zonas del acuario (inferior, media y superior) y se seleccionaron tres microhábitats diferentes (fondo, planta, agua abierta). En ausencia de indicadores químicos de peces y depredadores, *Notodromas* mostró un comportamiento antidepredador distintivo y un promedio del 17,26% de los animales prefirieron la zona inferior y el 68% la mitad vegetada del acuario. En los experimentos de preferencia alimentaria *Notodromas* prefirió claramente el alimento neustónico de los tallos del perifiton *Ceratophyllum*, indicando que *Notodromas* se alimenta preferentemente del neuston.

Palabras clave: Ostracoda, *Notodromas monacha*, preferencia alimentaria, selección del hábitat, disponibilidad depredativa.

INTRODUCTION

The main ecological controls on ostracods are habitat characteristics especially the size, depth and permanence of the waterbody (Bilton *et al*., 2001), the nature of the substrate and aquatic plants (Roca *et al*., 1993), food availability (Uiblein *et al*., 1994), predation (Uiblein *et al*., 1996), as well as water characteristics (temperature, pH, dissolved oxygen content, salinity and ionic composition) (Baltanas *et al*., 1990). A large number of freshwater ostracods live in the littoral and sublittoral zones of lakes where the macrovegetation in general provide both food and shelter from predation. Ostracods form a major food source for many vertebrates, but within the macrophyte zone a predator's foraging success is often low because of the structural complexity of such habitats. Ostracods have been found to respond to chemical signals derived from fish and other predators by adopting distinct antipredator behaviours. Benzie (1989) carried out a detailed field studies on ostracod abundance and distribution and several experiments to test survival on different foods, food preferences, and sediment particle size preferences of the three dominant ostracod species of a lake and concluded that each habitat had a discrete ostracod community. Few experimental studies dealed with the phytophilous *Cypridopsis vidua* which with the addition of chemical predator cue spent significantly more time in the lower vertical zone of micro-aquaria (Uiblein *et al*., 1996) and in contrast to many other species which reduce their mobility in response to chemical cues, *C. vidua* increase their swimming activity. *Cypridopsis vidua* show clear microhabitat preferences (Mbahinzireki *et al*., 1991) which are influenced by habitat structure and food supply.

Only limited information exist on the habitat preference and ecological demands of *Notodromas monacha* (Tetart, 1971; Hiller, 1972). This warm-stenoterm species is one of the rare freshwater ostracod which is usually present in samples collected from the zooplankton. *Notodromas* is an excellent swimmer and has high mobility level and is mostly found close to the surface film of the water.

The aim of this study was to detect the seasonal and spatial distribution of *Notodromas* populations and demonstrate the effect of habitat structure, food abundance and predation risk on the ostracod on the basis of 3 years field-work and laboratory observations.

STUDY AREA

The field-work was performed in the shallow Lake Fehér (Fehér-tó) (47° 41' N, 17° 21'E) which is situated in the northwestern part of Hungary in the area of the Fertő-Hanság National Park. The lake is small and very shallow (area: 2.69 km^2, open water: 0.25 km^2, mean depth: 50 cm, maximum depth: 110 cm) and the hydrology of the lake depends on the interplay of precipitation and evaporation. The littoral zone of the lake is characterised by beds of emergent macrophytes (*Phragmites australis* and *Typha angustifolia*). The reed-belt usually dries in summer and early autumn. Within the reed-belt there were three characteristic habitat types: 1. *Scirpo-Phragmitetum*, 2. *Typhetum angustifoliae* (the edge of the *Phragmites* zone) 3. *Lemno-Utricularietum* between the patches of *Phragmites* with *Utricularia vulgaris, Hydrocharis morsus-ranae, Lemna trisulca, Lemna minor* and *Spirodela polyrhiza*. In 1999 and 2000 the open water was covered by dense vegetation of *Najas marina*

Experiment			sediment powder	plastic plant	*Ceratophyllum*	fish chemicals	perch
1.	microhabitat selection	1.1	—	+	—	—	—
		1.2	—	—	+	—	—
		1.3	—	—	++	—	—
2.	food selection	2.1	+	—	—	—	—
		2.2	+	+	—	—	—
		2.3	+	—	+	—	—
3.	predation	3.1	—	—	+	+	—
		3.2	—	—	+	+	+

TABLE 1–Summary of the habitat parameters provided in eight different experimental treatments.

(95% PVI). The concentration of inorganic particles in the water was generally low, the dominant ion was HCO_3^-.

During the sampling period a diverse and abundant Ostracoda assemblages developed in the reed-belt. Out of 77 microcrustacean species 20 were ostracods (Kiss, 2002) The most frequent species were *Notodromas monacha*, *Cyclocypris ovum, Candona weltneri* and *Pseudocandona compressa*. The ostracod *Cypridopsis hartwigi*, which is new to Hungary, was recorded only once from the *Phragmites* beds. There was a diverse community of *Candonidae* (7 species) and most of the individuals (except *Candona weltneri*) were recorded only from sediment samples.

The fish assemblage was dominated by cyprinids. The most abundant species were *Carassius auratus, Rutilus rutilus* and *Perca fluviatilis* (G. Guti, personal communications). Because of the low oxygen concentration and extreme low water level, the reed-belt was unsuitable for fish except in spring when the predation pressure increased in the reed-belt because of high abundance of YOY fish. Invertebrates are also important predators in the reed-belt and affect the composition of littoral microcrustaceans (Paterson, 1993).

METHODS

Field sampling

The study was carried out from March 1998 to November 2000. Samples were collected at monthly intervals and biweekly in summer. One occasion in May 1999 and 2000 and August 1999 samples were collected every four hours between 5 a.m. and 21 p.m. in different habitats of the lake to study the diurnal changes of *Notodromas* populations. The tested habitats were: 1. Open water (mid-lake), 2. *Najas marina* beds (mid-lake, in 1999 and 2000), 3. Edge of the emergent macrophyte zone, 4. *Lemno-Utricularietum* (narrow channel among the *Phragmites* zone), 5. *Phragmites* beds, 6. *Typha* beds. The temperature, pH, conductivity and dissolved oxigen were measured in the field by using Multiline-P4 portable meter. *Notodromas* individuals were collected in one litre plastic box samplers gently closed over plants. Mixed five litres samples were collected and sieved through a 70 µm mesh net. The diurnal experiments were carried out in three replicates and the results are presented as mean values.

Laboratory processing

The laboratory experiments were performed in a micro-aquaria (22.5 x 9 x 9 cm) filled with 1.8 litres of filtered lake water, and were set up under uniform temperature (20ºC) and light (28 Lux) conditions. Adult specimens of *Notodromas monacha* were collected from the reed-belt of Lake Fehér. The experiments consisted of eight different treatments (see Table 2) and were aimed to test how *Notodromas monacha* respond to changes in plant structure, food abundance and predation risk. In each trial twenty adult *Notodromas* were introduced in the central part of the tank with a fine brush. The position of the ostracods with respect to three vertical zones of the aquaria (lower, middle and upper zone) and the selection of three different microhabitats (ground, plant, open water) were recorded every 30 second for a period of 15 minutes. Each experiment was repeated five times. At the start of each experiment 5 minute was given to each animal for acclimation. In the microhabitat selection experiment (1) uniform sized pieces of uncleaned *Ceratophyllum* *demersum* (1.2) and plastic plants (1.1), which closely resembled the natural ones, were used as plant structures in the vegetated half of the aquaria. In the beginning of the experiment 1. five replicates were carried out with 2 standardized piece of plant stems (1.2), then the number of the *Ceratophyllum* stems were doubled (1.3) in order to test how *Notodromas* react to the increased offer of plant structure. In the food selection experiments (2) desiccated lake sediment was scattered on the surface of unvegetated half of the aquaria as well as the other half of the aquaria was unvegetated in experiment 2.1, then vegetated with cleaned plastic plant (2.2) and uncleaned *Ceratophyllum* stems with a rich cover of periphyton (2.3). The fish used for predation experiments (3) belong to the species *Perca fluviatilis*, which is common in Lake Fehér. Juveniles of this species frequently prey on ostracods and other small crustaceans (Winfield, 1986). 5 mL of fish water from a tank containing young perch (*Perca fluviatilis*) was added into the aquaria (experiment 3.1), then 3 young perch were introduced to the aquaria (experiment 3.2).

Because there were no experimental studies of *Notodromas*, our laboratory experiments were based on the microhabitat selection tests of *Cypridopsis vidua* (Mbahinzireki *et al*, 1991, and Uiblein *et al*, 1996).

Statistical analyses were performed using STATISTICA 5.0 (StatSoft, Inc.). Significance of differences between the habitat parameters has been tested with one-way analysis of variance (ANOVA). Both treatments were tested for independence using G-test.

RESULTS AND DISCUSSION

Seasonal, daily and spatial differences in the density of *Notodromas* populations (field-work)

The spatial distribution of the species showed strong correlation with the habitat types in the lake. The individuals were recorded only from the reed-belt and the species was absent from the open water, the edge of the littoral zone and the *Najas marina* beds supposedly because of the strong wind effect and enhanced water movement in the open water and the channels. In 1998, there were no *Notodromas* individuals in the samples because the reed-belt was dry between March and October. In the reed-belt the stenoterm *Notodromas* was collected from April to October and the maximum was 32 ind./L in 1999 (September) and 29 ind./L in 2000 (April) (Fig. 1). This density was low compared to the observation of Tétart (1971) who collected 36000 ind./m^2 *Notodromas* juveniles in April. In 2000 the abundance was low throughout summer because the water-level was extremely low in the reed-belt and in some cases, the reed-belt dried completely. *Notodromas* individuals were found only in the upper water layers and no representatives of this species were present in the sediments.

The abundance of *Notodromas* varied markedly in the different habitats of the reed-belt. The density was significantly higher in the *Lemno-Utricularietum* than in the dense *Typha* and *Phragmites* beds throughout the 3 years of the investigation indicating that *Notodromas*

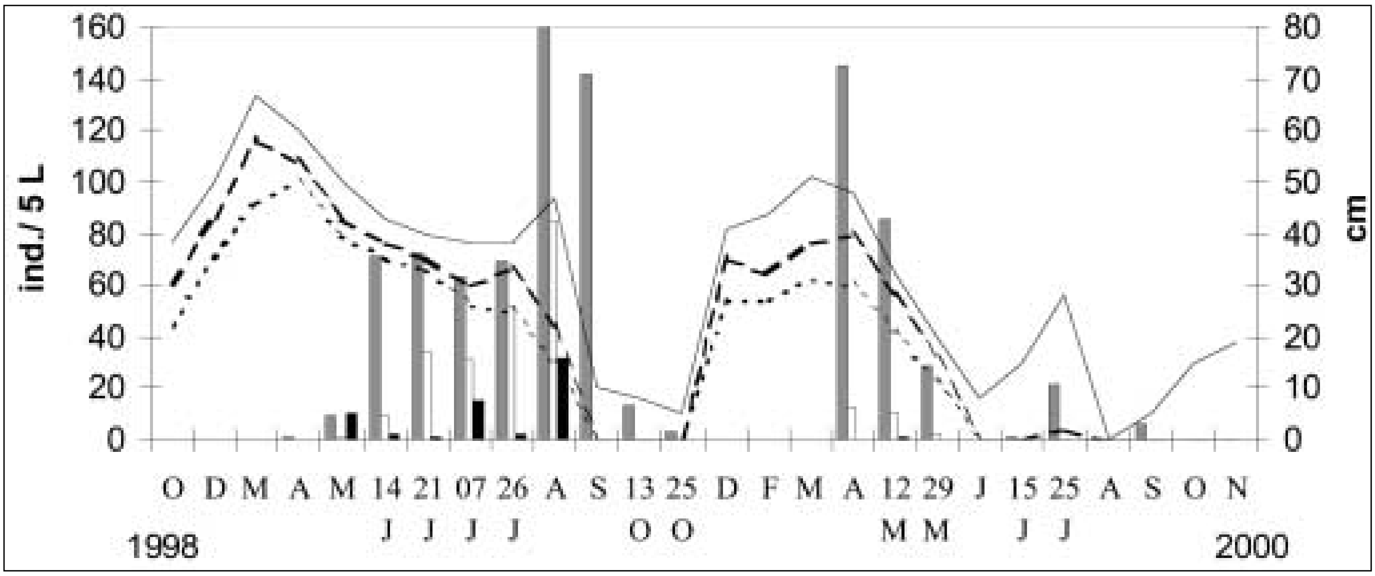

FIGURE 1–The density of the *Notodromas* populations (bars) and in the second axis the water level (lines) between 1998-2000, in the different habitats of the reed-belt: *Lemno-Utricularietum* (gray bar and black line), *Phragmites australis* (white bar and broken line) and *Typha angustifolia* (black bar and spotted line).

prefers the small patches and channels in the reed-belt covered by submerged macrophytes rather than the dense emergent macrophyte zone. In the reed-belt, during the presence of the species, the pH were ranged from 7.04-7.87, the temperature from 14.7-21°C, the conductivity from 367-1010 µs/cm and the oxygen content from 0.56-7.86 mg/L. In summer there were anoxic conditions in the reed-belt, and the dissolved oxygen content values were significantly low, sometimes 2-3 mg/L and the minimum (0.56 mg/L) was observed at the end of July in 1999. The results suggest that *Notodromas,* like many other non-marine ostracods, can tolerate wide ranges of dissolved oxygen levels and temporal anoxic conditions. There was no correlation between the *Notodromas* density and water chemistry parameters.

The composition of the *Notodromas* populations is shown in Fig. 2. Juveniles appeared in April and disappeared at the end of August. Males were always present in the samples. The sex ratio was near to 0.5 but in some cases in summer there were markedly more females than males. The ratio of males was higher in the dense *Typha* and *Phragmites* beds than in the *Lemno-Utricularietum*.

The maximum abundance of the *Notodromas* populations was in August in all habitats of the reed-belt, where more than 90 percent of the individuals were juveniles. The density was highest in the *Lemno-Utricularietum* in all the three sampling dates (in May 1999 and 2000 and August 1999). In 1999 the mean density was 3 ind./ L in May, 23 ind./ L in August, as well as in May 2000 was 9 ind./ L. In the *Lemno-Utricularietum,* the diurnal density changes of the populations were different in May and August (Fig. 3). In May 1999 and 2000 the maximum density was at night (5 and 17 ind./ L) and the minimum values were during day-time (2 and 3 ind./ L). In August, reverse diurnal changes were recorded, the maximum (32 ind./ L) was in the day-time and the minimum (15 ind./ L) was at night. A possible explanation of the day-time minimum in May might be predation by the visually hunting fish, especially newly hatched (YOY) zooplanktivorous fish. In early spring, the emergent macrophyte zone of the lake was flooded and different species of juveniles fish seek refuge and feed on microcrustaceans within the macrovegetation. In summer invertebrates were the most important predators in the reed-belt which strongly affects the composition of littoral microcrustaceans (Paterson, 1993). The most important invertebrate predators in the lake Fehér were tanypod chironomids, odonates and water mites. In the *Lemno-Utricularietum* the number of the *Notodromas* individuals was decreased by the predation of the carnivorous *Utricularia vulgaris* (personal observation), similarly to the observations of Mette *et al*. (2000).

In the *Typha* and *Phragmites* beds, there were no significant day-night differences in ostracod abundance. The density values were low throughout the day. In the *Phragmites* beds mean density was only 1-2 ind./L in May and 15 ind./L in August and 5 ind./L among the *Typha angustifolia.* Among the examined three habitats the density was always the highest in the *Lemno-*

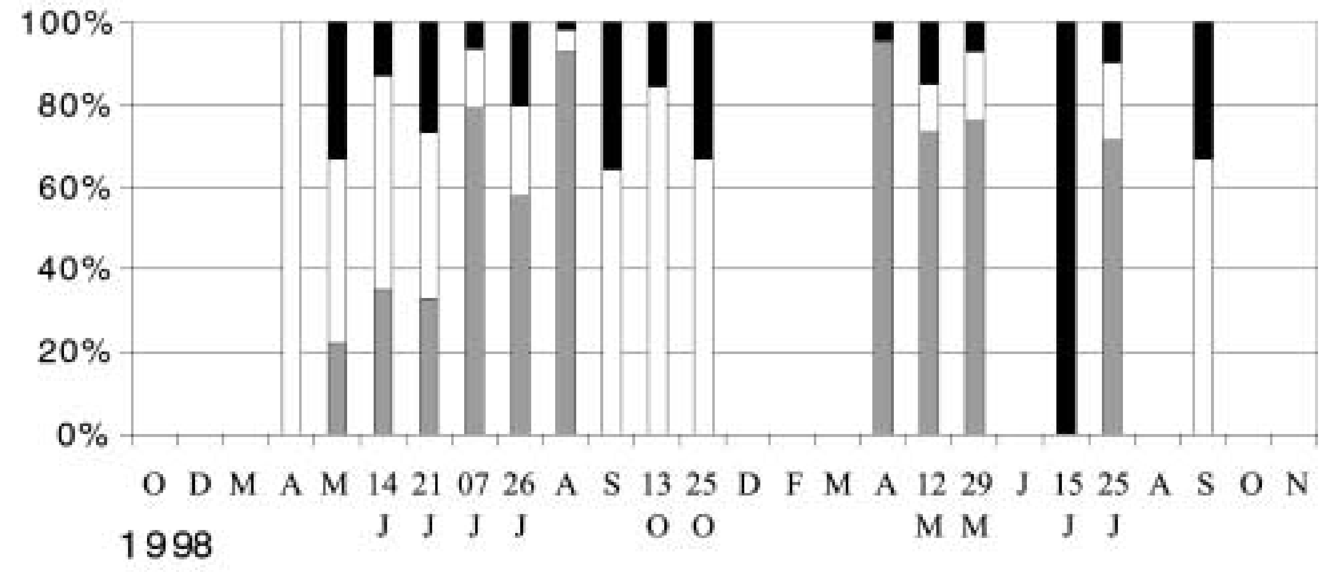

FIGURE 2–The composition of the *Notodromas* population (ind./5L) between 1998-2000 in the *Lemno-Utricularietum:* males (black bar), females (white bar) and juveniles (gray bar).

Utricularietum indicating that *Notodromas* show clear habitat selection and prefers the small patches and channels in the reed-belt covered by submerged macrophytes to the zone of dense, emergent macrophytes.

Laboratory observations

1. Microhabitat selection

The density of ostracods was significantly different in the 3 vertical zones of the aquaria both in treatment 1.1 and 1.2. On average, 93.6% were found in the upper, 4.6% in the middle and only 1.8% of the individuals in the lower zone of the aquaria indicating that *Notodromas* especially colonise the upper water layers of the lakes (Table 2). There were no noteworthy differences between the plastic and the natural plant, when plastic plants were used 88.9% of the individials found on the upper, 7.6 in the middle and 3.5% of the lower zone of the micro-aquaria.

There were also no differences between the two microhabitats (*Ceratophyllum* and plastic plant), on average 45% of the individuals were found among the *Ceratophyllum* stems and 43.3% among the plastic plants.

When the number of the *Ceratophyllum* stems was doubled (experiment 1.3) the mean density of the individuals increased ($p < 0.05$) on the uncovered part of aquaria. When two stems were used 54.9% of the individuals choosed the unvegetated part of the aquaria and when four stems were used 61.2% of the ostracods choosed the open water. Although *Notodromas monacha* clearly prefers the shallow water with rich vegetation of ponds and the littoral zone of lakes (Meisch, 2000), this experiment demonstrates that *Notodromas* does not prefer the very dense macrophyte beds.

These laboratory results conform well with the distribution pattern of *Notodromas monacha* in Lake Fehér where this species clearly preferred the *Lemno-Utricularietum* with 30-40% PVI (Plant Volume Infested) and the density of the population was significant lower in the dense (80-90% PVI) *Phragmites* and *Typha* beds. In addition the representatives of the spe-

Replicate	Lake water		UPPER	Fish water	
	Uncovered	Vegetated		Uncovered	Vegetated
1	49.33	44.33		22	39.33
2	50	44		19.67	42.33
3	50	44.66		28	35.67
4	60.67	31.33		23.67	34.33
5	51.33	42.34		24.34	32.67
Mean	52.27	41.332		23.54	36.87

Replicate	Lake water		MIDDLE	Fish water	
	Uncovered	Vegetated		Uncovered	Vegetated
1	1	3.67		4.67	17
2	1	3.34		5	18.33
3	0.67	3		3	15.66
4	1	4.33		5.33	17
5	2.67	2.33		6.33	19.33
Mean	1.268	3.334		4.866	17.464

Replicate	Lake water		BOTTOM	Fish water	
	Uncovered	Vegetated		Uncovered	Vegetated
1	1	0.67		5	12
2	1.33	0.33		3	11.67
3	1.67	0		3.67	14
4	1.67	1		3.67	16
5	1	0.33		2.33	15
Mean	1.334	0.466		3.534	13.73

TABLE 2–Percentage of individuals of *Notodromas* found in the uncovered and in the vegetated half of the aquarium without fish chemical cue (experiment 1.2) and after exposure of water fish water and juvenile perch (experiment 3.2) (n = 20 individuals per replicate and 15 observations per replicate).

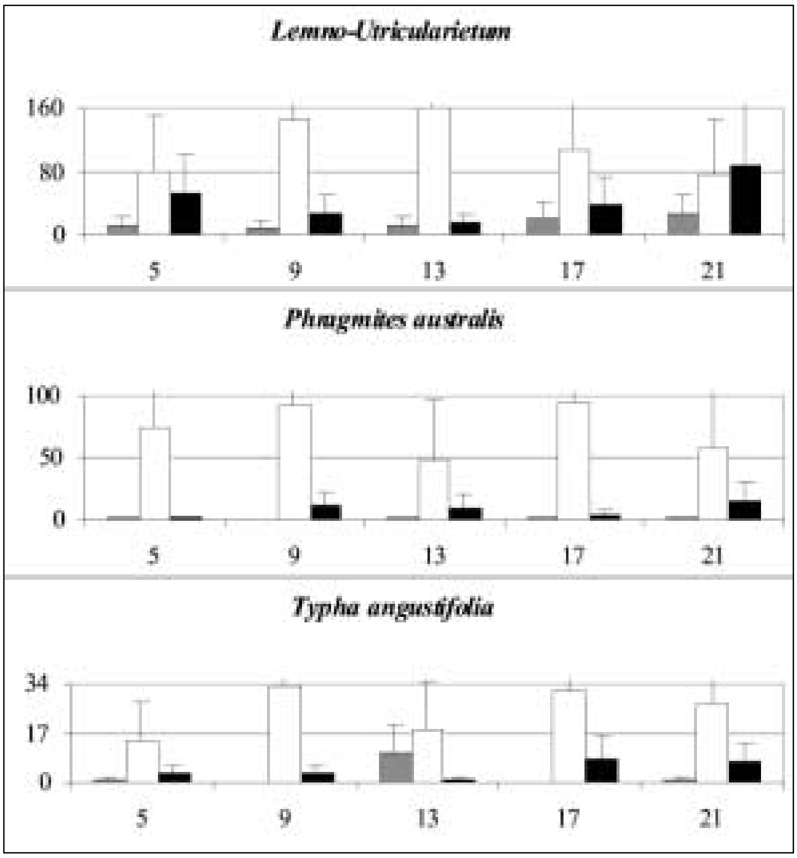

FIGURE 3–The mean diurnal density of the *Notodromas* populations (ind./5 L) in May 1999 (gray bar), in August 1999 (white bar) and in May 2000 (black bar) in the different habitats of the reed-belt. Error bars are 95% confidence intervals of the mean.

cies were found only in the upper (5-10 cm) water layers of the lake and there were no individuals in the sediment samples.

The presence of macrophytes in the microhabitat played a dominant role in determining the distribution and diversity of invertebrata species. Greater architectural complexity of habitat led to a higher number of invertebrata taxa on both natural and artificial macrophytes (Taniguchi *et al.*, 2003). Macrophytes can act as a refuge for microcrustaceans against predators and the plants with disserted leaves would provide more substrate for the growth of periphytic algae (Dvorak and Best, 1982) which is an important food source for invertebrates (Downing, 1981). The abundance of epiphytic invertebrates was significantly related to plant biomass, macrophyte bed size characteristics and sampling date (Cyr and Downing, 1988).

2. Food abundance

In treatment 2.1 the micro-aquaria was uncovered and in one half of the aquaria fine sediment powder was dispersed on the surface of the water. The density of the individuals in the upper zone of the aquaria was the highest in this treatment. On average 95.27 percent of the individuals were found on the upper zone and 56.2 percent chose the high food abundance part of the aquaria with the scattered sediment particles and 39 percent were recorded from the other part of the micro-aquaria. In this test without macrophytes and fish cue only an average of 0.79 percent of the animals moved to the lower zone. In treatment 2.2 when plastic plants were used an average of 57.53 percent of the *Notodromas* individuals chose the uncovered half of the aquaria with high food abundance and 42.47 percent the vegetated half of the aquaria. As compared to treatment 2.2 and 2.3 there were no significant differences between the plastic plant and the uncleaned *Ceratophyllum* and in treatment 2.3, the majority of the individuals (mean: 58.93%, SD: 0.936) choosed the uncovered part of the aquaria with sediment powder indicating that *Notodromas* discriminates between the *Ceratophyllum* covered with periphyton and the sediment with organic matter dispersed on the surface of the water.

The abundance and quality of food seem to be important determinants of microcrustacean density. Ostracods are active foragers which search for and select food based on chemical and tactile cues, making use of a well-developed sensory equipment and quickly detect those areas with highest food abundance. *Limnocythere inopinata* showed a highly significant preference for faecal material over old *Chara* (Benzie, 1989). The phytophilous *Cypridopsis vidua* was found to discriminate between different food types such as sediment with organic matter, dead chironomid larvae and pieces of *Chara* covered with periphyton (Roca *et al*., 1993) and congregated on uncleaned plants, but was not influenced by sediment particle size (Benzie, 1989). Uiblein *et al*. (1996) reported that hungry *C. vidua* remained on *Chara* for longer and they also visited the more exposed and riskier parts on the top of the plants especially when food abundance was higher in the upper zones and the incerased hunger level result in more time spent on *Chara*.

Opposite to *Cypridopsis*, *Notodromas monacha* preferred the fine sediment powder scattered on the surface of the water to periphyton-rich *Ceratophyllum* stems. These results conform well with the few earlier observations of the feeding strategy and preferred food type of *Notodromas*. According to Liperovskaya (1948), the gut contents of *Notodromas monacha* have been found to contain pollen and phytoplankton suggesting suspension feeding as well as feeding on the bacteria which colonize the air-water interface.

3. Predation risk

The effects of a fish chemical cue and the presence of juvenile fish on *Notodromas* were examined in treatments 3.1 and 3.2. If a fish cue was added (3.1) the vertical distribution and microhabitat preferences of the individuals changed as compared to distribution of individuals in microhabitat selection experiments (treatments 1.1, 1.2 and 1.3).

As on effect of fish cue, the average percentage of the individuals increased from 45 to 57.5 in the vegetated half of the aquaria as well as from 1.8 to 4.87 at the bottom of the aquaria. Comparing the number of individuals in the upper zone in experiment, the density decreased in the upper zone and the average percentage of individuals changed from 93.6 to 60.4 in the upper zone of the aquaria ($p < 0.0001$). These results are similar to former observations on *Cypridopsis vidua* (Uiblein *et al*., 1996) where *C. vidua* showed considerable variations in microhabitat choice and responded to predator signals by spending significantly more time in the lower zone of the aquaria and moved into shadowed and dense vegetated microhabitats.

These density differences increased even further when the synergic effect of fish presence and fish chemicals was examined. The average percent of the individuals increased from 57.5 to 68 in the vegetated half of the aquaria and from 4.87 to 17.26 at the bottom of the aquaria (Figs. 4, 5).

Ostracods frequently occur in the diet of juvenile fishes and are especially vulnerable to predation when exposed to light. Like *Cypridopsis vidua*, *Notodromas* individuals show distinct color patterns on their carapaces and possess pigmented carapaces, a feature that reduces visual detectability (Mbahinzireki *et al*., 1991) and result in a significant decrease of fish foraging success (Roca *et al*., 1993). In spring the juvenile perch frequently occurs in the reed-belt of the Lake Fehér and the YOY perch often move to the littoral zone and is an efficient forager among vegetation (Winfield, 1986). In the treatments *Notodromas* individuals showed antipredator response by moving to the lower and vegetated microhabitats. In addition the carapace of *Notodromas* also reduce the visual detectability and fish foraging success, resulting in a relatively high spring density (compared to other ostracod species) in the reed-belt of the lake.

SUMMARY

The effects of habitat structure, food abundance and predation risk on the ostracod *Notodromas monacha* was examined in the laboratory and compared to the results of field-work performed in the reed-belt of a shallow lake. In the different treatments the density of the individuals varied greatly among the different vertical zones and microhabitats indicating that *Notodromas* individuals are capable of actively choosing the most protective and profitable areas within the different microhabitats and show high behavioural flexibility in their responses and capabilities to explore their surroundings.

The experimental data are confirmed by field data, as *Notodromas* does not colonise habitats with strong

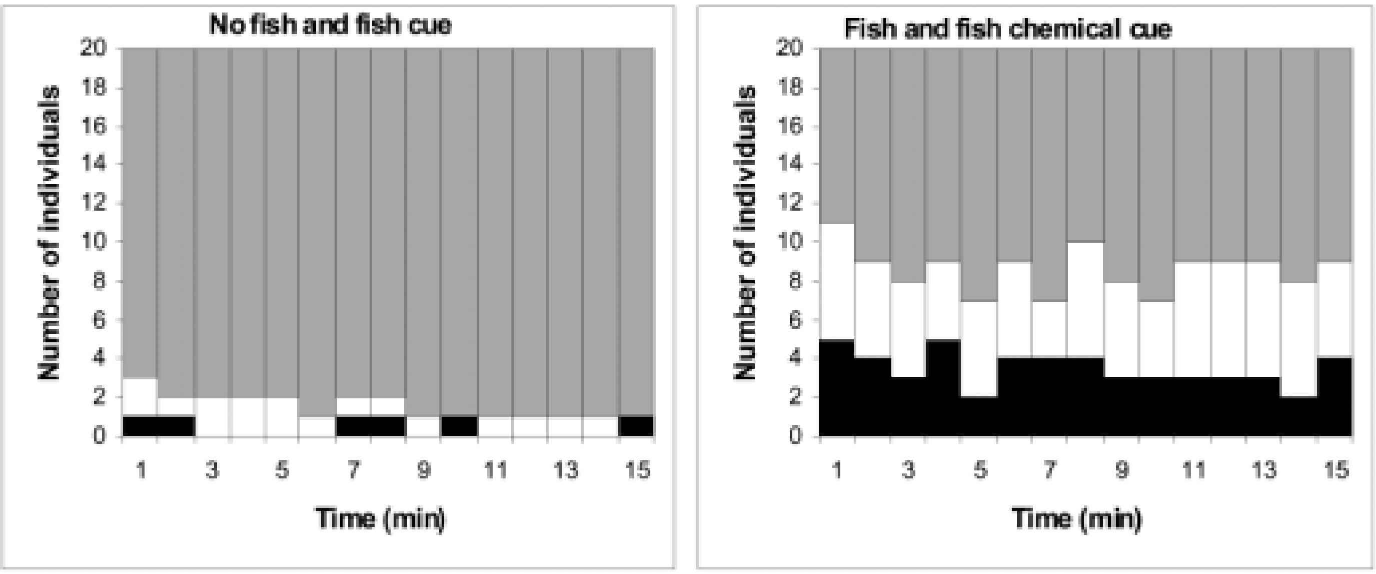

FIGURE 4–The number (mean values) of *Notodromas* individuals found in the different vertical zones of the aquaria without fish and fish cue (experiment 1.2) and after exposure to fish water and juvenile perch (experiment 3.2). Upper zone - gray bar, middle zone - white bar, lower zone - black bar.

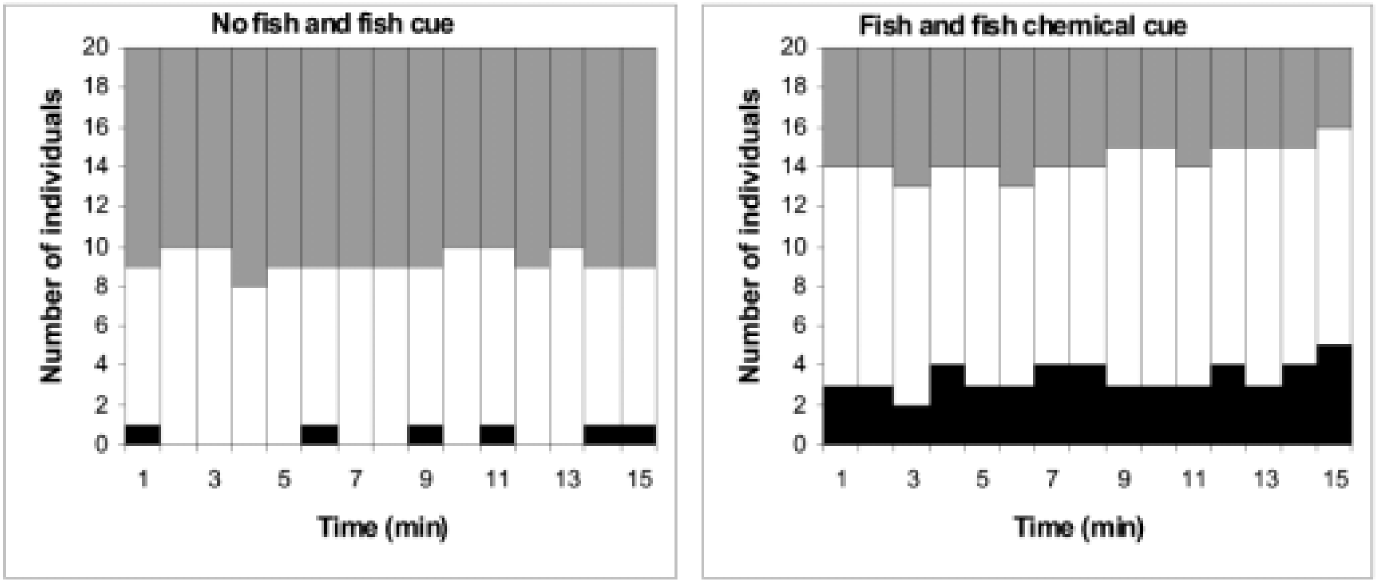

FIGURE 5–The number (mean values) of *Notodromas* individuals found in the different microhabitats of the aquaria without fish and fish cue (experiment 1.2) and after exposure to fish water and juvenile perch (experiment 3.2). Water - gray bar, plant - white bar, ground - black bar.

wind effect and enhanced water movements, nor prefers the very dense macrophyta beds, and usually moves in the surface water layers. It is able to discriminate different food types and shows a preference for the organic-rich food type on the surface of the water.

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OSTRACODE ASSEMBLAGES AND PALAEOENVIRONMENTAL EVOLUTION OF THE LATEST MESSINIAN LAGO-MARE EVENT AT PERTICARA (MONTEFELTRO, NORTHERN APENNINES, ITALY)

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Abstract

The latest Messinian *lago-mare* event, which affected the whole Mediterranean area, is well constrained both lithostratigraphically and biostratigraphically. The sediments lie between the evaporite deposition related to the Messinian salinity crisis and the clayey deposition related to the Early Pliocene transgression and it is marked by the appearance of ostracode assemblages with Paratethyan affinity. The Perticara section (Montefeltro, northern Apennines, Italy), characterised by a high sedimentation rate, has been sampled every 50 cm. Ostracode assemblages have been analysed from the topmost portion of the sedimentary succession, with the aim of reconstructing the palaeoenvironmental evolution of the last 15-20.000 years of this event and investigate possible environmental changes on a millennian scale. Statistical analyses have been performed on the relative abundance in percentages of the species identified in 31 sediment samples. Populational structure has been studied through several indexes such as Margalef, Shannon and equitability. Both species (R-mode) and samples (Q-mode) were grouped by cluster analyses and detrended correspondence analyses (DCA) using the software package PAST (ver. 1.06). The DCA analysis has shown that, during this short period, several environmental changes have been recorded. A short interval, 14 m below the Mio-Pliocene boundary, testifies to a shallow mesohaline waterbody dominated by Leptocytherinae and Loxoconchidae [*Loxoconcha (Loxocorniculina) djafarovi* and *Loxoconcha (Loxoconcha) eichwaldi* n. ssp.]. Within the upper intervals, salinity slowly shifts to oligo-freshwater conditions since Loxoconchidae and Leptocytherinae progressively decrease and Candoninae increase (with dominant *Caspiocypris pontica).* A few meters below the Mio/Pliocene boundary, Candoninae are still dominant but Leptocytherinae species increase again in frequency together with Loxoconchidae. These changes point to the restoration of oligo-mesohaline or mesohaline conditions. The uppermost 2 m of clays below the Mio-Pliocene boundary are barren of ostracodes preventing an investigation of the very late Miocene palaeoenvironment, but the first Lower Pliocene samples show clearly the abrupt restoration of fully marine conditions.

Key words: Ostracodes, latest Messinian, *lago-mare* event, northern Italy, palaeoenvironmental evolution, statistical analyses.

Resumen

El evento *lago-mare* del Messiniense final, que afectó al conjunto del área mediterránea, está bien caracterizado tanto litoestratigráficamente como bioestratigráficamente. Estos sedimentos se disponen entre los depósitos evaporíticos relacionados con la crisis salina del Messiniense y el depósito lutítico representativo de la transgresión del Plioceno Inferior, y está marcado por la aparición de asociaciones de ostrácodos con afinidad paratethysiana. La sección de Perticara (Montefeltro, Apeninos septentrionales, Italia), caracterizada por una alta tasa de sedimentación, ha sido muestreada cada 50 cm. Han sido analizadas las asociaciones de los ostrácodos de la parte superior de la sucesión sedimentaria, con el objetivo de reconstruir la evolución paleoambiental de los últimos 15.000-20.000 años de este evento, así como investigar posibles cambios medioabientales de escala milenaria. Se han realizado análisis estadísticos de los porcentajes relativos de las especies identificadas en 31 muestras de sedimento. La estructura poblacional ha sido estudiada por medio de los índices de Margalef, Shannon y equitabilidad. Tanto las especies (modo-R) como las muestras (modo-Q) han sido agrupadas mediante los análisis de Grupos y de Correspondencias (DCA) utilizando el paquete estadístico PAST (ver. 1.06). El análisis DCA ha mostrado que para este corto período temporal se han podido detectar varios cambios paleoambientales. Un corto intervalo, localizado 14 m por debajo del tránsito Mioceno-Plioceno, está representado por un medio acuoso somero, mesohalino, dominado por los Leptocytherinae y Loxoconchidae [*Loxoconcha (Loxocorniculina) djafarovi* y *Loxoconcha (Loxoconcha) eichwaldi* n. ssp.]. En los intervalos superiores, la salinidad cambia gradualmente hacia condiciones oligosalinas o de agua dulce, cambio atestiguado por la disminución de los Leptocytherinae y Loxoconchidae y el incremento de los Candoninae, con el dominio de *Caspiocypris pontica.* Unos pocos metros antes del tránsito Mio-Plioceno, los Candoninae son todavía dominantes, si bien las especies de Leptocytherinae incrementan su presencia, a la vez que las de Loxoconchidae. Estos cambios apuntan a la restauración de las condiciones oligo-mesohalinas o mesohalinas. Los 2 metros de arcillas superiores, previos al tránsito, están desprovistos de ostrácodos, lo que impide la investigación de los cambios paleoambientales del Mioceno terminal, si bien las primeras muestras del Plioceno Inferior indican claramente la restauración brusca de condiciones totalmente marinas.

Palabras clave: Ostrácodos, Messiniense final, evento *lago-mare,* Norte de Italia, evolución paleoambiental, análisis estadísticos.

INTRODUCTION

The *lago-mare* facies, characteristic of the Mediterranean area during the latest Messinian, has been widely investigated from a paleogeographic and paleontological point of view. Ostracode faunas, typical of this facies are characterised by an important contingent of ostracodes of Paratethyan affinity (Grekoff & Molinari, 1963; Gramann, 1969; Molinari Paganelli, 1975; Benson, 1976; Roep & Van Harten, 1979; Krstic & Stancheva, 1989; Bossio *et al.*, 1996; Gliozzi, 1999; Cipollari *et al.*, 1999a,b; Bonaduce & Sgarrella, 1999; Gliozzi *et al.*, 2002). Their migration into the Mediterranean area was due both to the western closure of the Mediterranean-Atlantic connection (Weijermars, 1988; Benson *et al.*, 1991; Cita & Corselli, 1993) and to the subsequent humid climate phase (Griffin, 2002) which diluted the hyperhaline Mediterranean waters after the Messinian “salinity crisis” (McCulloch & De Deckker, 1989). Ostracode assemblages mirror the dilution to oligo-mesohaline waters, being characterised by the presence of several Candoninae, *Cyprideis* and *Amnicythere* species. In the present paper the *Lago-mare* palaeoenvironment has been analysed in a new perspective: the detailed palaeoenvironmental reconstruction of the last 15.000-20.000 years before the marine ingression testifies to the restored Mediterranean-Atlantic connection and marks the beginning of the Pliocene.

GEOLOGICAL SETTING

The northern Apennines are part of the circum-Mediterranean orogen, developed through the convergence between the European and African plates mainly during Neogene times. The tectonic units of the northern Apennine chain derive from the deformation of both the Neotethyan oceanic realm and the Adria continental realm. In the Montefeltro area (Fig. 1), the oceanic-derived allochthonous Ligurian Complex overthrust the “autochthonous” succession of the Umbro-Marchean-Romagna domain, sedimented on the Adria continental microplate. Here, the allochthonous Ligurian Complex (Val Marecchia thrust sheet) is represented by the Mesozoic and Paleogene sedimentary cover of part of the Ligurian oceanic domain. In the northern Apennines, as well as on the Val Marecchia thrust sheet, Epiligurian deposits rest unconformably on the allochthonous Ligurian units. Epiligurian succession sedimented in wedge-top basins, above the forelandward migrating allochthonous Ligurian Complex (Ricci Lucchi, 1986; Roveri *et al.*, 1999).

The Umbro-Marchean-Romagna “autochthonous” succession is characterised mainly by Meso-Cenozoic deep-water deposits (pelagic basin). The Neogene terms of this basinal succession extensively crop out at the footwall of the Val Marecchia thrust sheet (Fig. 2).

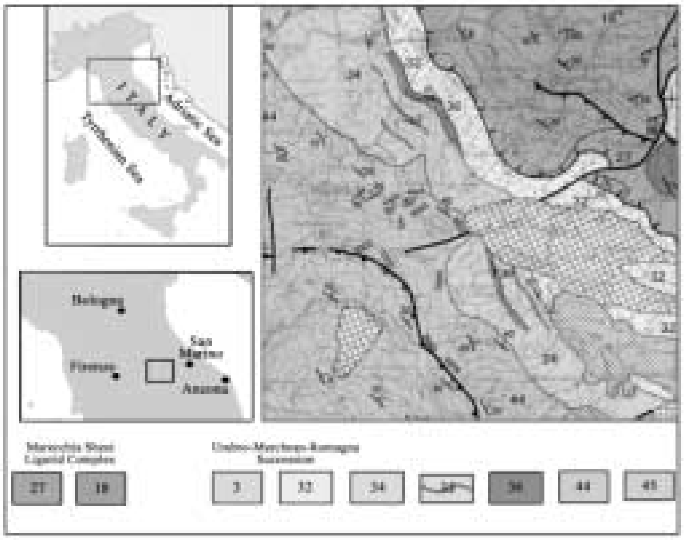

FIGURE 1–Location map of the study sections and geological sketch-map of the Perticara area. Legend: MARECCHIA SHEET LIGURID COMPLEX – 27. Sillano Fm. (Upper Cretaceous-Lower Eocene); 19. Campaolo Fm. (Upper Oligocene-Aquitanian); UMBRO-MARCHEAN-ROMAGNA SUCCESSION – 3. Yellowish-grey limestones (Lower Pliocene, *G. puncticulata* Zone); 32. *Peliti grigio-azzurre* Fm. (Lower Pliocene, *Sphaerodinellopsis* spp. to *G. puncticulata* Zone); 34, 35, 36. *“Colombacci”* Fm. (Upper Messinian); 44. *Gessoso-solfifera* Fm. (Upper Messinian); 45. *Ghioli di Letto* Fm. (Tortonian-Lower Messinian) (from Conti, 1989, modified).

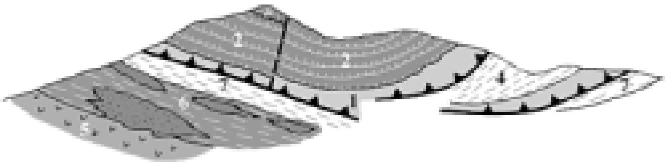

FIGURE 2–Schematic section showing the geometrical relations between the Marecchia sheet Ligurid Comples and the Umbro-Marchean-Romagna Succession. Legend: MARECCHIA SHEET LIGURID COMPLEX – 1. Ligurid Complex; 2. Campaolo Fm.; 3. S. Marino Fm.; 4. *Arenarie di Perticara* Fm.; UMBRO-MARCHEAN-ROMAGNA SUCCESSION – 5. *Marnoso-Arenacea* Fm.; 6. *“Colombacci”* Fm.; 7. *Peliti grigio-azzurre* Fm. (from Bortolotti *et al.*, 1992, modified).

Close to the Val Marecchia thrust sheet the uppermost part of the “autochthonous” Umbro-Marchean Romagna succession crops out (Roveri *et al.*, 1999). The upper turbiditic lobes of the *Marnoso-Arenacea* Fm. (Late Tortonian) are capped by the *Ghioli di letto* Fm. (Late Tortonian – Messinian), a thick fine-grained unit made up by thin bedded-turbidites, hemipelagites and submarine slide deposits. This fining-upward sequence (T2 sequence *sensu* Ricci Lucchi, 1986) is abruptly overlain by the *Gessoso-Solfifera* Fm, here exclusively made up by resedimented evaporites. In turn, the evaporites are capped by the late Messinian Lago-Mare “*Colombacci*” Fm. and by the *Peliti grigio-azzurre* Fm., which mark the re-establishment of marine conditions in the Mediterranean basin during the Early Pliocene.

In the Montefeltro area the Messinian terms of the autochthonous succession crop out, resting on the Tortonian *Marnoso-Arenacea* Formation. The Perticara section (Fig. 3), studied in detail in the present paper, includes the “*Colombacci*” Fm. and the Early Pliocene *Peliti grigio-azzurre* Fm. which conformably overly them. The “*Colombacci*” Fm. is represented by the association of several lithofacies: varicoloured, thin laminated pelites bearing abundant brackish ostracodes; intercalated sandstones and conglomerate lenses (not found at Perticara), black sandy-clays and chemically precipitated white limestones (“*colombaccio*” s.s.) of variable thickness from 30 to 80 cm. These litofacies, included the “*colombacci*” levels, are repeated at least five times along the “*Colombacci*” Fm. which reaches its maximum thickness of about 250 m at the Cella section (Romagna Apennines) (Casati *et al.*, 1978; Colalongo *et al.*, 1978). In the studied portion of the Perticara section only one “*colombacci*” level is included.

The *Peliti grigio-azzurre* Fm., on the contrary, is characterised by bluish-grey clays with rare intercalation of yellowish-grey sandy levels. The formation

FIGURE 3–Panoramic view of the Perticara section.

bears rich planktic foram assemblages which testifies to the fully restored marine conditions during the Early Pliocene (*Sphaeroidinellopsis seminulina* Zone).

Nineteen meters of sedimentary succession have been sampled every 50 cm (being each samples around 8-10 cm of thickness), 17 m below the Mio/Pliocene boundary and 2 m above it (Fig. 4). At the base, grey-greenish clays are intercalated with thin reddish silty laminations (7,5 m of thickness). They are covered by ca. 1 m of alternating marls and clayey marls with a 20 cm thick limestone level ("*colombaccio*"). Green and grey clays follows (40 cm thick) overlain by ca 1 m of varicoloured (greenish, whitish and reddish) clays. Above the varicoloured clays an alterntion of grey and greenish clays (5 m of thickness) is followed by ca 2 m of "black marls" (dark marly clays), rich in organic matter. Taking into account a sedimentation rate of about 1m / 1.000 year (this figure is based on the maximum thickness of the "*Colombacci*" Fm. in the Romagna area (Colalongo *et al*., 1978) and on the duration of the Lago-Mare event of 260.000 years deduced from Krijgsman *et al*., 1999, and Lourens *et al*., 1996), it is possible to assume that the investigated seventeen meters of the "*Colombacci*" Fm. were deposited during a period of about 15-20 ka. Thus each sample possibly corresponds to a sedimentation interval of about one hundred years and the sampling frequency is about every five hundred years.

The *Peliti grigio-azzurre* Fm., which rest conformably upon the "black marls" is easily distinguished and characterised by a decimetric alternation of light and dark grey clays.

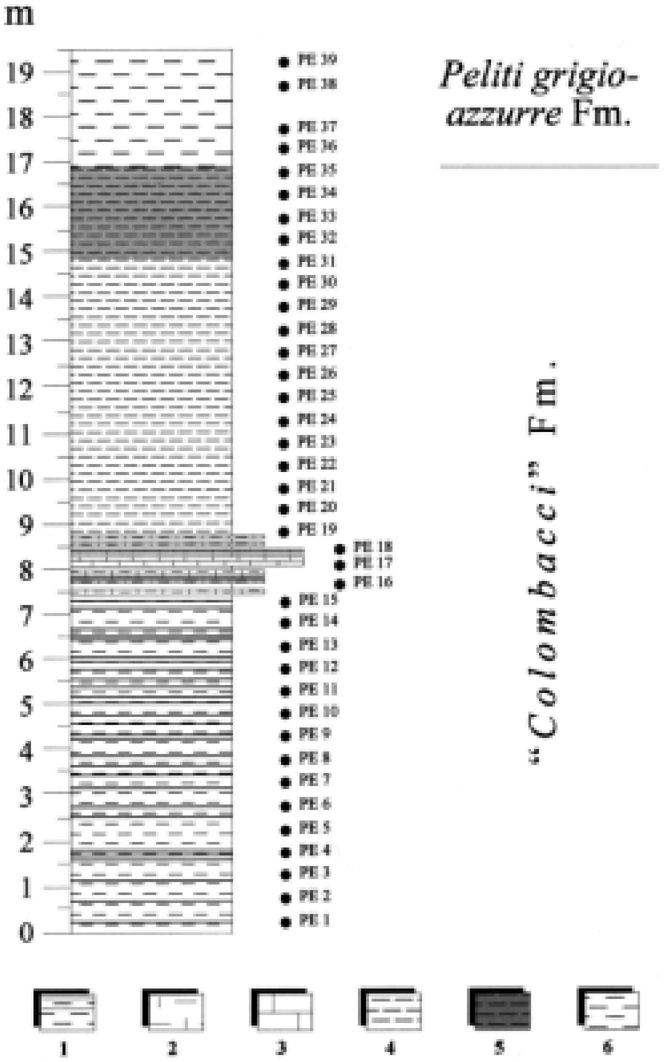

FIGURE 4–Stratigraphical log of the Perticara section, with the sample locations. Legend: 1. Varicoloured silty clays with alternations of thin reddish clayey layers; 2. Marly levels; 3. "*colombaccio*" limestone level; 4. Varicoloured silty clays; 5. Black marls; 6. Grey-bluish clays.

MATERIAL AND METHODS

Each sample has been desegregated in a 5% H_20_2 solution, washed using a 0.125 mm mesh sieve and dried. Not less than 300 ostracode valves for sample where handpicked under the stereomicroscope. Ostracodes were mainly represented by carapaces whereas loose valves were few. On the whole they were medium to well-preserved, except for the samples collected from the upper portion of the "*Colombacci*" Fm. characterised by a high amount of deformed specimens, probably due to the tectonic stress linked to the overthrust which settled the Val Marecchia thrust sheet. Some samples were barren of ostracodes (PE 32-PE 35 from the "*Colombacci*" Fm. and PE 36-PE 39 from the *Peliti grigio-azzurre* Fm.), others yielded few valves (PE 16-PE 19, corresponding to the "*colombaccio*" limestone) but, in general, the majority of the samples were characterised by high frequencies. Each species frequency was normalised to 10 g of dried sieved sample and the relative abundance in percentage was calculated for each taxon. Community structure analyses [frequency, Margalef index, Shannon index and equitability index) (Dodd & Stanton, 1990)] and multivariate analyses (cluster analysis and Detrended Correspondence Analysis (DCA) in Q-mode and in R-mode) have been used. These latter analyses have been performed using the software package PAST – Palaeontological Statistics (ver. 1.06) (Hammer *et al.*, 2003).

PALEONTOLOGICAL ANALYSES

The ostracode fauna collected at Perticara contains 22 species referable to 12 genera: *Amnicythere* sp. 1., *Amnicythere* sp. C Miculan in Bassetti *et al.* (2003), *Amnicythere* sp. D Miculan in Bassetti *et al.* (2003), *Amnicythere costata* (Olteanu, 1989), *Amnicythere idonea* (Markova, 1962) vel *pontica* (Sheydaeva, 1951), *Amnicythere multituberculata* (Livental, 1929), *Amnicythere palimpsesta* (Livental, 1929), *Amnicythere propinqua* (Livental, 1929), *Amnicythere subcaspia* (Livental in Agalarova *et al.*, 1940), *Euxinocythere* (*Maeotocythere*) *praebaquana praebaquana* (Livental in Agalarova *et al.*, 1940), *Euxinocythere* sp. 1, *Cyprideis* sp. 5, *Cyprideis anlavauxensis* Carbonnel, 1979, *Acanthocythereis* cf. *A. hystrix* (Reuss, 1950), *Tyrrhenocythere* cf. *T. taurica* Krstic, 1977, *Loxoconcha (Loxoconcha) eichwaldi* Livental, 1929 (ssp.), *Loxoconcha* (*Loxocorniculina*) *djafarovi* Schneider in Suzin, 1956, *Pseudocythere limata* Schneider in Agalarova, Djafarov, Halilov, 1940, *Camptocypria* sp. 1, *Lineocypris* sp. 1, *Caspiocypris pontica* (Sokac, 1972), *Pontoniella pontica* Agalarova, 1961 (ssp.) and *Zalanyiella venusta* (Zalanyi, 1929).

Six of these genera (*Euxinocythere*, *Camptocypria*, *Caspiocypris*, *Lineocypris*, *Pontoniella* and *Zalanyiella*) are widespread during Miocene in the Paratethys domain and migrated into the Mediterranean area only during the latest Messinian *lago-mare* event [*Loxoconcha* (*Loxocorniculina*) *djafarovi* Zone as defined by Carbonnel, 1979] (Bonaduce & Sgarrella, 1999; Carbonnel, 1979; Gliozzi, 1999; Gliozzi *et al.*, 2002 *cum bibl.*). Four genera are widespread in the Neogene/Quaternary of both the Paratethyan and Mediterranean domains (*Loxoconcha*, *Pseudocythere*, *Tyrrhenocythere*, *Amnicythere*), but here at Perticara they are represented only by Paratethyan species which migrated in the Mediterranean exclusively during the latest Messinian *Lago-mare* event (Bonaduce & Sgarrella, 1999; Carbonnel, 1979; Gliozzi, 1999; Gliozzi *et al.*, 2002 *cum bibl.;* Gliozzi *et al.*, in press). Finally, the genus *Cyprideis* is here represented only by Mediterranean species, although widespread in both the Paratethyan and Mediterranean realms. At Perticara, the genus *Acanthocythereis,* which is widely represented in the Mediterranean area during the Late Tortonian, is here considered as reworked since it is represented by a single fragment of *A.* cf. *A. histrix*.

At the species level, the taxa recognised at Perticara were characteristic of the late Pontian (Bosforian) (*sensu* Nevesskaya *et al.*, 1984; Papp, 1985; Pantic, 1989; Marinescu, 1989, 1995; Stevanovic, 1989; Krstic & Stancheva, 1989) of the Eastern Paratethys (Euxinic and Caspian-Aral basins), the early Dacian (Getian) *sensu* Marinescu (1989; 1995; Sacchi & Horvath, 1997) of the Central Paratethys (Dacian Basin) and of the early Pontian (Novorossian) (*sensu* Stevanovic, 1989; Krstic & Stancheva, 1989) of the Western Paratethys (Pannonian basin) which, on the whole, correspond to the latest Messinian. In particular, *A. subcaspia*, *A. palimpsesta*, *E.* (*Maeotocythere*) *praebaquana praebaquana* and *L.* (*Loxocorniculina*) *djafarovi* are widespread in all the four Paratethyan basins, *P. limata* and *A. idonea* vel *pontica* are distributed only in the Euxinic and Caspian-Aral basins, whereas *A. costata*, *Z. venusta* and *C. pontica* are present in the Pannonian and Dacian basins and *A. multituberculata* has been collected in the Dacian, Euxinic and Caspian-Aral basins. Only *A. propinqua* seems to be reported exclusively in the Pannonian basin during latest Messinian. Anyway this species is widespread in the Euxinic and Caspian-Aral basin from Early Pliocene to Recent. Thus, it seems that the Paratethyan species able to spread into the Mediterranean realm during the latest Messinian *Lago-mare* event were those living in the Dacian and Euxinic areas. Those areas represented the more probable areas in connection with the Mediterranean, according to the palaeogeographic reconstruction proposed by several authors (Hámor, 1988; Cipollari *et al.*, 1999a; Cipollari *et al.*, 1999b; Gliozzi *et al.*, in press).

Since few of the studied species are extant, little data exists on their ecology. At present, *A. multituberculata* and *A. palimpsesta* live in the Caspian Sea, *A. propinqua*, lives in the Caspian Sea, the Aral Sea, the Pahlavi Lagoon (Iran), the Black Sea and in the Azov Sea (Gofman, 1966; Schornikov, 1966; Naydina, 1970, Yassini & Ghahreman, 1976; Boomer *et al.*, 1996). All three species seem to be characteristic of shallow waters (around 10-12 m depth) and oligo-mesohaline waters (12-13.25‰ for *A. multituberculata* and *A. palimpsesta*, 4-13.25‰ for *A. propinqua*). No ecological data have been found regarding the Candoninae species collected at Perticara, but at a generic level it seems that the living species of *Caspiocypris* and *Pontoniella* in the Caspian Sea are characteristic of less saline and deeper waters (down to few hundred meters) (Gofman, 1966; Schornikov, pers. com.). The fresh/oligohaline conditions for the latest Messinian *lago-mare* Candoninae seem to be supported by the stable isotopic analyses performed by

Casati *et al.* (1978) on the "*colombacci*" limestones of the "*Colombacci*" Fm. outcropping in the Romagna Apennines.

COMMUNITY STRUCTURE ANALYSES

Community structure analyses have been performed on the ostracode assemblages collected at Perticara in the "*Colombacci*" Fm. samples. Three assemblage structure indices were calculated for each sample: Margalef index (richness), Shannon index (diversity) and equitability index (Fig. 5).

The samples show a medium richness coupled with a rather high equitability. These parameters mirror rather stable environments, which lead to the establishment of several mature ostracode communities. In particular, the first two samples (PE 1-PE 2) and the samples from the upper portion of the Perticara Messinian succession (PE 19-PE 31) show the presence of several species with high equitability and high diversity. On the contrary, in the interval PE 3-PE 12, low values of equitability and Shannon indexes, coupled with a rather low richness mirror rather unstable environments, with low-diversity communities dominated by *Caspiocypris pontica*. Although in samples PE 16-PE 19 (corresponding to the "*colombaccio*"), few species have been collected, they show rather high equitability and diversity values, pointing to a rather stable but specialised environment able to support a mature, but oligotypic assemblage (made only by Candoninae species).

MULTIVARIATE ANALYSES

A Q-mode hierarchical cluster analysis of the total association was computed using the Morisita distance measure and the un-weighted pair-group method using arithmetic average (UPGMA). By selecting a cut-off value of 0.6 for the across-cluster similarity, samples were statistically discriminated into three groups (Fig. 6). The first cluster is represented by the basal PE 1-PE 2 and PE 4 samples, the second by samples PE 25, PE 29-PE 31 taken near the top of the "*Colombacci*" Fm. and the third cluster includes all the remaining samples, mirroring the high similarity of their ostracode assemblages.

It is worth noting the partial coincidence of community analyses results and cluster analysis results, particularly for the basal and the higher samples in the Perticara succession. This is in accordance with the results of the paleontological analyses and was rather predictable taking into account that the different ostracode assemblages come from sediments deposited in a short time interval (probably not more than 20 ka) inside the latest Messinian *lago-mare* Event.

For a more detailed statistical analysis of the structure of the ostracode assemblages, DCA was performed on the data set both in Q- and R-mode (Figs. 7, 8). The eigenvalues are 36.7% for Axis 1 and 17.1% for Axis 2.

The Q-mode DCA further subdivides the samples into nine different groups (Fig. 7). The overlapping species distribution indicates that only three groups are characterised by "typical" taxa: Group IX characterised by *A. palimpsesta* (in Fig 7: pal), *A. multituberculata* (mul) and *A. idonea* vel *pontica* (ido); Group VII, characterised by the presence of all the Candoninae [*Lineocypris* sp. 1 (LIN), *Camptocypria* sp. 1 (CAMP), *P. pontica* ssp. (PON), *Z. venusta* (ZAL), and *C. pontica* (CAS)]; Group III, characterised by *C. pontica* (CAS), *Amnicythere* sp. D (spD), *A. costata* (cos) and *L. eichwaldi* ssp. (eich). Some groups seem to be characterised by a low ostracode frequency rather than a different taxonomic composition. For example, Group VI, whose samples (PE 16-PE 18) correspond to the "*colombaccio*", shows a taxonomic composition very similar to that of Group VII (dominant Candoninae) but with much lower frequencies. Most of the species are located in the central area of the plot of Fig. 7, pointing to a more or less similar distance from all the groups and further emphasising the high grade of similarity of the Perticara ostracode assemblages. Particularly significant is the central position of *Caspiocypris pontica*, characteristic of Group III (where it is dominant) but always present in all the analysed samples with rather high frequencies.

The R-mode DCA plot (Fig. 8), shows the distribution of the 20 species (except *Acanthocythereis* and *Tyrrhenocythere*, considered reworked or displaced) in four groups (A-D). The species *C. pontica* and *Amnicythere* sp. 1 are isolated. The first, probably because it shows high frequencies in all the samples (it seems to be an euryplastic taxon). The second, on the contrary, because is represented by very few valves in scattered samples.

Considering the few ecological data relating to the Perticara species, it is possible to suggest that Group C (which includes *A. multituberculata*, *A. palimpsesta*, *A. idonea* vel *pontica* and *Amnicythere* sp. C) represents a mesohaline (12-13‰) assemblage, while Group B (with *A. propinqua*, *Z. venusta*, *C. anlavauxensis* and *P. limata*) clusters taxa of a low mesohaline/oligohaline environment. If this interpretation is true, Group A

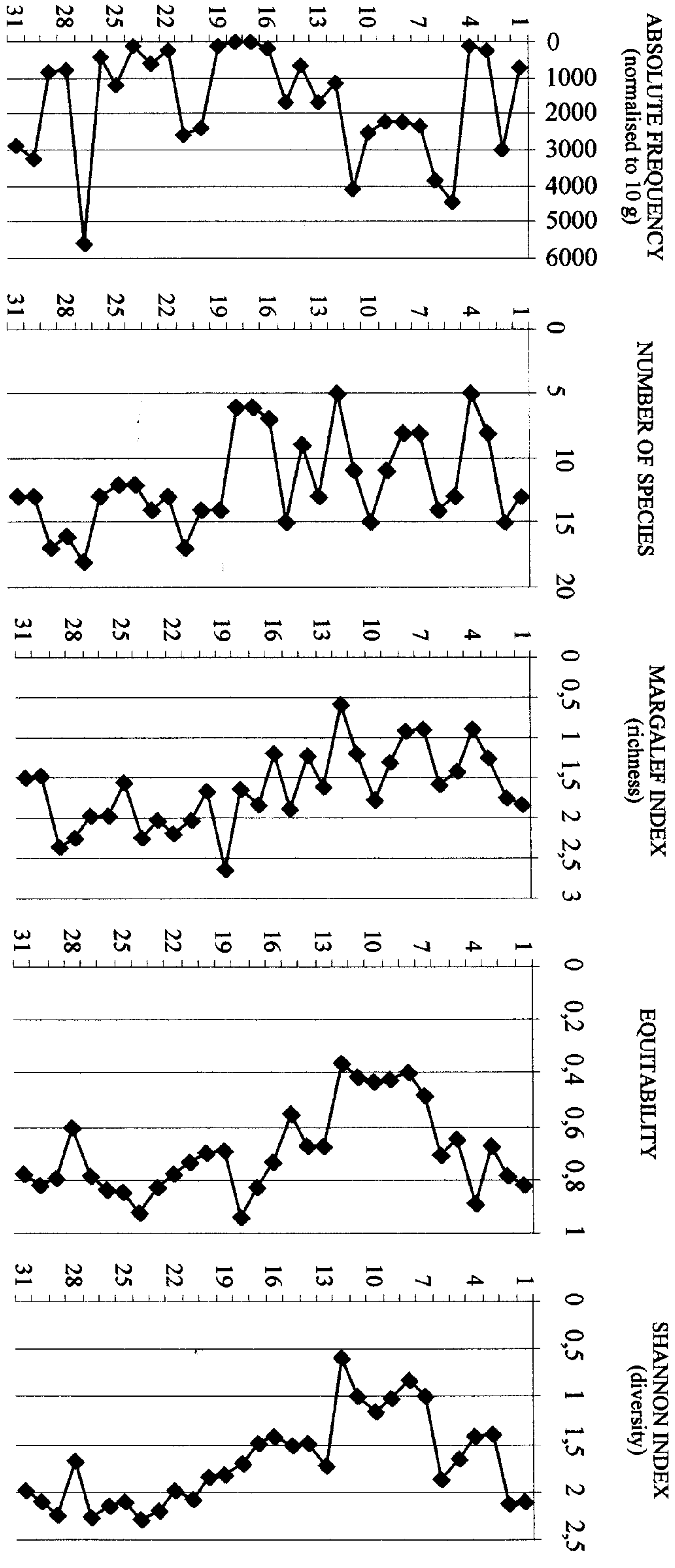

FIGURE 5–Diagrams of the community structure indexes.

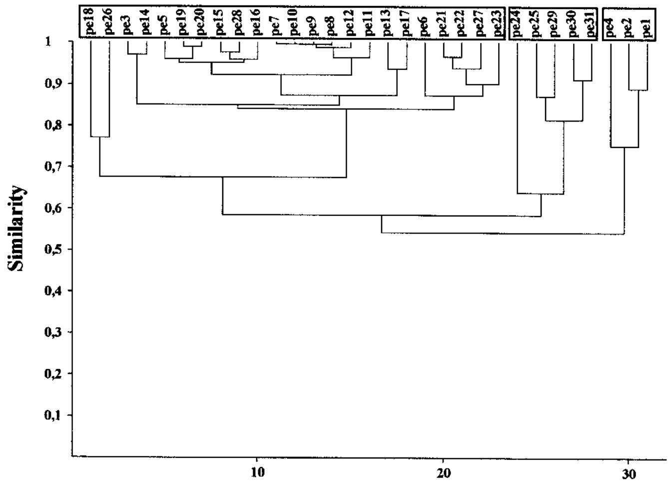

FIGURE 6–Dendrogram resulting from cluster analysis using UPGMA method and Morisita distance applied to the Perticara samples.

(*Camptocypria* sp. 1, *Lineocypris* sp. 1 and *P. pontica* ssp.) should be the less saline assemblage and Group D (with *L. eichwaldi* ssp., *Amnicythere* sp. D, *A. costata*, *A. subcaspia*, *E.* (*M.*) *praebaquana praebaquana*, *L.* (*L.*) *djafarovi* and *Cyprideis* sp. 5) an oligo-mesohaline assemblage. Thus, Axis 1, which accounts for 36.7% of the relative variance, should represent the ecological parameter “salinity”. Group D and Group B, both characterised by species tolerating similar salinities, are separated on the basis of their different behaviour respect to the Axis 2. According to the few ecological parameters found in the literature (Gofman, 1966; Schornikov, 1966; Naydina, 1972; Yassini & Ghahreman, 1976; Boomer *et al.*, 1996) Candoninae (Group A) and Leptocytherinae (distributed in the other groups) inhabit different water depths: up to few hundred meters for the first and few tens of meters for the second. Thus, Axis 2, which account for 17.1% of the relative variance, should represent the ecological parameter “depth” and Group D should be represented by oligo/mesohaline shallow-water species, while Group B would include oligo/mesohaline deeper species. If this interpretation is the correct one, the ostracode assemblages are more significative for the paleosalinity fluctuations.

DISCUSSION

Paleontological, assemblage and multivariate analyses have been used to depict the detailed palaeoenvironmental evolution of the last 17 m thick portion of the “*Colombacci*” Fm., corresponding to the last 15-20 ka of the latest Messinian *lago-mare* event. The 20 ostracode species collected at Perticara are not simultaneously present in the same samples but are associated in various assemblages each one with different frequencies. Although the cluster analysis indicates the high level of similarity of the different sample assemblages, DCA and community analyses have given important informations that distinguish several palaeoenvironmental intervals within the “*Colombacci*” Fm. succession. Tab. 1 and Fig. 9 summarize the palaeoenvironmental evolution recorded by the analysed section. It is worth to note the similar conclusions arised by independent methods (paleontological, geochemical and mineralogical) concerning the palaeoenvironmental interpretation of Interval F (PE 16-PE 18), which corresponds to the “*colombacci*” limestone lithofacies. In these samples Candoninae are the absolutely dominant taxa, with all the genera recovered at Perticara (*Pontoniella*, *Zalanyiella*, *Camptocypria*, *Caspiocypris* and *Lineocypris*). *L. eichwaldi* ssp., and Leptocytherinae valves are very few, probably displaced. From the paleontological analyses, this interval most likely records a true fresh water and deep waterbody mirroring an environment rather different than those previously recorded, characterised by brackish and rather shallow waters. This palaeoenvironmental interpretation is supported by the results of stable

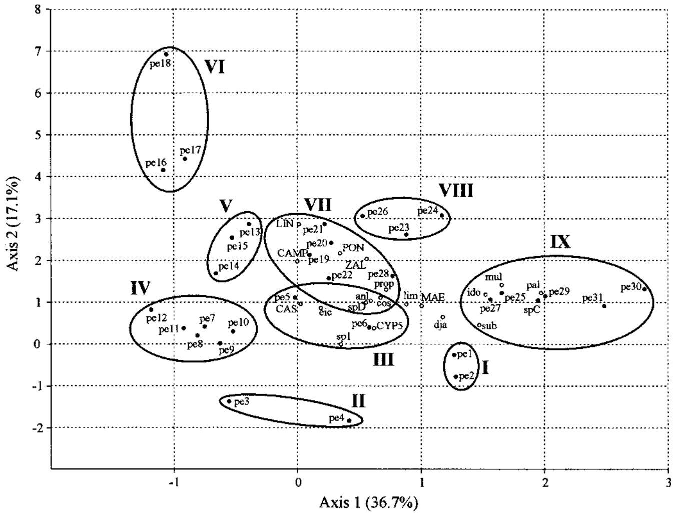

FIGURE 7–DCA ordination plot (Axis 1/Axis 2) of sites and species (Q-mode).

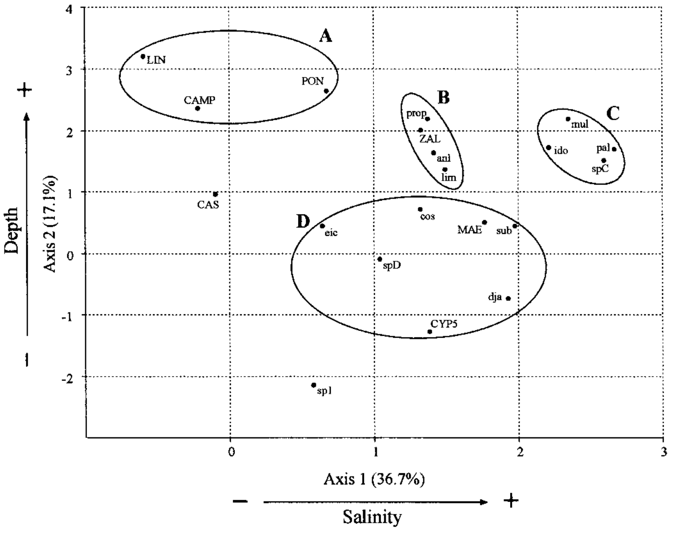

FIGURE 8–DCA ordination plot (Axis 1/Axis 2) of species (R-mode).

isotopes analyses performed by Casati *et al.* (1978) on the “*colombacci*” limestones cropping out in the Romagna (northern Apennine) area. The authors report low $\delta^{18}O$ values (from -5.03 to 1.63) which are explained, at an average temperature of 20-25°C, as the result of $CaCO_3$ precipitation in a freshwater environment. Moreover, the mineralogical analyses carried out by Colalongo *et al.* (1978) on the “*colombacci*” levels show the dominance of calcite over dolomite, pointing to a freshwater depositional environment.

Two metres below the Messinian/Zanclean boundary, i.e. the topmost part of the *lago-mare* interval, samples are barren of ostracodes. The sedimentary succession here is characterised by “black marls”, i.e. clays and marly clays rich in organic matter. Such organic matter accumulation suggests very shallow marshy or palustrine environment characterised by low pH conditions, unfavourable to ostracode life. Black marl levels have been found elsewhere in the northern Apennine “*Colombacci*” Fm. Mineralogical

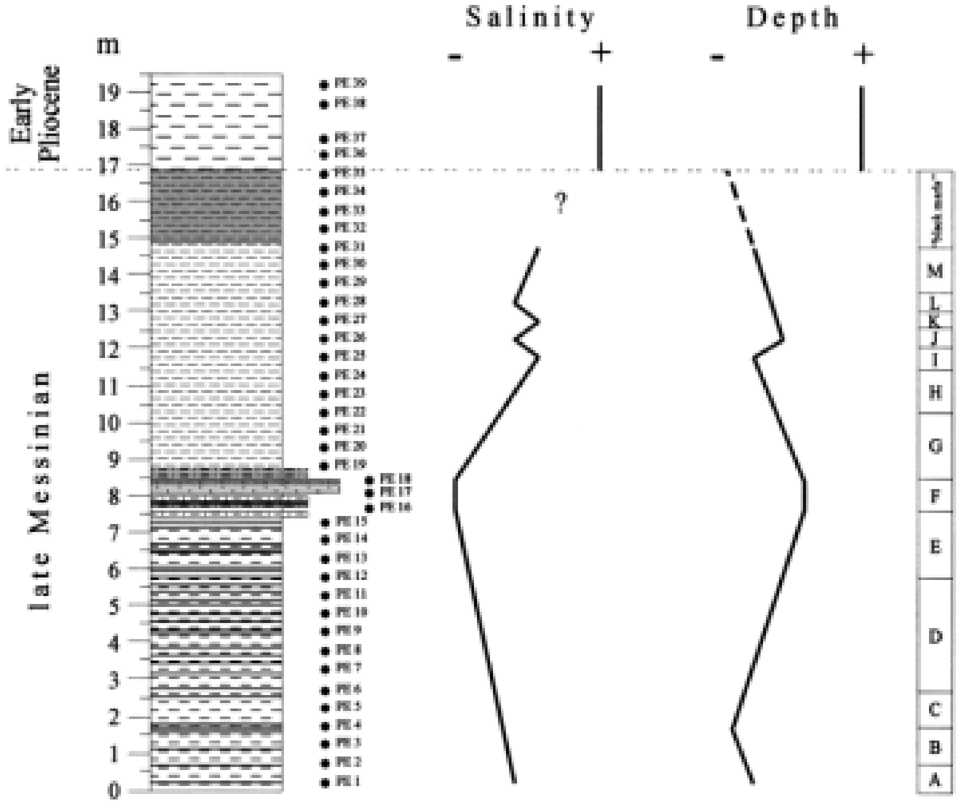

FIGURE 9–Palaeoenvironmental evolution (salinity and depth changes) of the upper portion of the *“Colombacci”* Fm. cropping out at Perticara.

INTERVAL	SAMPLES	COMMUNITY TYPE	DCA GROUP	ENVIRONMENT	ASSEMBLAGE
Interval A	PE 1-PE 2	High equitability High diversity	I	Shallow, oligo-mesohaline	Dominant Loxoconchidae and Leptocytheriane (particularly *Amnicythere* sp. D)
Interval B	PE 3-PE 4	Low richness Very low frequency	II	Progressively decreasing salinity and depth (possibly less than 10m).	Dominant Loxoconchidae (particularly *L. eichwaldi* spp.) and *Cyprideis* sp. 5. Leptocytherinae decrease.
Interval C	PE 5-PE 6	Medium equitability Medium diversity High frequency	III	Slightly deeper and less saline waterbody than Interval A (for the presence of *Caspiocypris*)	Dominant Loxoconchidae and Leptocytherinae (particularly *A. costata* and *Amnicythere* sp. D). Presence of *C. pontica* Dramatic decrease of *Cyprideis* sp. 5.
Interval D	PE 7-PE 12	Low equitability Low diversity	IV	Oligohaline waterbody; depth increases.	Dominant *C. pontica* over *Cyprideis*. Loxoconchidae and Leptocytherinae are scarce.
Interval E	PE 13-PE 15	Medium diversity Medium diversity	V	Progressively deeper and less saline waterbody.	Dominant Candoninae (*Pontoniella*, *Zalanyiella*, *Camptocypria* and *Caspiocypris*) over *Cyprideis*, Leptocytherinae and Loxoconchidae.
Interval F	PE 16-PE 18	High equitability High diversity	VI	Fresh and rather deep waterbody.	Dominant Candoninae (*Pontoniella*, *Zalanyiella*, *Camptocypria, Caspiocypris* and *Lineocypris*).
Interval G	PE 19-PE 22	Medium equitability High diversity	VII	Restoration of less deep and slightly saline waters.	Leptocytherinae (particularly *Amnicythere* sp. D) and Candoninae.
Interval H	PE 23-PE 24	Medium equitability High diversity	VIII	Salinity is still increasing.	Dominant Leptocytherinae (particularly *A. palimpsesta*); Candoninae (*Caspiocypris* and *Camptocypria*) decrease.
Interval I	PE 25	Low equitability Low diversity	IX	Mesohaline waterbody.	Dominant Leptocytherinae (particularly *A. palimpsesta* and *Amimicythere* sp. D).
Interval J	PE 26	Medium equitability High diversity	VIII	Salinity is still increasing. Oligohaline waters.	Decreasing Leptocytherinae, increasing Candoninae (*Caspiocypris* and *Camptocypria*).
Interval K	PE 27	Medium equitability High diversity	VII	Mesohaline waters.	Dominant Leptocytherinae (particularly *A. palimpsesta, A. multituberculata* and *A. idonea* vel *pontica*).
Interval L	PE 28	Medium equitability Medium diversity	VII	Salinity decreases.	Dominant Candoninae.
Interval M	PE 29-PE 31	High equitability High diversity	VII	Shallow mesohaline waters.	Dominant Leptocytherinae (particularly *A. palimpsesta, A. multituberculata* and *A. idonea* vel *pontica*); frequent Loxoconchidae [*L. eichwaldi* ssp. and *L. (Loxocorniculina) djafarovi*]

TABLE 1–Palaeonvironmental interpretation of ostracode assemblages from Perticara samples.

analyses carried out by Colalongo *et al*. (1978) support evidences of a pH lowering: these dark levels are characterised by a lower cristallinity degree of the illite (that point to a decreasing of alkalinity) and an abrupt lowering of smectite, a clay mineral which is typical of medium/high alkaline environments.

The palaeoecological analyses carried out on the upper portion of the "*Colombacci*" Fm. cropping out at Perticara reveals several palaeoenvironmental changes of the waterbody linked mainly to salinity and, to a less degree, to depth variations. The lower 9 m of the studied succession testify to a continuous progressive trend of salinity reduction, from a mesohaline to an oligohaline/fresh waterbody. At the same time, a less marked but still progressive deepening is recorded, from few meters to several tens of meters. The maximum salinity decrease and waterbody depth is reached during the deposition of the "*colombaccio*" limestone. In the upper portion of the succession, however, the salinity increase and the depth decrease are reached through several short-time oscillations.

Bassetti *et al*. (2003) studied from a sedimentological and paleontological point of view a portion of the "*Colombacci*" Fm. below the one studied in the present paper, cropping out in the same area, a few km to the NW of the Perticara section (Sapigno section, Fig. 1). Here, two *colombacci* limestones crop out along the "*Colombacci*" Fm., the topmost corresponding to the "*colombaccio*" of Perticara section. The ostracode taxonomic composition revealed in the Sapigno section is very similar to that recovered at Perticara. From Bassetti *et al*. (2003) data it is possible to recognise a similar palaeoenvironmental trend below and above the lower *colombaccio* level, thus confirming a cyclicity in the palaeoenvironmental changes. Within the Sapigno section, the ostracode assemblages below and above the first *colombaccio* are dominated by Leptocytherinae and Loxoconchidae, while close to the *colombaccio* level, those assemblages become progressively dominated by Candoninae. In the Romagna-Marche area (northern Apennine) the "*Colombacci*" Fm. is characterised by high thickness (up to 260 m) (Casati *et al*., 1978; Colalongo *et al*., 1978) and up to five *colombacci* levels have been recognised along the entire succession. Ostracode assemblages studied in different Romagna-Marche outcrops point everywhere to palustrine/marshy waterbodies with alternate salinities. On the basis of the results of the detailed palaeoenvironmental study of the Perticara section it is possible to suggest that, during the late Messinian *lago-mare* event at least 5 complete mesohaline/freshwater cycles are represented which are probably driven by cyclic climatic variations. Although the present palaeoenvironmental analysis has been carried out at a very small temporal scale (about five hundred years) at present it is not possible to detail neither the cyclicity period nor the nature of the climatic variations. Further investigations are needed, such is the aim of the authors: a longer and more constrained palaeontological record and the eventual integration of palinological analyses.

CONCLUSIONS

The ostracode analyses carried out on the upper part of the late Messinian "*Colombacci*" Fm. cropping out at Perticara (Montefeltro, northern Apennines), indicate a lagoon/marshy brackish environment typical of a *lago-mare* facies. The taxonomical composition, dominated by taxa of Paratethyan affinity, confirms the stratigraphical correlation of this facies to the late Messinian "*Lago-Mare*" event.

Detailed palaeoecological analyses on ostracode assemblages, using community structure analyses and multivariate analyses (UPGMA and DCA) lead to the recognition of a complete cyclical palaeoenvironmental change from mesohaline to fresh and deep to shallow waterbodies. These changes took place progressively in the lower portion of the studied succession and with short-living pulses in its upper part. The "*colombaccio*" level proved to be deposited in fresher and deeper palaeoenvironmental conditions. Other literature data record the presence of at least 5 "*colombacci*" limestones within the "*Colombacci*" Fm., cropping out in the Romagna-Marche area. This suggests that the late Messinian *Lago-Mare* event was generally characterised by a *lago-mare* environment subject to cyclical changes in water salinity and depth, probably linked to astronomically driven minor climatic oscillations.

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EARLY AND LATE DEVONIAN OSTRACOD FAUNAS FROM THE IBERIAN CHAINS (NE SPAIN)

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Abstract

Ostracod records from two localities in the Eastern Iberian Chain are described. These two sections have been demonstrated during the EOM excursion in 2003 (see Carls *et al.*, 2003). The lithological characteristics of the first section from the mid-Lochkovian to early Pragian of the Axial Depresion of the Cámaras river suggest a continuation of the Ibero-Armorican Trough for, at least, Early Devonian times. The presence of *Zygobeyrichia* sp. on mid-Lochkovian bedding planes does not support the former opinions that the benthic beyrichiacean ostracods could not reach Gondwana before the Emsian because of the Rheic ocean. These two results disproof the existence of a large Rheic Ocean during the Early Devonian between Gondwana and Baltica. The rich ostracod diversity of the second section from the Upper Devonian of Tabuenca allows the establishment of two different ostracod zonations. The zonation by benthonic ostracods has been developed for Frasnian and Fammenian rocks, but only with local application. In contrast, the Entomozoaceans, which have only been found in Frasnian rocks, allow an accurate correlation with the european and chinese entomozoacean zonations.

Key words: Ostracods, Devonian, palaeogeography, biostratigraphy, Entomozoacean Zonation, Spain.

Resumen

Se describen los ostrácodos estudiados en dos localidades en la Cadena Ibérica Oriental. Estas dos secciones han sido visitadas durante la excursión del EOM-V en 2003 (ver Carls *et al.*, 2003). Las características litológicas de la primera sección, de edad Lochkoviense medio a Praguiense inferior de la Depresión Axial del río Cámaras, permiten suponer la continuidad de la Cuenca Ibero-Armoricana durante, al menos, todo el Devónico Inferior. La presencia de *Zygobeyrichia* sp. en niveles del Lochkoviense medio pone en duda las opiniones previas en las que los ostrácodos bentónicos beyrichiaceos no alcanzarían Gondwana antes del Emsiense, debido a la presencia del océano Rheico. Estos datos cuestionan la existencia de un océano Rheico entre Gondwana y Báltica durante el Devónico Inferior. La rica diversidad de los ostrácodos de la segunda sección del Devónico Superior de Tabuenca permite establecer dos zonaciones diferentes basadas en los ostrácodos. La zonación con ostrácodos bentónicos ha sido desarrollada para el Frasniense y el Fameniense, pero solamente con una aplicación local. Por el contrario, los Entomozoos, que han sido hallados sólo en rocas frasnienses, permiten una correlación precisa con las zonaciones europeas y chinas.

Palabras clave: Ostrácodos, Devónico, paleogeografía, bioestratigrafía, Zonación de Entomozoidos, España.

INTRODUCTION

The intensive and detailed studies carried out by Carls and his German and Spanish disciples for the last 40 years (see review in Carls, 1999) in the Upper Palaeozoic of the Iberian Chains (IC), have demonstrated the worldwide importance of Devonian (mainly Early Devonian to middle Givetian) strata from the Axial Depression of the Río Cámaras (ADRC). The best sequence of rhenish faunas is known from the Early Devonian, and the ADRC can be considered as a reference area for such faunas. Within the Emsian, a deepening of the basin allowed the entry of hercynian faunas, which in turn allows a direct correlation of rhenish and hercynian faunas for this interval. The importance of the area gave rise for excursions of many interested groups (e.g. SDS, the International Subcommission on Devonian Stratigraphy). Another area of special relevance for Devonian strata is situated near Nigüella, which represents the northeastermost outcrop of Lochkovian to Early Emsian strata of the IC (Valenzuela-Ríos, 1984; Carls and Valenzuela-Ríos, 1998). Within the Montalbán Anticline Emsian to Frasnian and Carboniferous strata are exposed. Finally the Tabuenca area (Gozalo, 1994; Gozalo *et al.*, 2001) shows very thick Late Devonian strata.

The purpose of this paper is to analyse the Early and Late Devonian ostracod record in two of these areas, the Lochkovian and Praguian from Barranco de Santo Domingo in the ADCR and the Frasnian from Tabuenca.

GENERAL ASPECTS OF THE DEVONIAN OF THE IBERIAN CHAINS

Outcrops of pre-Mesosoic rocks in the IC occur in the core of alpine anticlines or anticlinorial structures, often bounded by high-angle reverse faults (Ábalos *et al.*, 2002). These preserved Palaeozoic rocks have been included into three geological units: Badules Unit, Mesones Unit and Herrera Unit (Lotze, 1929; Carls, 1983; Gozalo and Liñán, 1988). Devonian outcrops are limited to five areas within the Herrera Unit (Fig. 1) which is built of Late Cambrian to Late Carboniferous rocks. From south to north these five areas are: Cabezos Altos and Anadón-Huesa Devonian outcrops, both in the Montalbán Anticline, Axial Depression of the Río Cámaras (ADRC), Nigüella and Tabuenca-Rodanas areas.

The ADRC is the largest and more important area for Early to Middle Devonian rocks and faunas. In addition, important Early Devonian faunas from the Nigüella area are relevant for palaeogeographical connections between the IC and the "Rhenohercynicum" (Carls and Valenzuela-Ríos, 1998). Middle Devonian strata are best represented in the ADRC and in the Montalbán Anticline. At the Montalbán Anticline, Late Devonian is partly known from disconnected sections; however, a continuous section of about 1,300 m of siliclastic rocks is documented in the Tabuenca area (Gozalo, 1994; Gozalo *et al.*, 2001).

The known thickness of Devonian strata in the IC is close to 4,000 m (Carls, 1988, 1999; Carls and Valenzuela-Ríos, 2002), but there is not a single outcrop, or larger area, to show a complete Devonian sequence. Numerous, short sections have been studied for high-resolution stratigraphy, subsequently they have been correlated to evaluate a complete stratigraphic column. This correlation partially benefits from the horizontal stability of the faunas and faunal horizons, especially in the Early Devonian. Most of the rock sequence is composed of siliciclastic rocks (shales, fine-grained sandstones and quartzites); carbonate rocks (shelly limestones and marls) are common, but thinner. This sequence was mainly deposited in a shallow marine, neritic environment. Most of the strata are fossiliferous; most common are the neritic turbidicolous brachiopods (Carls and Valenzuela-Ríos, 1998, 1999). In some cases, pelagic faunas from black shales and limestones provide a high potential for correlations between neritic and pelagic environments. The correlations have been based on conodonts, brachiopods, trilobites, dacryoconarids, ostracods and ammonoids; microichtyoliths are less commonly used.

The following formations can be recognized in ascending order in the ADRC and in the Montalbán Anticline: Luesma, Nogueras, Santa Cruz, Mariposas, Castellar, Ramblar, Loscos, Peña Negra, Molino, Monforte, Moyuela, Recutanda, Barreras, Salobral, Cabezo Agudo, Huesa, Bandera and Fuenpudrida Fms. (Carls and Valenzuela-Ríos, 2002). In the Tabuenca area the following continuous Upper Devonian succession is observed: Rodanas, Bolloncillos, Hoya and Huechaseca Fms. (Gozalo, 1994; Gozalo *et al.*, 2001). The succession from ADRC and Montalbán Anticline is not yet complete and there are some gaps of information between the Ramblar and Loscos formations, upper and lower limits of the Barreras Fm., Cabezo Agudo and Huesa, Huesa and Bandera. Between Ramblar and Loscos Fms. (late Emsian) there are 6 disjointed sections measuring at least 500 m that cannot be yet precisely integrated within the general stratigraphic scheme. In the Tabuenca area the Rodanas, Bolloncillos, Hoya and Huechaseca Fms. are dated as Frasnian and Famennian.

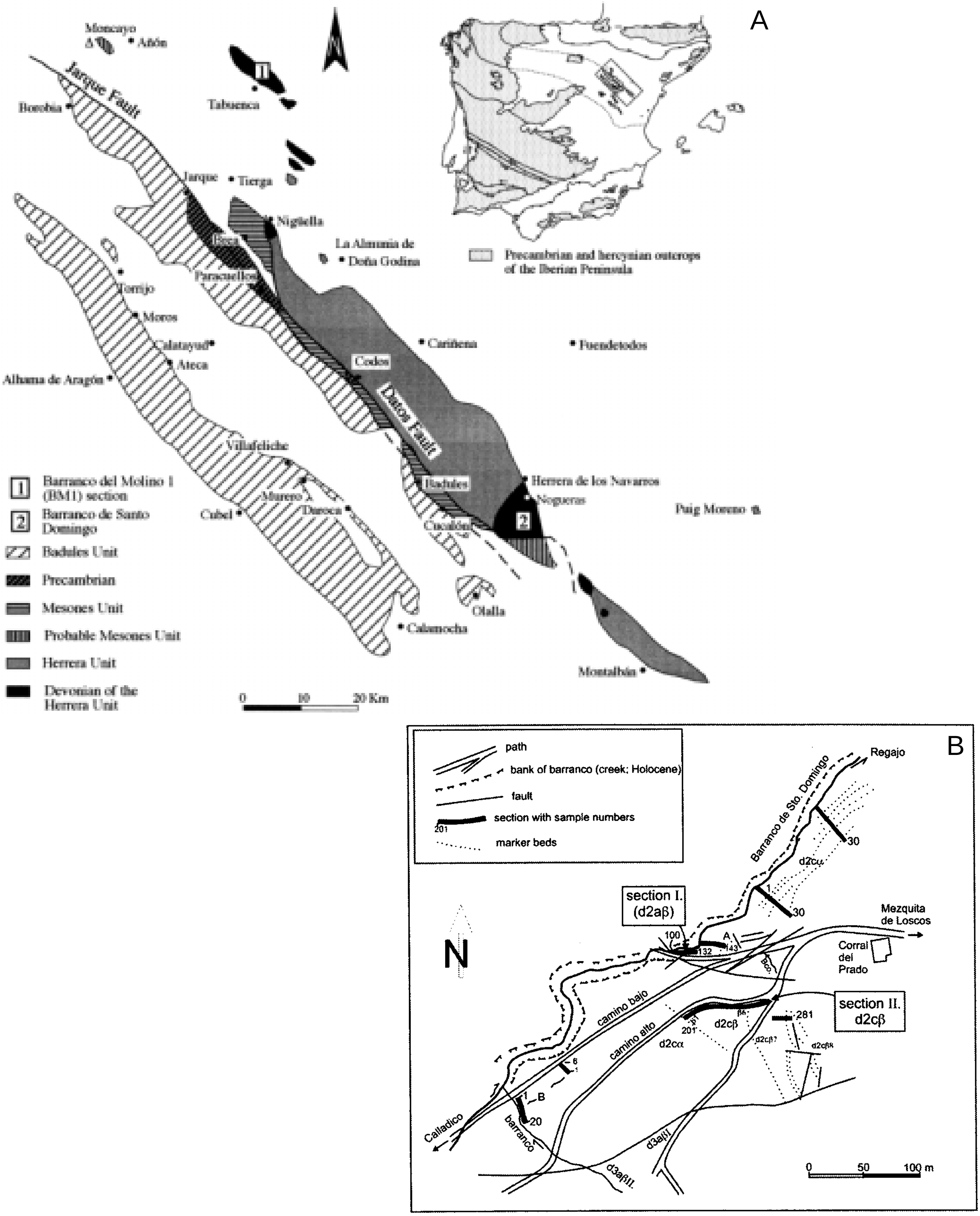


FIGURE 1–A: Precambrian and Palaeozoic Units of the Iberian Chains (based on Gozalo and Liñán, 1988). B: Geological sketch of South Barranco de Santo Domingo area showing partial sections and location of samples.

The Rodanas Fm. can partly be correlated with the Bandera Fm. A detailed discussion of the ostracod bearing formations can be found in the next chapter.

OSTRACODS OF THE NOGUERAS FM. (PRAGIAN, EARLY DEVONIAN)

The Nogueras Fm. (d2) is about 140 m thick, contains the Lochkovian/Pragian (L/P) boundary and it is composed of shelly limestones, marls, siltstones, and occasionally sand lenses (palaeochannels) or more continuous thin sand beds interbedded between shales. These sand beds, which mostly correspond to "lag-deposits", are horizontally persistent in the ADRC, and some of them are even recognized in Nigüella. The Lochkovian part of the Nogueras Fm. measures about 55 m, whereas the equivalents in the Guadarrama are about 200 m thick. There, a slight deepening allowed the invasion of pelagic elements like cosmopolitan conodonts (*Ancyrodelloides*, *Pedavis*; Carls, 1975) and oldest Nowakiids (*Homoctenowakia senex* and *H. bohemica*). These differences in taxa composition between both margins of the basin, was observed in the benthonic faunas as well; in Guadarrama more claricolous brachiopods appeared, while the turbidicolous brachiopod taxa remained in the IC (Carls and Valenzuela-Ríos, 1998).

The L/P boundary is traced in the IC at the top of a 35-50 cm thick sandy-mudstone dark-brown bed (bed A), where the index brachiopod *Vandercammenina sollei* appears. Lithostratigraphically, the L/P boundary corresponds with the local boundary d2bα/d2bβ.

In ADRC as well as in the Guadarrama, slightly above the L/P boundary, very shallow sediments were deposited in subtidal to emergent environments, their thicknesses are greater in the Guadarrama (230 m) compared with those in the ADRC (30 m). They correspond with the d2cα2-6 units (ADRC) and their equivalents MS12b-g (Guadarrama). One of the best proofs for the continuation of this succession into the l'Armorique Fm. (Armorica, northwestern France), even in fine details, have already been stated by Carls and Valenzuela-Ríos (1999).

Near the boundary of the d2cα/d2cβ in the ADRC and the MS12/MS13 in the Guadarrama, a rhythmothem *sensu* Carls (1988) started that even reached Armorica. This synchronous facies change, that took place just after the entry of the conodont *Icriodus simulator* and the beginning of the "*Spirifer*" *rousseaui* group, is linked to a transgressive pulse produced by a slight sea level rise (Carls, 1988; Valenzuela-Ríos and Carls, 1996). This moderate deepening is recorded as 30 m of alternating marls and shales in the upper part of the Nogueras Fm. that contains a brachiopod fauna, which is also found in Armorica and in north-western Africa. Because of the tentative conodont correlation this level is dated close to the *kitabicus* boundary (beginning of the Emsian, *sensu* SDS; within the classic Early Siegenian). Ostracods from the Nogueras Fm. have been studied from a composite section named Sur Barranco de Santo Domingo that is located about 2 km southwest of Mezquita de Loscos (Fig. 1B).

Ostracods of the section Sur Barranco de Santo Domingo (Fig. 2, Pls. 1-2)

The succession Sur Barranco de Santo Domingo is composed of several faulted sections, and consists of shales with intercalated limestones and marls and, in the lower parts, a few beds of sandstone. The age ranges from mid Lochkovian to Early Pragian in original sense (Nogueras Fm., units d2aβ5 to d2cβ8). Ostracods occur on bedding planes (unit d2aβ5), and can be washed from marls with H_2O_2 and NH_3 (submember d2cβ). In this paper only data from section I and II, which show materials from the units d2aβ and d2cβ respectively, are analysed (Fig. 1B).

About 50 ostracod taxa have been determined from the section (Fig. 2). Most of them have been cited in open nomenclature, only 16 of them can be identified specifically. The detailed description of the ostracods will be part of a Ph. D. thesis (Dojen, in prep.). Smooth Podocopina have not yet been studied.

The first records of ostracods from this section (see Fig. 1B) are of mid Lochkovian age with *Zygobeyrichia* sp. on bedding planes of silty limestones (unit d2aβ5; section I, beds 117–119). This is the oldest known occurrence of beyrichiacean ostracods besides those of Groos-Uffenorde (1983: 344) in Gondwana. The presence of these relatively large benthic ostracods refute the arguments of Cocks and Fortey (1982) and McKerrow (1994) that beyrichiid ostracods could not reach Gondwana before the Emsian because of the Rheic ocean (see also Dojen, this vol.) The accompanying fauna consists of pelecypods (e.g. *Nuculites*, *Grammysia*), (par)authochthonous centronellid brachiopods respectively *Iridistrophia* in mass populations and fish remains. Moreover, reworking of phosphoritic nodules and some channeling prove the shallow neritic environment of the habitat.

Additionally, a few poorly preserved ostracod taxa (*Zygobeyrichia* sp., *Poloniella* sp., *Cryptophyllus* sp., *Bollia* sp.) have been found in conodont samples from etched limestones (units d2bα1 and d2bα2, unit d3aβ1).

x: 0 - 10 specimens
xx: 10 - 50 specimens
xxx: 50 - 100 specimens
xxxx: > 100 specimens

d2cβ1	d2cβ2		d2cβ3	d2cβ4	d2cβ5		d2cβ6	d2cβ7	d2cβ8	unit
×	×	×	×	×	×	×	×	×	×	sample positions
										taxa
		x		x		xx	xx	x	x	"*Aparchites*" ? sp. 1
			x			x	x		x	"*Aparchites*" sp. sp.
								x	x	*Ctenoloculina* cf. *cicatricosa*
							x	x		*Ctenoloculina longivelum*
					x		x	x		*Ctenoloculina cicatricosa* vel *longivelum*
							x	x		*Tetrasacculus curtus*
							xx			*Bollia lavibadia*
xx		x	xx	xx	xx	xx	xxxx	xxx	x	*Bollia* aff. *ungula*
				x	xx	xx	xxxx	xxx	x	*Bollia* sp. B
							xx	xx		*Bollia* sp., cf. *Bollia* sp. B
x		x	x	x	xx			xx	xx	*Bollia* ? sp. 3
x		x	x	x	xx	xx	xx	xxx	x	*Bollia* ? sp. 4
							x	xx	x	*Ulrichia (U.)* cf. *elegans*
							x	xx		*Ulrichia (S.)* cf. *fragilis* sensu ZAGORA
			x		x			x		*U. (S.)* cf. *fragilis* sensu B.& G.
				x	x	x				*Torella* ? n.sp. 7
				x				xx		*Placentella* aff. *heraultiana*
								x		*Placentella* ? n.sp. 8
						x		x		*Berdanella* sp. K
						x		x		*Refrathella* aff. *bissousensis*
						x		xx		Palaeocopida gen. et sp. indet 2
		x				x		x	x	Palaeocopida gen. et sp. indet 5
				x						*Punctoprimitia africana*
	x	xx	x	x			xx	xx	x	*Punctoprimitia europaea*
		x					x	x		*Punctoprimitia* aff. *europaea*
				x			x	xx	xx	*Punctoprimitia* n.sp. 13
							x		x	*Birdsallella* sp.
		x		x				x		*Sulcella (S.) kloedenellides*
x				xx	x	xx	xx	x	xx	*Bythocyproidea* ? *polaris*
				xx	x		xx	xx	x	*Punctomosea* cf. sp. 29
		x						x		*Polyzygia beckmanni antecendens*
			x				x	xx	xx	*Polyzygia grekoffi*
x	x	xx	x	x	xx		xx	xxxx		*Polyzygia kroemmelbeini*
x	x	x	x	xx	x	x	xxxx	xxx	x	*Polyzygia normannica*
x		xx						x		*Polyzygia vinea*
		x	x	x	x		x	x	x	*Jenningsina thuringica*
		x			xx		xx	xx	xx	*Jenningsina* aff. sp. 28
x	x	xx	xx	xxx		xx	xx	xx	x	*Jenningsina* ? n.sp. 14
				x			x	x		*Ovatoquasillites* ? sp.
				x		x				Thlipsuridae, gen. et sp. indet 2
				x		x				Thlipsuridae, gen. et sp. indet 3
x	x	x	xx	xx	xx	x	xx	xx	xx	*Ponderodictya aggeriana*
x	x		x	xx		x	x		x	*Ponderodictya* cf. *aggeriana*
x	x	x	x	x	xx		xx	xx		*Ponderodictya jeanlefevrei*
x			x		x					*Ponderodictya inventeplicata*
x			xx	x	xx		xx	x		*Leptoprimitia balbiniensis*
					x		x	x		*Leptoprimitia* cf. *ornata*
							x	xx		*Zeuschneria* n.sp. 19
x		x		x			x	x		*Eridoconcha* sp. 23
x		xx	x	x			xx	x		*Cryptophyllus* ? sp. sensu WEYANT

FIGURE 2–Distribution of some ostracod taxa from Sur Barranco de Santo Domingo section, Early Devonian, Nogueras Fm., submember d2cβ.

Ten samples from the marly intercalations of the submember d2cβ (section II; Early Pragian in the original sense; approximately *pireneae* Conodont Zone) bear highly diverse neritic ostracod faunas. They consist mainly of thick shelled and heavyly-sculptured palaeocopids and of thin shelled and fine-sculptured metacopids, whereas kloedenellid and ropolonellid ostracods and also Eridostraca occur less frequently. This 40 m thick submember is composed of lutites deposited in a low energy environment and marls. The macrofauna is the "*Spirifer*" *rousseaui* fauna with various brachiopods (often *in situ*), trilobites (Homalonotinae, Asteropyginae), branched and bulbous Favositidae, solitary Rugosa, bryozoans, crinoids and orthoconic cephalopods. The biotopes of the neritic bottom level environment were little below the wave base, at depths about 20 m, usually without reworking, with low contents of suspended matter and therefore in euphotic conditions.

Upper Devonian ostracods from Tabuenca (Fig. 3, Pls. 3-4)

The Upper Devonian of Tabuenca (Fig. 1A) comprises a thick siliciclastic sequence of more than 1,300 m. Ostracods are abundant in the Rodanas and Boloncillos formations, and are scarce in the lower and upper parts of the Hoya Fm.

The main outcrops at Tabuenca are situated on the local road between Tabuenca and Ainzón. There, the section Barranco del Molino 1 (BM1) has been studied in detail by Gozalo (1986, 1994). 17 fossiliferous levels have been examined, including some with very abundant ostracods. Additionally six sections have been studied in the same region (Gozalo, 1994).

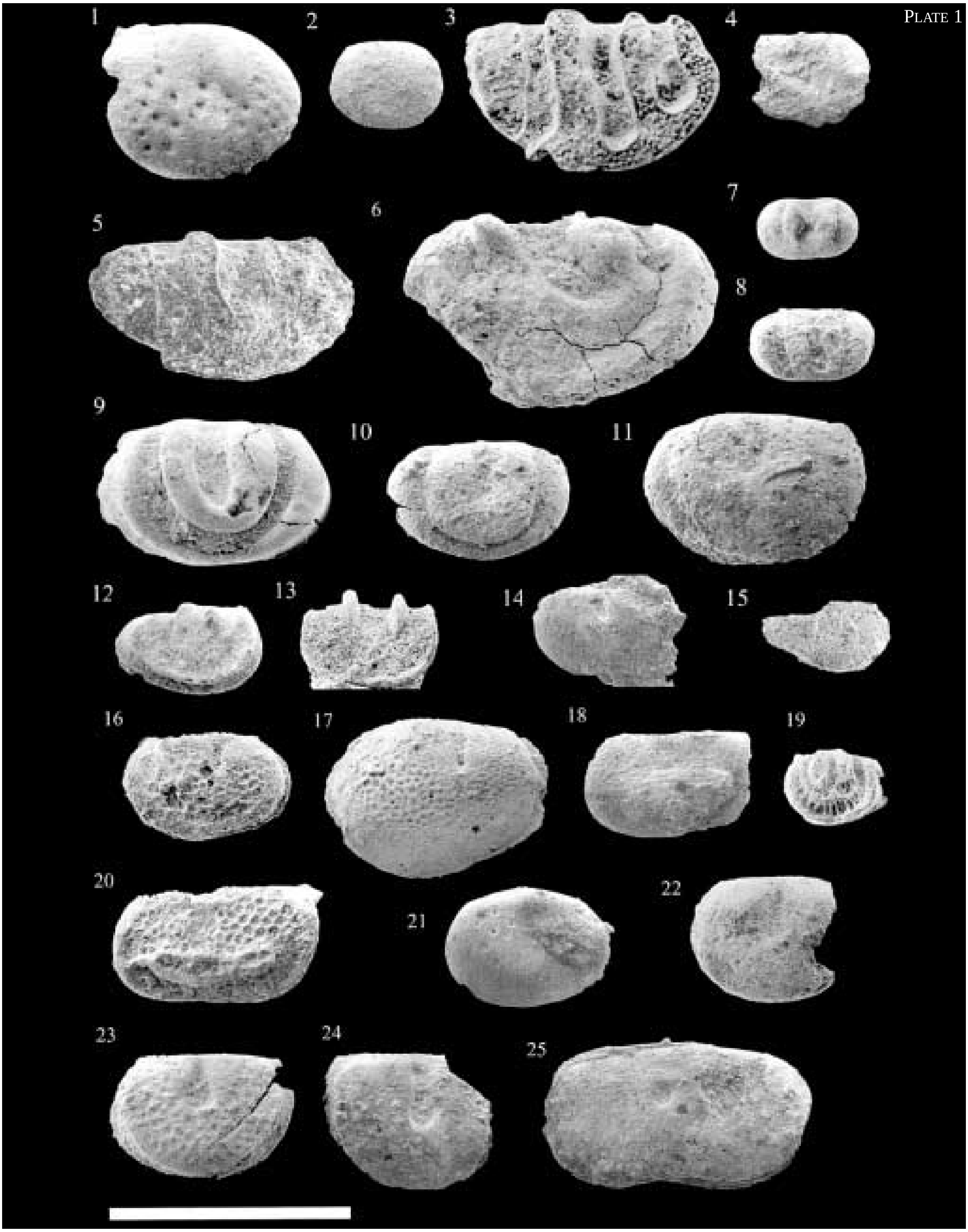
The fossils from shaly levels are frequently preserved as moulds. For our study and for demonstration purposes (e.g. plates 3 and 4) latex or silicone casts (see Siveter, 1982) have been used.

The **Rodanas Fm.** measures 450 m and it is subdivided into two parts. The lower part consists of 300 m of a siliciclastic alternation of predominant quartzitic sandstones; individual beds are from 0.5 to 3 m thick. The upper surface of the quartzitic sandstones beds commonly shows an irregular relief, bioturbation and a cover of a ferruginous patina; they are interpreted as hard ground. Shaly intercalations are scarce and very thin (decimetre thicknesses and only occasionally metres). The base of the Rodanas Fm. is assigned to the Frasnian *torleyi-cicatricosa* interval by ostracods (Gozalo and Sánchez de Posada, 1986; Gozalo, 1994) and ammonoids (*Schindewolfoceras* cf. *chemungense, Aulatornoceras (Truyolsoceras)* sp. A and *Tornoceras uniangulare* ssp., *sensu* Montesinos and Gozalo, 1987). These faunas hint at a deep sublittoral or even

→

PLATE 1–Early Devonian ostracodos from Sur Barranco de Santo Domingo section. All specimens in calcareous preservation and x50. *1, "Aparchites"* ? sp. 1, unit d2cβ4, 7 m below top of unit d2cβ5; left valve; length: 0.85 mm. *2, "Aparchites"* sp., unit d2cβ, + 7.25 m; left valve; length: 0.53 mm. *3, Ctenoloculina* cf. *cicatricosa* (Warthin, 1934), unit d2cβ7, + 0.6 – 0.8 m; heteromorph right valve; length: 1.10 mm. *4, Tetrasacculus curtus* K. Zagora, 1968, unit d2cβ7, + 0.6 – 0.8 m; heteromorph left valve; length: 0.552 mm. *5, Ctenoloculina longivelum* K. Zagora, 1968; unit d2cβ7, + 0.6 – 0.8 m; heteromorph right valve; length: 1.10 mm. *6, Bollia lavibadia* Becker, 1996; unit d2cβ6, + 0.3 m; right valve; length: 1.33 mm. *7, Bollia* ? sp. 3; unit d2cβ7, +0.6 – 0.8 m; right valve; length: 0.42 mm. *8, Bollia* ? sp. 4; unit d2cβ6, + 0.3 m; right valve; length: 0.56 mm. *9, Bollia* aff. *ungula* sensu Weyant, 1976; unit d2cβ1; right valve; length: 0.95 mm. *10, Bollia* sp. B sensu Zagora, 1968; unit d2cβ6, + 0.3 m; left valve; length: 0.77 mm. *11, Bollia* sp., cf. *Bollia* sp. B sensu Zagora, 1968; unit d2cβ6, + 0.3 m; left valve; length: 0.925 mm. *12, Ulrichia (Subulrichia)* cf. *fragilis* sensu Becker and Groos-Uffenorde, 1982; unit d2cβ3, +3 m; right valve; length: 0.625 mm. *13, Ulrichia (Ulrichia)* cf. *elegans* Abushik, 1968; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.575 mm. *14,* Palaeocopida, gen. et sp. indet. 2; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.55 mm. *15, Ulrichia (Subulrichia)* cf. *fragilis* sensu K. Zagora, 1968; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.51 mm. *16, Placentella* aff. *heraultiana* Groos-Uffenorde, 1976; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.62 mm. *17, Placentella* ? n.sp. 8; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.92 mm. *18, Berdanella* sp. K; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.63 mm. *19, Torella* ? n.sp. 7; unit d2cβ4, 7 m below top of unit d2cβ5; left valve; length: 0.45 mm. *20, Refrathella* aff. *bissousensis* Groos-Uffenorde, 1979; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.83 mm. *21,* Palaeocopida, gen. et sp. indet. 5; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.69 mm. *22, Punctoprimitia africana* Becker, 1998; unit d2cβ4, 7 m below top of unit d2cβ5 left valve; length: 0.58 mm. *23, Punctoprimitia europaea* Weyant, 1967; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.765 mm. *24, Punctoprimitia* aff. *europaea* Weyant, 1967; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.70 mm. *25, Sulcella (S.) kloedenellides* Adamczak, 1968; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 1.12 mm.

PLATE 1



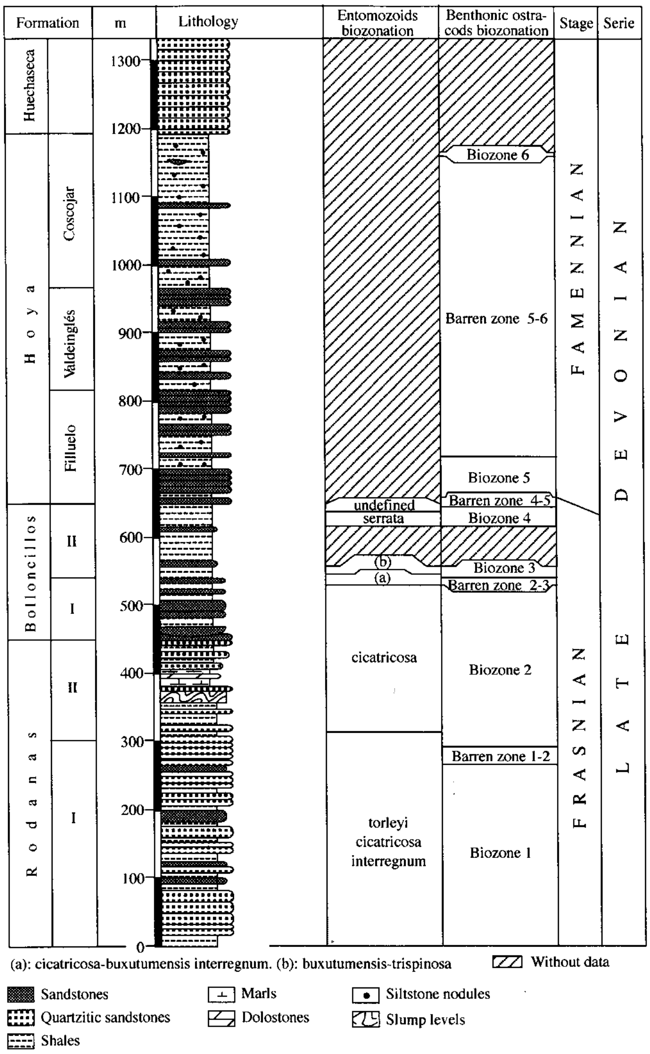


FIGURE 3–Late Devonian composite section of Tabuenca, with the benthonic and entomozoacean ostracod zonations (Gozalo, 1994; Gozalo *et al.*, 2001).

circalittoral environment, besides very important siliciclastic sedimentation, indicative of shallower environments. Faunas from the highest part indicate sublittoral environments. Probably, the lowest shale levels belong to another formation, but they are only known from this locality.

The Ostracod species from this lower part are *Falsipollex tabuencensis*, *Parabolbinella* cf. *postaculeata*, *Hollinella (Keslingella)* cf. sp. D, *Skalyella* sp., ?*H. (K.)* aff. *samarensis*, *Rozhdestvenkayites sencielensis casier*, *Amphissistes* cf. *parvulus*, *Sinessites*? *micronodus*, *Healdia* sp., *Bythocyproidea weyanti*, *Polyzygia neodevonica aragonensis*, *Svantovites spinosus*, *Microcheilinella postfecunda*, *Tricornina (Ovornina)* sp., *Franklinella (F.) calcarata*, and *Cryptophyllus* cf. *materni*.

The upper part consists of 150 m of a detrital alternation. It differs from the lower part in the higher content of lutites representing more than 50% of the thickness. Also, some calcareous levels appear in the upper part. Quartzitic sandstones are of the same kind than in the lower part, but thinner (0.3-1.5 m thick). In the upper half carbonate sediments occur (dolomite and marls). Between 55 and 75 m above the base of this upper part, several slumps have been observed. Numerous ostracods, tentaculitids, trilobites, bivalves, conodonts and Machaeridia have been found (Gozalo, 1994; Gozalo *et al.*, 2001).

The Ostracod species from the upper part of Rodanas Fm. in BM1 are *Parabolbinella lethiersi*, *Hollinella (Keslingella) lignani*, *H. (K.)* aff. *praecusor*, *H. (K.)* cf. sp. D, *Rozhdestvenkayites sencielensis casieri*, *Amphissistes* cf. *parvulus*, *A.* aff. *remesi*, *Sinessites*? *micronodus*, *Bythocyproidea weyanti*,

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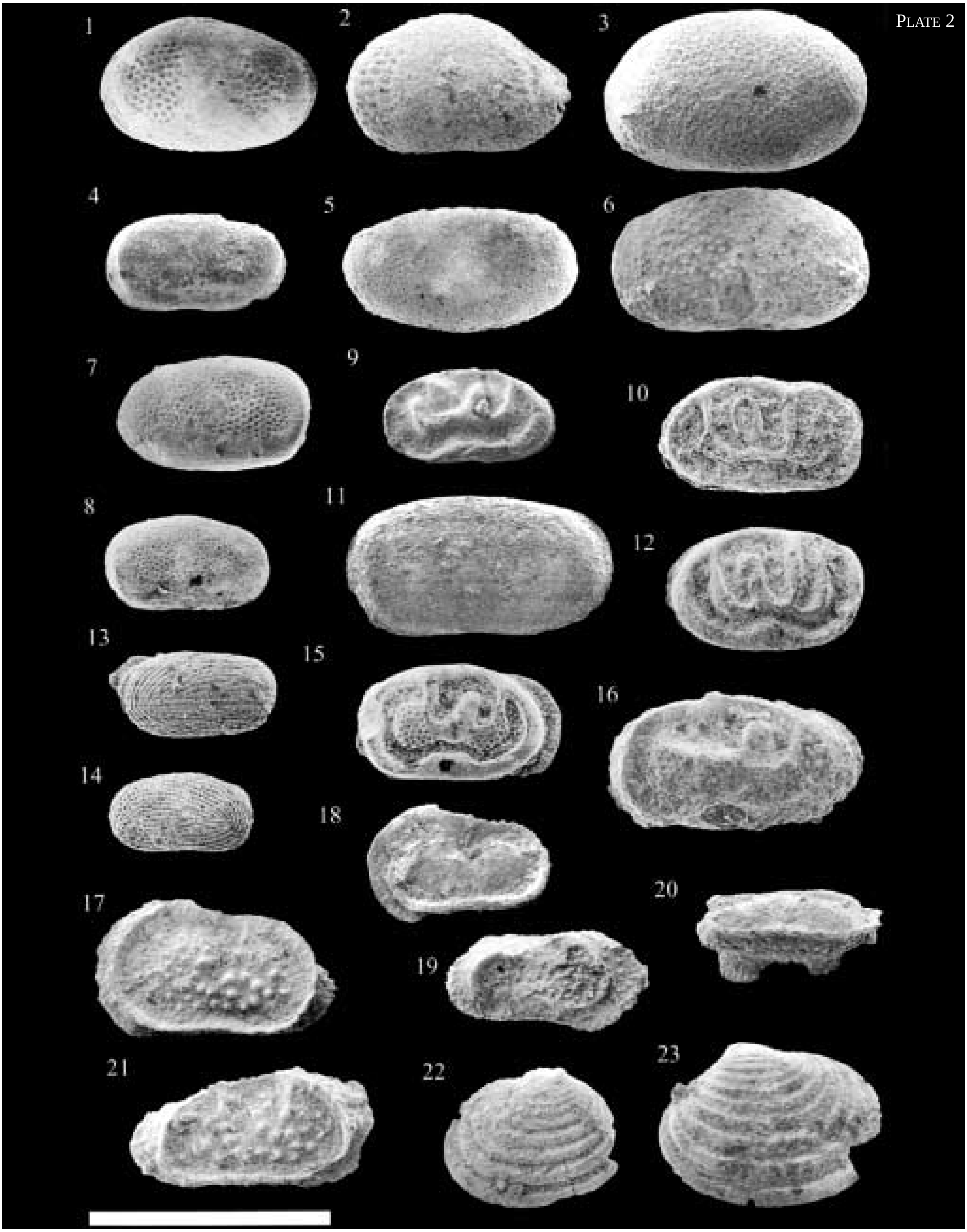
PLATE 2–Early Devonian ostracodos from Sur Barranco de Santo Domingo section. All specimens in calcareous preservation and x50. *1, Bythocyproidea*? *polaris* (Gürich, 1896); unit d2cβ4, 7 m below top of unit d2cβ5; right valve; length: 0.91 mm. *2, Punctomosea* sp. 29 sensu Groos-Uffenorde, 1979; unit d2cβ6, + 0.3 m; right valve; length: 0.92 mm. *3, Ponderodictya aggeriana* Groos, 1969; unit d2cβ76, + 0.3 m; right valve; length: 1.10 mm. *4,* Thlipsuridae gen et sp. indet 2; unit d2cβ5, midpoint of unit; right valve; length: 0.75 mm. *5, Ovatoquassillites* ? sp.; unit d2cβ5, 7 m below top of unit d2cβ5; left valve; length: 0.96 mm. *6, Ponderodictya inventeplicata* Becker, 1989; unit d2cβ3, + 3.0 m; right valve; length: 1.08 mm. *7, Jenningsina* ? n.sp. 14; unit d2cβ5, 7 m below top of unit d2cβ5; left valve; length: 0.8 mm. *8, Jenningsina* ? n.sp. 14; unit d2cβ5, 7 m below top of unit d2cβ5; right valve; length: 0.69 mm. *9, Polyzygia kroemmelbeini* LeFèvre and Weyant, 1966; unit d2cβ2, 7.25 m above base of submember; right valve; length: 0.72 mm. *10, Polyzygia beckmanni antecedens* K. Zagora, 1968; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.82 mm. *11,* Thlipsuridae, gen et sp. indet 3; unit d2cβ5, midpoint of unit; right valve; length: 1.10 mm. *12, Polyzygia grekoffi* Weyant, 1980; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 0.82 mm. *13, Jenningsina* aff. sp. 28 sensu Groos-Uffenorde, 1979; unit d2cβ7, + 0.6 – 0.8 m; right valve; length: 0.59 mm. *14, Jenningsina thuringica* K. Zagora, 1968; base of unit d2cβ5; left valve; length: 0.675 mm. *15, Polyzygia normannica* Weyant, 1967; unit d2cβ5, 7 m below top of unit d2cβ5; right valve; length: 0.86 mm. *16, Polyzygia vinea* Michel, 1972; unit d2cβ6, + 0.3 m; right valve; length: 1.05 mm. *17, Leptoprimitia* cf. *ornata* K. Zagora, 1968; unit d2cβ7, + 0.6 – 0.8 m; left valve; length: 1.02 mm. *18-20, Zeuschneria* n.sp. 19; unit d2cβ7, + 0.6 – 0.8 m; *18,* left valve; length: 0.74 mm; *19,* right valve; length: 0.82 mm; *20,* dorsal view. *21, Leptoprimitia balbiniensis* Weyant, 1967; unit d2cβ6, + 0.3 m; right valve; length: 1.05 mm. *22, Eridoconcha* sp. 23; unit d2cβ1, midpoint of unit; right valve; length: 0.68 mm. *23, Cryptophyllus* ? sp. sensu Weyant, 1976; unit d2cβ1, midpoint of unit; left valve; length: 0.92 mm.

PLATE 2



Favulella aff. *spissa*, *Polyzygia neodevonica aragonensis, Quasillites ovetensium, Ponderodictya blessi, Microcheilinella postfecunda, Nehdentomis tenera, N. pseudorichterina, Waldeckella (Waldeckella) trappi, Franklinella (F.) calcarata, F. (Arnoldella) trispinosa*, and *Cryptophyllus* cf. *materni*. Furthermore, we have found the following species in the nearest section Barranco del Filluelo 1 (BF1: Gozalo, 1994): *Roundyella* aff. *pokornyi*, *Favulella spissa*, *Polyzygia neodevonica neodevonica*, *Craspedographylus*? sp., *Svantovites inops, S. magnei* and *Waldeckella (Rabienella) cicatricosa*.

Based mainly on ostracods, the lower part is also assigned to the *torleyi-cicatricosa* Interregnum and the top of this part to the *cicatricosa* Zone. Faunal assemblages indicate always a sublittoral environment with a slow deepening. The upper part represents the unique carbonate episode of the whole sequence.

The **Bolloncillos Fm.** consists of 200 m of detritic rocks and has been subdivided into two parts. The lower part is 90 m thick and consists of an alternance of coarse to fine grain sandstones and lutites, being the former predominant. Channel structures showing cross-bedding appear at the basal part. Sandstone beds are 0.5-2 m thick. Lutitic levels increase their thickness upward from 0.5 to 2 m; they consist of an alternance of fine sandstone and lutites, being the latter predominant. A rich ostracod fauna, together with some conodonts (*Palmatolepis gigas*, *Ancyrognathus* cf. *ancyrognathoideus* and *Ancyrodella* sp., *sensu* Valenzuela-Ríos *et al.*, 2002), trilobites, tentaculitids (*Styliolina* spp. and *Homoctenus* spp.), and ammonoids indicate that the lower beds belong to the *cicatricosa* Zone and the upper ones to the *cicatricosa-buxutumensis* Interregnum (Gozalo, 1994). The beginning of this formation represents a shallowing, that was followed by a deepening, but environments keep always within the sublittoral.

The ostracod species are *Parabolbinella lethiersi*, *Hollinella (Keslingella) lignani*, *Rozhdestvenkayites sencielensis casieri*, *Amphissistes* cf. *parvulus*, *Sinessites*? *micronodus*, *Bythocyproidea weyanti*, *Quasillites ovetensium*, *Ponderodictya blessi*, *Microcheilinella postfecunda*, *Nehdentomis tenera*, *N. pseudorichterina*, *Richterina (Volkina) zimmermanni*, *Posadaella alcaldei*, *Waldeckella (Waldeckella) trappi*, *Waldeckella (Rabienella) cicatricosa*, *Franklinella (F.) calcarata*, *F. (Arnoldella) trispinosa* and *Cryptophyllus* cf. *materni*.

The upper part is 110 m thick. The amount of lutites increases and metric levels of sandstones disappear. The top beds are exclusively lutites. Rich ostracod faunas, tentaculitids and conodonts indicate an age between the *cicatricosa-buxutumensis* Interregnum and above the *serrata* Zone. Topmost levels did not yield fauna and they can either belong to the Frasnian or to the Fammenian (Montesinos *et al.*, 1990; Gozalo, 1994; Valenzuela-Ríos *et al.*, 2002). The presence of organic matter together with *Chondrites*? would indicate a poorly oxygenated biotop.

The ostracod taxa in the lower part of this 110 m thick sequence are *Parabolbinella lethiersi*, *Hollinella (Keslingella)* aff. *radiata*, *Adelphobolbina* sp., *Rozhdestvenskayites sencielensis casieri*, *Kummerowia blessi*, *A.* cf. *cantabricus*, *A.* aff. *cononodus*, *Amphissites* cf. *parvulus*, A. aff. *remesi*, *A. saalfeldensis valdeonensis*, *A. inflatus*, *A. (Ectodemites)* sp., *Bythocyproidea weyanti*, *Favulella lecomptei brevis*, *Jenningsina (Aragonella) carlsi*, *Craspedographylus*? sp., *Microcheilinella postfecunda*, *Nehdentomis tenera*, *N. buxutumensis*, *Richterina (Volkina) zimmermanni*, *Waldeckella (Waldeckella) trappi*, *Franklinella (F.) calcarata*, *F. (Arnoldella) trispinosa*, and *Cryptophyllus* cf. *materni*. Ostracod taxa from the upper part are *Parabolbinella*? cf. *vomis*, *Kullmannissites* aff.

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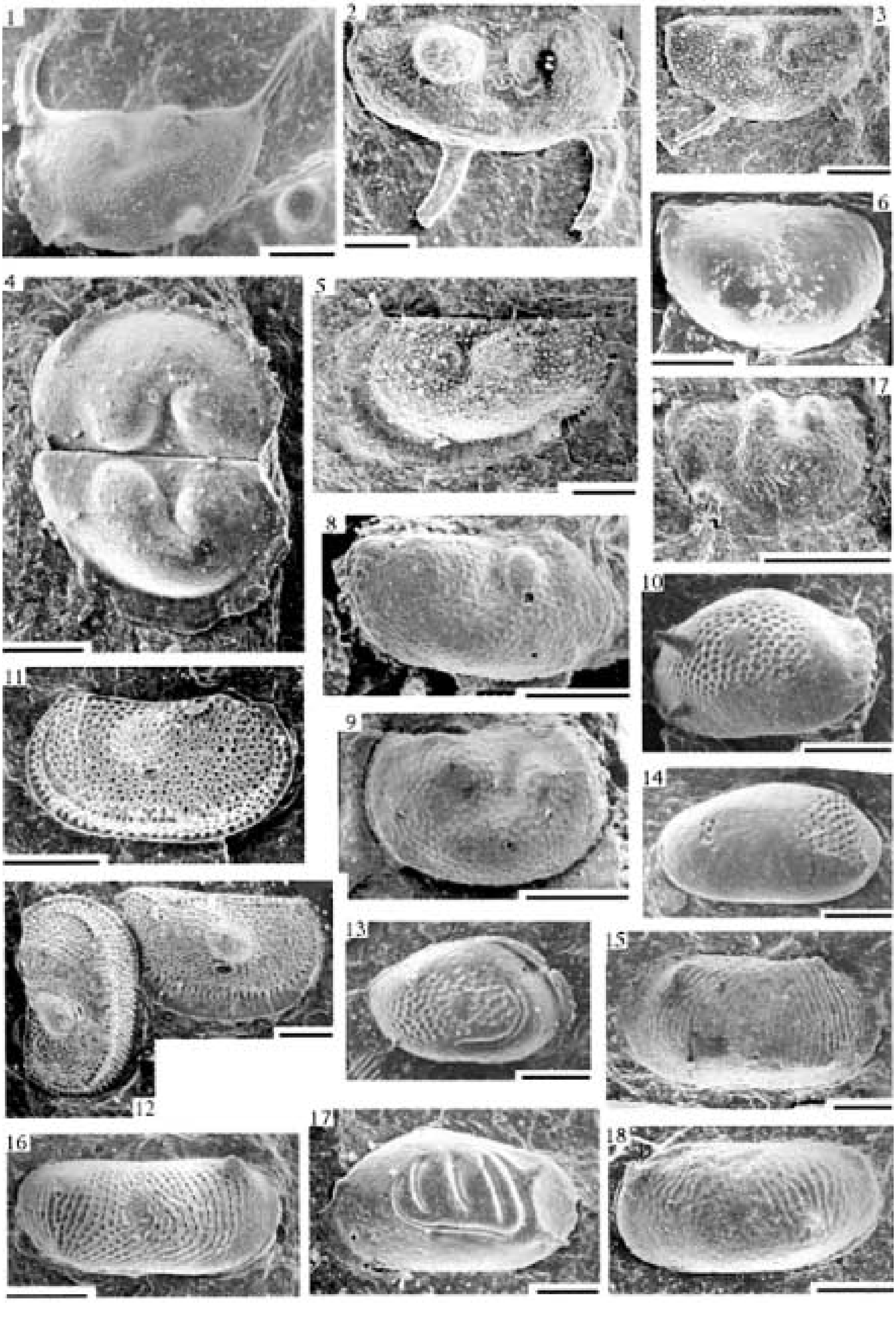
PLATE 3–Late Devonian ostracodos from Tabuenca area. All specimens are silicone casts of external moulds. Scale bars 0.25 mm. *1-3, Parabolbinella lethiersi* Gozalo, 1994; Bolloncillos Fm.; *1,* heteromorph left valve; *2,* tecnomorph right valve; *3,* juvenil right valve. *4, Hollinella (Keslingella) lignani* Gozalo, 1994; Bolloncillos Fm., heteromorph left and right valves. *5, Hollinella (Keslingella)* aff. *radiata* (Jones & Kirkby, 1886); Bolloncillos Fm., tecnomorph left valve. *6, Coryellina* sp.; Hoya Fm., tecnomorph right valve. *7, Tmemolophus sequeirosi* Gozalo, 1994; Hoya Fm. *8-9, Knoxites perplexa vini* Gozalo, 1994; Hoya Fm.; *8,* heteromorph right valve; *9,* tecnomorph right valve. *10, Ponderodyctia blessi* Gozalo, 1994; Rodanas Fm.; right valve. *11, Amphissites saalfeldensis valdeonensis* Becker, 1981; Bolloncillos Fm.; left valve. *12, Amphissites inflatus* Gozalo, 1994; Bolloncillos Fm.; left and right valves. *13, Favulella lecomptei brevis* Gozalo, 1994; Bolloncillos Fm.; right valve. *14, Bythocyproidea weyanti* (Becker, 1971); Rodanas Fm.; left valve. *15, Svantovites spinosus* Gozalo, 1994; Rodanas Fm.; left valve. *16, Jenningsina (Aragonesites) carlsi* Gozalo, 1994; Bolloncillos Fm.; right valve. *17, Polyzygia neodevonica aragonensis* Gozalo & Sánchez de Posada, 1986; Rodanas Fm.; left valve. *18, Quasillites ovetensium* Gozalo, 1994; Rodanas Fm.; left valve.

PLATE 3



kullmanni, *Nehdentomis tenera*, *N. pseudorichterina*, *Richterina (Volkina) zimmermanni*, *Entomoprimitia (E.) inconstans*, *Waldeckella (Waldeckella) trappi*, *Waldeckella (Rabienella) serrata*, and *Franklinella (F.) calcarata*.

The **Hoya Fm.** is 545 m thick and it has been subdivided into three members, the Filluelo Mb., the Valdeinglés Mb. and the Coscojar Mb.

The Filluelo Mb. consist of 165 m of a detritical alternance. Coarse to middle grain sandstone with some microconglomerates are predominant. Beds are 1-3 m thick but without large lateral continuity and with irregular surfaces. Lutitic levels are mostly silty, have thickness around 1 m and are more abundant and thicker to the upper part of the member. Most of the beds are barren, and fauna is restricted to the lower 70 m where ostracods, conodonts, bivalves, brachiopods and specially the ammonoid *Falcitornoceras* point to a Fammenian age (Montesinos *et al.*, 1990). These sediments were deposited in restricted sublittoral environments (Gozalo *et al.*, 2001).

The very scarce famennian ostracods taxa are: *Hollinella (Keslingella)* sp., *Coryellina* sp., *Tmemolophus sequeirosi*, *Knoxites perplexa vini* and *Glyptopleura?* sp.

The Valdeinglés Mb. is 160 m thick and consists of an alternation of sandstone and lutite. Its limit with the underlain Filluelo Mb. is based on the increase of lutitic material and in a change of colour (white to green and brown colours). Sandstones are coarse to medium grainsize; there are scattered conglomerate levels with pebbles of 2-4 mm. Beds have a thickness between 0.5-1.5 m. On some beds big medusoids with radial or flat ornamentation have been recorded (Gozalo *et al.*, 2001). Clay rocks are the predominant lutites. Bed thickness increases to the upper part. In these levels, silty nodules are common.

The Coscojar Mb. consists of 220 m of lutites. The base is drawn by the disappearance of sandstone beds thicker than 1 m. Lutites are mostly clay beds with some fine-grained sandstone interbedded (from centimetre levels to scattered decimetre levels). Silt nodules are common and can reach up to 10 cm in diameter. A fossiliferous horizon at the top of the member contained a few ostracods, bivalves, and one trilobite, a *Trimerocephalus* sp. cranidium, that indicates a Fammenian age, probably upper Fammenian.

The ostracod taxa found in the top of the Hoya Fm. are: Hollinellidae sp. indet., Primitiopsidae sp. indet. and *Marginohealdia* cf. *marginata*.

The **Huechaseca Fm.** consists of at least 140 m of middle to fine grained, well-sorted quartzitic sandstones. This formation is unfossiliferous, but because of continuity with the underlain formation an upper Fammenian age can be inferred. The top of this formation is not known.

The Frasnian Biostratigraphy and the Frasnian/Fammenian boundary in Tabuenca

The ostracod taxa diversity allows us to establish two different ostracod zonations (see Gozalo, 1994), based on benthonic and entomozoacean ostracods. The zonation by benthonic ostracodes has been developed for Frasnian and Fammenian rocks, but it has only a local application.

In contrast, Entomozoacean ostracods have only been recorded in Frasnian rocks from Tabuenca area, where Gozalo (1994) established five biozones (Fig. 4). This biozonation permits us an accurate correlation with the European and Chinese entomozoacean zonations (see Groos-Uffenorde and Rabien, 1996); the concurring conodonts enable a correlation with the conodont standard zonation (Valenzuela-Ríos *et al.*, 2002).

The Frasnian/Fammenian boundary was identified in two sections: Barranco del Molino 1 (BM1) and Collado de la Hoya (CH). The boundary lies close to

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PLATE 4–Late Devonian ostracodos from Tabuenca area. All specimens are silicone casts of external moulds. Scale bars 0.50 mm, except 1, 10 and 13 scale bars 0.25 mm. *1, Richterina (Volkina) zimmermanni* (Volk, 1939); Bolloncillos Fm.; left valve. *2, Entomoprimitia (Entomoprimitia) inconstans* Müller-Steffen, 1964; Bolloncillos Fm.; right valve. 3, *Nehdentomis tenera* (Gürich, 1896); Bolloncillos Fm.; right valve. *4, Nehdentomis pseudorichterina* (Matern, 1929); Bolloncillos Fm.; right valve. *5, Posadaella alcaldei* Gozalo, 1994; Bolloncillos Fm.; left valve. *6, Nehdentomis buxutumensis* Casier, 1977; Bolloncillos Fm.; left valve. *7, Waldeckella (Rabienella) serrata* (Gozalo, 1994); Bolloncillos Fm.; right valve. *8-9, Franklinella (Franklinella) calcarata* (Rhein. Richter, 1856); Bolloncillos Fm.; *8,* right valve with original relief; *9*, flatened right valve. *10, Waldeckella (Rabienella) cicatricosa* (Matern, 1929); Bolloncillos Fm.; right valve. *11-12, Franklinella (Arnoldella) trispinosa* (Gozalo, 1994); Bolloncillos Fm.; *11*, tecnomorph right valve; *12*, heteromorph right valve. *13, Cryptophyllus* cf. *materni* (Bassler & Kellet, 1934) *sensu* Becker, 1971; Bolloncillos Fm.; right and left valves.

PLATE 4

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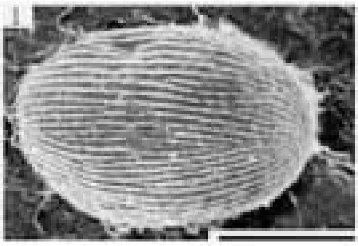

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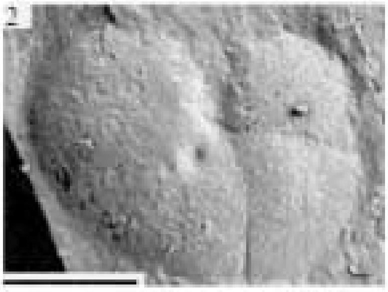

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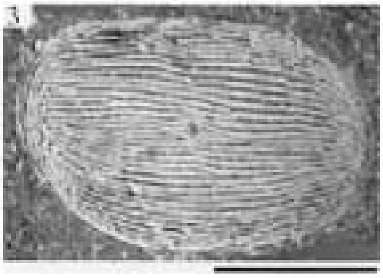

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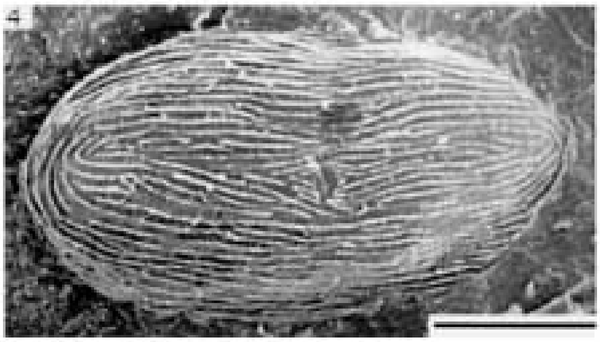

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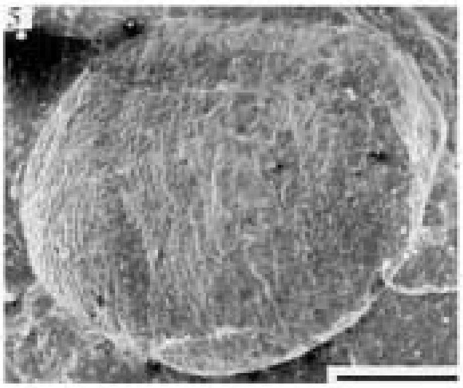

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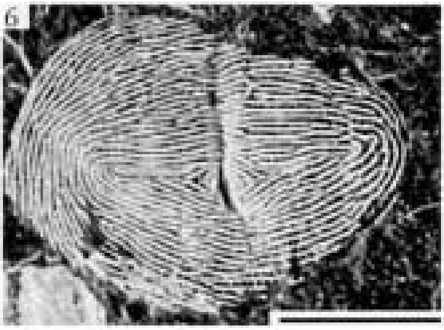

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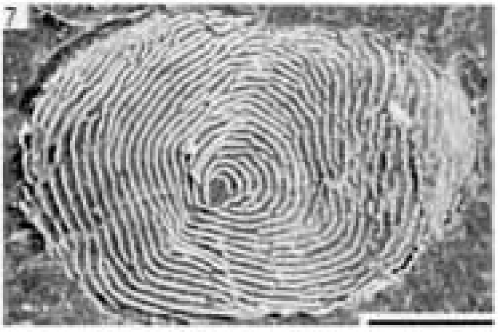

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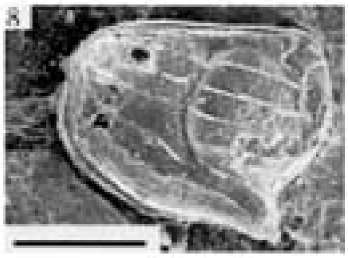

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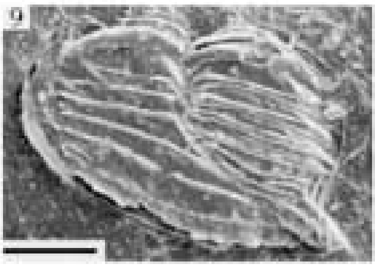

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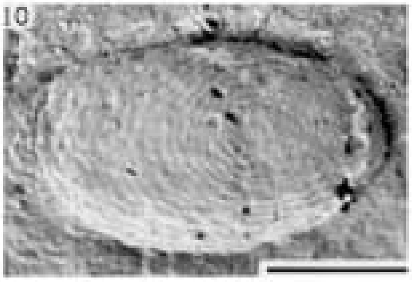

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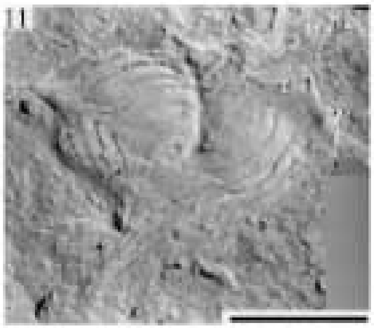

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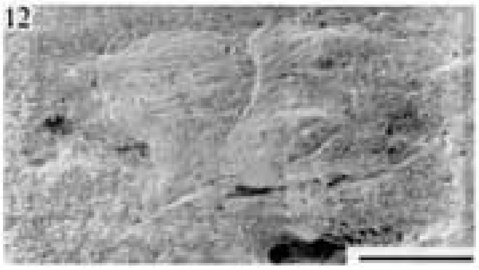

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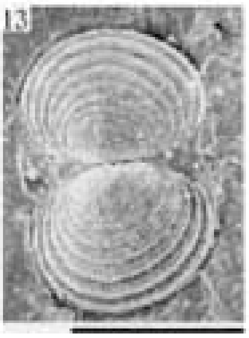

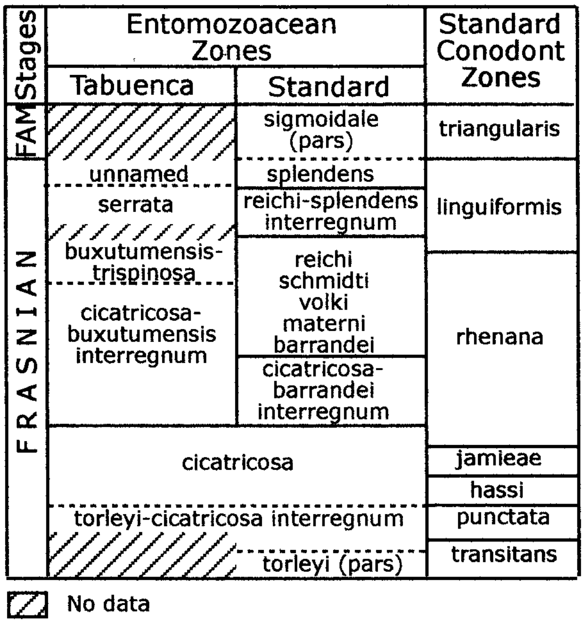

FIGURE 4–Correlation chart of entomozoacean (Tabuenca and standard) and conodont zonation within the Frasnian (modified from Gozalo, 1994, and Groos-Uffenorde and Rabien, 1996).

the lithostratigraphical limit between the upper parts of the Bolloncillos Fm.; and the lower parts of the Hoya Fm. It is marked by the change from green and grey shales, with some intercalations of decimetre thick fine sandstones, to thicker bedded sandstones showing channel structures.

The uppermost fossil record from the Bolloncillos Fm. was found 8 m below the top of this formation, and it is composed of entomozoaceans (see above), homoctenids (*Homoctenus krestrovnikovi, H. ultimus ultimus, H. ultimus* cf. *derkaouensis* and *H. deflexus, sensu* Montesinos *et al.*, 1990), conodonts (*Ancyrognathus* cf. *coeni, A. triangularis* and *Ancyrodella curvata*, sensu Valenzuela-Ríos *et al.*, 2002) and bivalves, which suggest a Frasnian age (levels BM1/32 and CH/6). The next fossiliferous level lies 4 m above the base of the Hoya Fm., and contains ostracods, ammonoids, brachiopods, conodonts and bivalves. Because of the presence of *Falcitornoceras falciculum* ssp. this level is dated as lower Famennian in age (BM1/34 and CH/9) (Montesinos *et al.*, 1990; Montesinos and Sanz-López, 1999). According to these data the Frasnian/Famennian boundary is drawn between beds 32 and 34 at BM1 section, and between beds 6 and 9 at CH section.

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EARLY DEVONIAN NERITIC OSTRACODS OF CELTIBERIA, SPAIN – BIOSTRATIGRAPHICAL, PALAEOECOLOGICAL AND PALAEOGEOGRAPHICAL ASPECTS

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Abstract

Celtiberian neritic ostracods of Lochkovian to late Early Emsian age are associated with conodonts, trilobites and brachiopods and bear a high potential for biostratigraphy, palaeoecology and palaeogeography. Pragian neritic ostracods are highly diverse in Celtiberia, whereas only low diversities were hitherto known in NW Europe and N Africa. Thirteen taxa appear in Celtiberia earlier than elsewhere in Europe. The biofacies of the benthic ostracods reach from harsh neritic to deeper water conditions with dacryoconarids and ammonoids. Neritic ostracod taxa common with NW Africa and Armorica corroborate the continuity of the Ibarmaghian Faunal Province (= Mauro-Ibero-Armorica). The occurrence of beyrichiacean ostracods in Ibero-Armorica, at least from the Lochkovian onwards disprove a Devonian "Rheic Ocean" between Baltica-Avalonia and "Perigondwana".

Key words: Neritic ostracods, biostratigraphy, palaeogeography, Early Devonian, Celtiberia, Spain.

Resumen

Los ostrácodos neríticos del Lochkoviense al Emsiense Inferior de Celtiberia están asociados a conodontos, trilobites y braquiópodos y presentan un alto potencial bioestratigráfico, paleoecológico y paleobiogeográfico. Incluso los ostrácodos neríticos del Pragiense son altamente diversificados en Celtiberia, donde solamente se conocían asociaciones de baja diversidad en el conjunto del NW de Europa y N de África. Trece taxones aparecen antes en Celtiberia que en el resto de Europa. Las biofacies de ostrácodos bentónicos abarcan desde las severas condiciones neríticas hasta las aguas profundas, con dacryoconáridos y ammonoideos. Taxones de ostrácodos neríticos comunes con el NW de África y Armórica corroboran la continuidad de la Provincia Faunística Ibarmaghiense (= Mauro-Ibero-Armórica). La presencia de ostrácodos beyrichiáceos en Ibero-Armórica, al menos a partir del Lochkoviense, está en desacuerdo con la presencia de un "océano Rheico" entre Báltica-Avalonia y "Perigondwana".

Palabras clave: Ostrácodos neríticos, bioestratigrafía, paleogeografía, Devónico Inferior, Celtiberia, España.

INTRODUCTION

The mainly neritic Devonian of Celtiberia has been studied by several authors for many years (see historical review in Carls, 1999). It is well known as regards the stratigraphy, the fossil contents and the palaeoecological conditions. Through trilobites, brachiopods, conodonts, ammonoids and dacryoconarids the succession is well correlated with the Devonian of Europe and N Africa (Carls, 1987, 1988, 1996) and is therefore of special interest for biostratigraphical purposes. However, there are only few studies on Early Devonian ostracods of this area (Groos-Uffenorde, 1983; Lethiers & Raymond, 1993). Moreover, not many neritic ostracods of Pragian age of NW Europe and N Africa have been studied.

GEOLOGICAL SETTING

Celtiberia is composed of southern Aragón and northeastern Castilla, in the NE of central Spain. As regards the Early Devonian, important outcrops are in the NW-SE striking Eastern Iberian Chains (Cordillera Ibérica Oriental = CIO) in the NE, in the easternmost spur of the Guadarrama in the W, and near Henarejos in the S of Celtiberia (fig.1). The thickness of the Early Devonian in the CIO is about 1600 m, mainly composed of siliciclastics (shales and fine-grained sandstones). Intercalations of limestones and marls are frequent, but thinner. The complete succession was mainly deposited in shallow neritic marine environments within the intracontinental Ibero-Armorican Trough (Carls, 1988; Carls & Valenzuela-Ríos, 2002).

In the following, the Pragian is referred to in the original sense, beginning with the appearance of *Eognathodus irregularis* (correlated near the boundary of d2bα/β) and ending between the entries of *Icriodus gracilis* in the basal bed of unit d4aβ2 and *I. bilatericrescens* about 1.3 m above the base of submember d4aγ). The Emsian is referred to in the traditional German sense, beginning with the entries of *Arduspirifer prolatestriatus* and "*Acrospirifer*" *fallax* (Mittmeyer, 1982: 262, tab. 1).

THE OSTRACOD FAUNAS

Ages and biostratigraphical correlation

About 50 Early Devonian ostracod samples were studied, mainly from the Axial Depression of Río Cámaras (DARC) in the CIO, and partly from the eastern Guadarrama. Some collections were washed from marly shales with hydrogen peroxide plus ammonia, others were obtained from limestones etched for conodonts, and a few were found on bedding planes. More than 100 taxa are identified from mid-Lochkovian (Luesma Fm., submember d1cγ) to late Early Emsian age (Mariposas Fm., submember d4bα); smooth podocopid ostracods have not yet been studied. The taxonomy will be published in a forthcomming thesis. Several Pragian ostracods of the section S of Sto. Domingo are listed and figured in Dojen *et al.* (this volume).

High diversities of Early Devonian neritic ostracods in SW Europe and N Africa are mainly known from the Emsian, e.g. in Morocco (Antiatlas, Becker *et al.*, 2003), in the Cantabrian Mountains (e.g. Becker & Sanchez de Posada, 1977; Becker, 2001), in the Montagne Noire (Feist & Groos-Uffenorde, 1979) and in the Thuringian Slate Mountains (e.g. K. Zagora, 1968). Not so many European neritic ostracods of Pragian age have been studied (e.g. in the Armorican Massif, Weyant 1976, 1980), and they are known in lower diversity. As a result, numerous taxa have been considered as index fossils of the Emsian, as they have been obtained hitherto exclusively from the Emsian. Although in Celtiberia, several such taxa have their oldest records already in the Pragian or even in the Lochkovian. Table 1 indicates the formerly known records of 15 taxa and their currently known entries in Celtiberia. The ages of their records elsewhere are herein revised and correlated with the Celtiberian succession, as many of the taxonomic works are rather old and their biostratigraphical concepts have undergone various changes.

The Armorican taxa of Weyant, 1976 (St. Céneré Fm., beds Sc49 – Sc63), occur little above the entry of *Nowakia acuaria* (bed Sc47); this record correlates with submember d2bβ and slightly younger levels (Early Pragian). The entry of *Bollia* ? sp. 2 sensu Weyant, 1976, in Celtiberia (Guadarrama) corresponds to submember d2aα (mid Lochkovian). Wether *Ulrichia* cf. *fragilis* sensu Weyant, 1976, is conspecific with the Thuringian *U.* cf. *fragilis* sensu Zagora 1968, is still uncertain.

The oldest reported faunas of Early Devonian ostracods in Cantabria are from the LaVid Fm., Units 2 and 3, in León (Becker, 1998, loc. 46/2). Unit 2 can be correlated with an interval from the lower part of submember d3bγ onwards, because Unit 1 (= Felmín Member) contains brachiopods (Faunal interval 7, García Alcalde, 1996: 64, Text-Fig. 2, 4), which indicate age equivalence with the Sta. Cruz Fm. up to the basal part of d3bγ (Carls, 1999: Text-Fig. 3). Unit 3 of the LaVid Fm. begins at the entry of *Nowakia cancellata* (Early Dalejian, corresponding to little above the base of submember d4bβ). Celtiberian ostracods beginning in the interval of Units 2 and 3 of LaVid are: *Bollia lavibadia* Becker, 1996; *Bollia* sp. B sensu K. Zagora, 1968; *Punctoprimitia africana*, Becker, 1998; *Polyzygia beckmanni antecedens* K. Zagora, 1968; *Jenningsina thuringica* K. Zagora, 1968; *Ponderodictya inventeplicata* Becker 1989, and *Ponderodictya jeanlefevrei* Becker 1998. These enter in Celtiberia already early within the submember d2cβ (first half of the original Pragian).

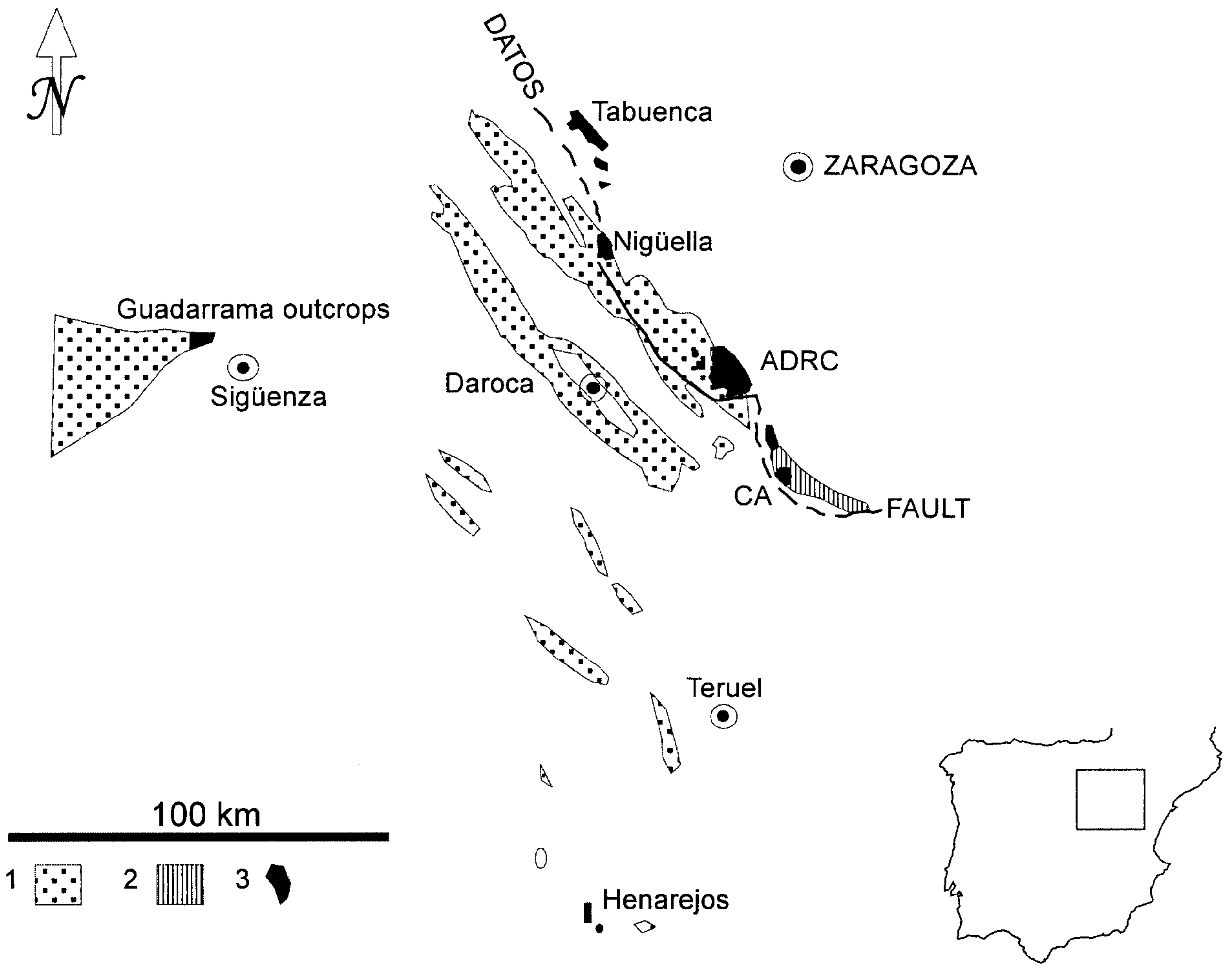

FIGURE 1–Simplified geological scheme of Celtiberia showing the Devonian outcrops of the Eastern Iberian Chains and the easternmost spur of the Guadarrama Mountains (after Carls & Valenzuela-Ríos, 2002). ADRC: Axial Depression of the Río Cámaras; CA: Cabezos Altos Devonian outcrops in the Montalbán Anticline. 1: Basement; 2: Carboniferous of the Montalbán Anticline; 3: Devonian outcrops.

Thus, the known ranges of these Celtiberian and Cantabrian ostracod taxa are extended downward at least by the span between d3bγ and d2cβ. According to Carls (1999: Text-Fig. 3) this span lasted approximately 2.8 ma.

The entry of *Punctomosea* sp. 29 sensu Groos-Uffenorde 1979 in the Montagne Noire (Feist & Groos-Uffenorde, 1979) is above a bed with *Anetoceras* (*Erbenoceras*), which indicates Late Zlichovian and warrants equivalence to the upper parts of submember d4bα. In Celtiberia, the oldest record of this taxon is in submember d2cβ. The difference in age between both levels is about 7 ma, according to Carls (1999).

As regards ostracods of Thuringia, those of the Horizon III of the Tentakuliten-Schiefer (Zagora, 1968) with *Nowakia cancellata* correlate with the middle and upper parts of submember d4bβ (Early

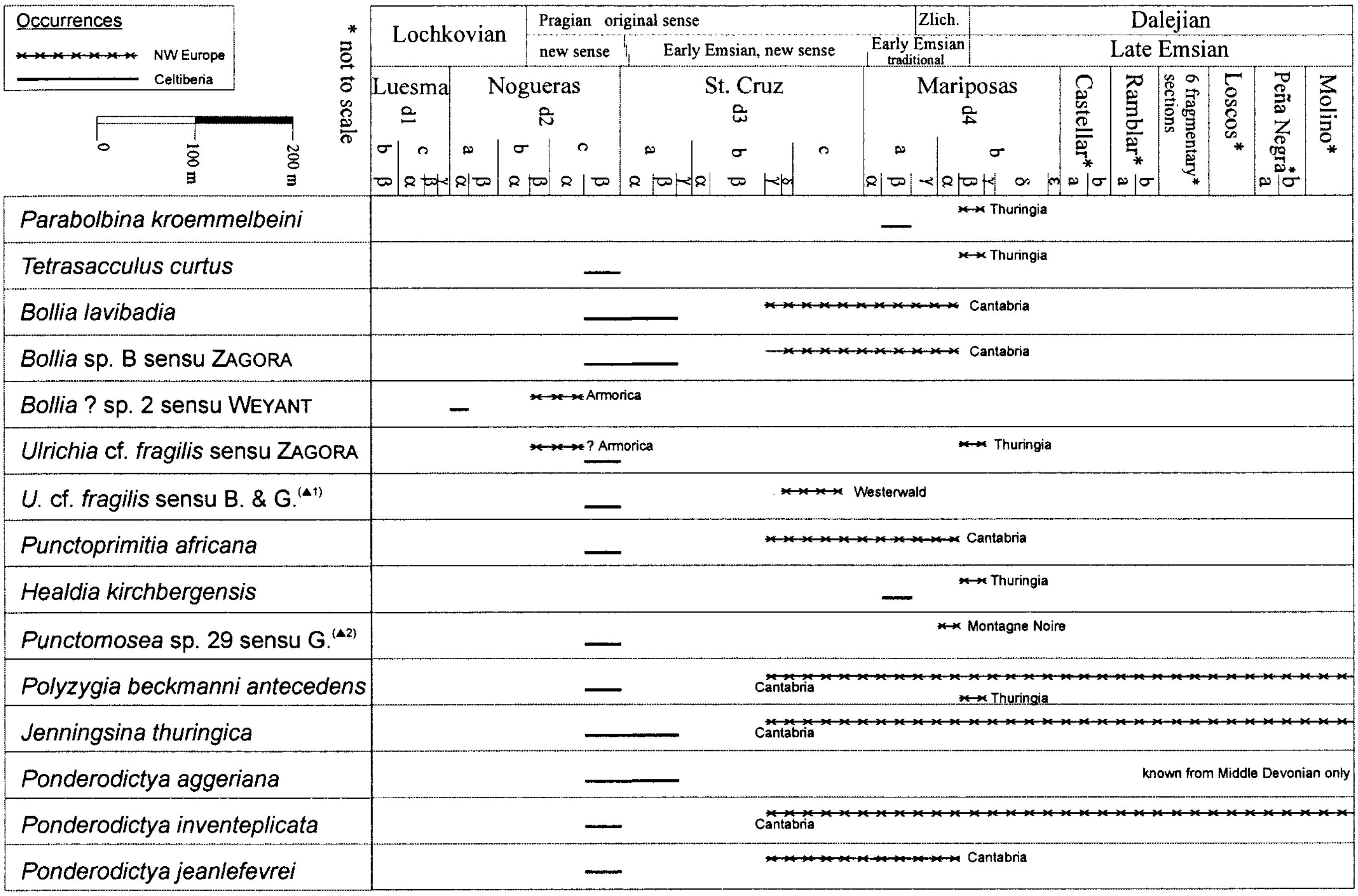

TABLE 1–Records of some neritic ostracod taxa in Europe and Celtiberia. Indicated are the formerly known entries, not the ranges of the taxa. (▲1): sensu Becker & Groos-Uffenorde, 1982; (▲2): sensu Groos-Uffenorde, 1979.

Dalejian). *Parabolbina kroemmelbeini* K. Zagora, 1968, and *Healdia kirchbergensis* K. Zagora, 1968, occur in Celtiberia in submember d4aβ (Late Pragian in the original sense = Early Emsian in the traditional German sense). *Tetrasacculus curtus* K. Zagora, 1968, and *Ulrichia* cf. *fragilis* sensu K. Zagora, 1968, occur in Celtiberia in submember d2cβ, i.e. over 7 ma before the former record.

Ulrichia cf. *fragilis* sensu Becker & Groos-Uffenorde, 1982, was hitherto known from the Seifen Schichten in the Westerwald (Germany), corresponding to most of submember d3bδ and parts of d3c (Carls, 1996, 1999). The same form in submember d2cβ is over 3 ma older.

Lethiers & Raymond (1993: 321, Fig. 2) postulated the Pragian/Emsian boundary (traditional sense) within the Nogueras Fm. (member d2c) of the CIO, as the assemblages of their samples 8 and 9 bear ostracods, which they considered as Emsian index fossils. The authors referred especially to the occurrence of *Bythocyproidea lefevrei* Adamczak, 1976; *Polyzygia beckmanni antecedens* K. Zagora, 1968, and *Jenningsina thuringica* K. Zagora, 1968. This biostratigraphical age assignment by means of ostracods, against the evidence for Early Pragian age provided by the successions of conodonts, brachiopods and trilobites (Carls, 1987, 1988, 1996), overtaxes the potential of the ostracods. Brachiopod faunas of the "*Spirifer*" *rousseaui* group in the Nogueras Fm. (submember d2cβ) plead unambiguously for a mid Pragian age in the traditional sense. Even in the sense of the current Pragian/Emsian boundary at the entry of *Polygnathus kitabicus*, that is correlated close to the limit d2/d3 in Celtiberia, the samples 8 and 9 of Lethiers & Raymond would be "latest Pragian".

PALAEOECOLOGY

All Celtiberian ostracods are from level bottom environment; three assemblages can be distinguished palaeoecologically. In harsh neritic environments, often with palaeochannels (low within the Nogueras Fm.; high Castellar Fm.; low in the Molino Fm.), oligospecific ostracod assemblages with abundant beyrichiid ostracods like *Zygobeyrichia* and *Carinokloedenia* occur. The ostracods occur on bedding planes of silty limestones and were also found in limestones etched for conodonts (with *Icriodus* faunas of low diversity). The occurrence of oldest beyrichiid ostracods known from Perigondwana in shelly limestones of mid-Lochkovian age (Nogueras Fm., unit d2aβ5, with *Acastello tiro* Rh. & E. Richter, 1954) is important for palaeogeography (see below).

Highly diverse ostracod assemblages were found in marly shales and marls of the Early Pragian (section S of Sto. Domingo, Nogueras Fm., submember d2cβ) and in limestones of the Early Emsian (section El Manchón, Mariposas Fm., submember d4aβ, bed d4aβ). They consist mainly of thick shelled and heavily sculptured palaeocopids and of thin shelled and finely sculptured metacopid ostracods. The habitats were level bottom environments, where the ostracods lived in particular microbiotopes among the brachiopods, bryozoans, solitary rugosa and favositid corals, little below wave base in euphotic depths.

Samples with dacryoconarids and ammonoids (section Regajo Parideras, Mariposas Fm., submember d4bα) still bear some benthic ostracod taxa (roponellids and few primitiopsid) in moderate diversity. Insulation still favourable for the growth of algae is proven by *Receptaculites* in the lower third of the submember, and water depths of hardly 60 m are indicated by phacopid trilobites with unreduced eyes. The top of the submember is characterized by the increasing occurrence of Hercynic elements like goniatites (*Anetoceras, Mimagoniatites*) and dacryoconarids (e.g. *Nowakia barrandei*).

PALAEOGEOGRAPHICAL RELATIONSHIPS

The palaeogeography of Variscan Europe is a matter of discussion for years. The postulation of several Devonian oceans was partly based on the distribution of neritic ostracods. Cocks & Fortey (1982) postulated the "Rheic Ocean" between Baltica-Avalonia and Perigondwana since the Ordovician. Ziegler (1988) postulated an additional ocean between N Africa and Iberia. However these plate kinematic models neglected numerous important geologic and faunistic facts (Carls, 2001, 2003).

Close faunal links between NW Africa and Ibero-Armorica, as indicated by common associations of shallow neritic brachiopods and trilobites (Racheboeuf *et al.*, 1981; Gandl, 1972) and lithological similarities led to the coining of the Ibarmaghian Faunal Province (= Mauro-Ibero-Armorica). Emsian ostracods of NW Africa were studied by LeFèvre (1963) and by Rabaté (1976), and were recently listed (Becker *et al.*, 2003). Lethiers & Raymond (1993:327) reported 8 neritic ostracod taxa common to the CIO and NW Africa (Algeria; Morocco); own studies recognize 13 shared taxa (Table 2). Although Becker classes the majority of his faunas as of "Thuringian provenance", the shared taxa are mainly neritic ones and refute therefore an oceanic separation between Morocco and Celtiberia, but corroborate the Ibarmarghian Faunal Province.

The close relationships of facies and fauna between Iberia and Armorica have repeatedly been described in detail (e.g. Carls, 1971, 2003; Carls & Valenzuela-Río, 1998, 1999). The coeval similarities in shallow neritic facies and faunas from the Pridoli to the Givetian prove a connection from Celtiberia around the Cantabrian Knee to Armorica through the intracontinental Ibero-Armorican Trough. The Armorican neritic ostracod faunas of Pragian age (Weyant, 1967, 1976, 1980) share 14 species out of 36 described Armorican taxa with Celtiberia (table 2). *Bollia*? sp. 2 Weyant, 1976; *Punctoprimitia europaea* Weyant, 1967, and *Leptoprimitia balbiniensis* Weyant, 1967, are known only from these two areas so far. Thus, the ostracod distribution corroborates the continuity of the Ibero-Armorican Trough against the "Rheic Ocean" postulated by P. Ziegler (1988) between both regions.

Cocks & Fortey (1982) postulated the Rheic Ocean as a faunal barrier between Baltica-Avalonia and Gondwana since the Ordovician. The model is based on the assumed lack of faunal exchange between these two areas. They referred to benthic ostracods, which "today have a development without a planktonic larval stage" and whose "mobility for migration is limited". Therefore, they "would have been unable to cross an ocean barrier, even one that was quite narrow" (Cocks & Fortey, 1982:474). The authors relied particularly on Pridoli beyrichiacean ostracods like *Frostiella* and *Londinia*, which occur in Baltica-Avalonia but are unknown in Perigondwana (Cocks & Fortey, 1982:474, Fig. 6). According to McKerrow (1994) the appearance of beyrichiacean ostracods in Gondwana

Regions Taxa	Armorica (Pragian)	Celtiberia (Pragian to Emsian)	NW Africa (Emsian)
Zygobeyrichia subzylindrica ? (RH. RICHTER, 1863)	x	x	
Parabolbina kroemmelbeini K. ZAGORA, 1968	? sp.	x	x
Ctenoloculina cf. *cicatricosa* (WARTHIN, 1934)	x	x	
Ctenoloculina longivelum K. ZAGORA, 1968		x	x
Bollia aff. *ungula* sensu WEYANT, 1976	x	x	
Bollia sp. B sensu ZAGORA, 1968		x	x
Bollia ? sp. 2 sensu Weyant, 1967	x	x	
Ulrichia cf. *fragilis* sensu WEYANT, 1976	x	x	x
Placentella heraultiana GROOS-UFFENORDE, 1976		x	cf.
Refrathella bissousensis GROOS-UFFENORDE, 1976		aff.	x
Punctoprimitia africana BECKER, 1998		x	x
Punctoprimitia europaea WEYANT, 1967	x	x	
Bythocyproidea ? *polaris* (GÜRICH, 1896)	x	x	x
Polyzygia kroemmelbeini LEFÈVRE & WEYANT, 1966	x	x	x
Polyzygia grekoffi WEYANT, 1980	x	x	
Polyzygia normannica WEYANT, 1976	x	x	
Polyzygia vinea MICHEL, 1972	x	x	x
Ponderodictya inventeplicata BECKER, 1989		x	x
Ponderodictya jeanlefevrei BECKER, 1998	x	x	x
Jenningsina planocostata JORDAN, 1964		x	x
Leptoprimitia balbiniensis WEYANT, 1967	x	x	
Loquitzella mesodevonica K. ZAGORA, 1968		aff.	x
Cryptophyllus ? sensu WEYANT, 1976	x	x	

TABLE 2–Some shared ostracod taxa of Armorica, Celtiberia, and NW Africa (Algeria, Morocco). x: evidence of taxon; cf./ aff.: closely related taxon; ? sp: doubtful evidence of genus.

should prove the closure of the Rheic Ocean in the Emsian.

Numerous faunistic and facies evidences against this model were itemized by Carls (e.g. 2003) and Carls & Valenzuela-Ríos (1998, 1999). With regard to the ostracods, the lack of beyrichiacean ostracods in Gondwana in the Late Silurian is due to conditions of biofacies, as throughout Ibero-Armorica in the Luesma Formation (CIO) and its equivalent thick white quartz sands were deposited; this habitat was not favourable for beyrichiacean ostracods. Also in Bohemia and Thuringia the deeper water environments with graptolites did not offer convenient habitats. Against McKerrow (1994), beyrichiacean ostracods (*Zygobeyrichia*, *Carinokloedenia*) appear in Perigondwana (Celtiberia) for the first time in mid-Lochkovian (unit d2aβ5), as was already reported by Groos-Uffenorde (1983). As well, Groos-Uffenorde (in Robardet *et al.*, 1991) stated that most of the ostracod taxa of the Ossa Morena Zone in southern Spain are large beyrichiacean ostracods; those strata are of mid-Pragian age, as they can be correlated by the occurrences of trilobites (Robardet *et al.*, 1991, Fig. 4) with the interval d3bγ-δ in Celtiberia. Additionally, Weyant (1966) studied beyrichiacean ostracods of the Normandy, which included *Londinia* in the Early Pragian. Lethiers & Raymond (1993) commented that the distribution of *Polyzygia* disproves the presence of a Rheic Ocean as a hermetic faunal barrier in the Devonian. Thus, the argument of Cocks & Fortey for the "Rheic Ocean" based on beyrichiacean ostracods do not remain valid.

CONCLUSIONS

In the Early Devonian of Celtiberia, the biostratigraphy and palaeoecology of benthic ostracods is assessed according to their associations with rich brachiopod, trilobite and conodont faunas. The ostracods prove to be palaeoecologically sensitive. The biostratigraphic ranges of some taxa prove to begin earlier than had been known before. The knowledge of Pragian benthic ostracods of "Perigondwana" has considerably improved.

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A CARBONIFEROUS NECROPHAGOUS MYODOCOPID OSTRACOD FROM DERBYSHIRE, ENGLAND

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Abstract

A monospecific population of cypridinid ostracods (Myodocopida) has been recovered from an ammonoid-bearing concretion of Namurian (Kinderscoutian, R_{1a-b}) age in the Bowland Shale Formation of Central England. These deposits represent sedimentation on the northern margin of a Carboniferous marine basin, the WNW-ESE orientated Widmerpool Gulf, where water depth probably exceeded 100 m. The ostracods occur in close association with the cranium of a shark (*Orodus*), on which they had most likely been scavenging. The shark carcass apparently formed a refuge to which the ostracods were restricted: they do not occur elsewhere within the concretion or surrounding strata. Adults and possibly as many as six moult stages are present so that the assemblage represents the original conspecific ostracod biocoenosis. The carapace morphology of this myodocopid ostracod, *Eocypridina carsingtonensis* sp. nov., is described and compared with related taxa. It is the oldest known myodocope to provide firm evidence of traces of an integumental circulatory system, present in positive relief on internal moulds as a series of anastomosing sinuses radiating away from the adductor muscle scar area, and comparable with modern cypridinids such as *Vargula*.

Key words: Crustacea, Ostracoda, Carboniferous, Myodocopida, palaeoecology, England.

Resumen

Una población monoespecífica de ostrácodos cypridínidos (Myodocopida) ha sido recogida de una concreción que contiene ammonoideos de edad Namuriense (Kinderscoutiense, R_{1a-b}), en la Formación Bowland Shale del centro de Inglaterra. Estos depósitos son representativos de la sedimentación del margen septentrional de una cuenca marina del Carbonífero, el golfo Widmerpool, de orientación WNW-ESE, donde la profundidad del agua pudo ser superior a los 100 m. Los ostrácodos aparecen en estrecha asociación con el cráneo de un tiburón (*Orodus*), del cual han sido depredadores. El cadáver del tiburón constituyó probablemente un refugio en el que fueron restringidos los ostrácodos, que no aparecen en el resto de la concreción ni en el sedimento adyacente. Están presentes los adultos y posiblemente hasta seis estadios juveniles, con lo cual esta asociación representa la biocenosis específica original de los ostrácodos. La morfología del caparazón de este ostrácodo myodocópido, *Eocypridina carsingtonensis* sp. nov., es descrita y comparada con otros taxones próximos. Esta especie constituye el myodocópido más antiguo conocido que proporciona evidencia firme de un sistema circulatorio tegumentario, presente en relieves positivos de los moldes internos, como una serie de senos anastomosados, dispuestos radialmente alrededor del área de las huellas musculares centrales y que es comparable con el sistema de los cypridínidos modernos, como *Vargula*.

Palabras clave: Crustacea, Ostracoda, Carbonífero, Myodocopina, paleoecología, Inglaterra.

INTRODUCTION

In 1986, during an investigation by the British Geological Survey of the Carsington Reservoir site, Derbyshire, England (Fig. 1), a large concretion (1 m in diameter, 0.4 m thick) was collected from the Lower Hays Farm Borrow Pit (extending from National Grid Reference SK 2478 5033 to 2496 5042). The spheroidal concretion (locally known as a 'bullion') comprises very hard, dark grey micrite with conchoidal fracture, which accumulated around the cranial part of a shark (*Orodus*). It formed in the sediment subsurface during an early phase of lithification, by a concentration of $CaCO_3$, caused or initiated by carbonate supersaturation related to microbial decay of organic matter (cf. Canfield & Raiswell, 1991). In addition to the shark remains, the concretion contains a number of goniatites, several small bivalves, very small orthocones, spat of bivalves, fragments of wood and over 250 valves (and several hundred smaller fragments) of the large, myodocopid ostracod, *Eocypridina*. Wilby *et al.* (in press) concluded that the intimate relationship between ostracods and the shark teeth and dermis suggested that the myodocopids had been scavanging on the carcass, which acted as a necrobenthic island on the soupy, dysaerobic sea floor.

The most detailed taxonomic work on Carboniferous myodocopes from Britain is that by Jones *et al.* (1874). They described Cypridinidae, including two species of *Eocypridina*, *E. brevimentum* and *E. radiata*, of late Asbian to early Brigantian and Namurian age, respectively. Mason (1983, unpublished thesis) documented the Dinantian ostracods from central England and North Wales, including *E. brevimentum* and two species of *Eocypridina* of late Asbian to early Brigantian age, which were left in open nomenclature. These four species represent the previous record of the genus in Britain, although other members of the genus are known from the Devonian of the USA (Kesling & Ploch, 1960) and the Carboniferous of Europe (Bless, 1973).

Cypridinidae in general, and *Eocypridina* in particular, form a scant element of the Carboniferous ostracod population of Britain. Little has been documented about the environmental preferences and ecology of the genus.

STRATIGRAPHY

The Kinderscoutian part of the Bowland Shale Formation (formerly the Edale Shales), is poorly exposed in the Carsington-Wirksworth region of northern Derbyshire (Frost & Smart, 1979; Chisholm, *et al.*, 1988). It was best exposed in the Lower Hays Farm borrow pit (now flooded by the Carsington Reservoir), near Carsington, to the south west of Wirksworth (Fig. 1). It comprises up to about 87m of dark grey, unfossiliferous, calcareous mudstones, together with numerous fossiliferous marine-bands of organic-rich, dark grey to black, fissile mudstone (Fig. 2). The succession extends from the lower Chokierian (H_{1a}) to the upper Kinderscoutian (R_{1c}) of the Namurian.

Only a few thin (up to 6cm thick) beds of sandstone are present in the succession except immediately above the highest exposed (*Reticuloceras reticulatum*) marine band, where 9.7 m of silty mudstone with interbeds of sandstone, siltstone and sideritic ironstone (each up to 0.1 m thick) occur. These beds have been interpreted as distal turbidites (Chisholm *et al.*, 1988) and are situated below the highest R_{1c} marine band (*R. coreticulatum*).

Micritic concretions are present in several of the marine bands (Fig. 2). The ostracods forming the subject of this paper were found in a concretion that had fallen from the side of the borrow pit. Although the precise marine band from which it came is not known, it can be assigned to the Kinderscoutian R_1 Zone by the occurrence of the goniatite *Reticuloceras*. Furthermore, as the sandier R_{1c} Subzone sediments lack micritic concretions in the Lower Hays Farm borrow pit, it must have been derived from either the R_{1a} or R_{1b} subzones (Fig. 2).

The marine bands yield bivalves, such as *Dunbarella rhythmica*, *Coryella squamula*, *Posidonia minor* and *P. obliquata*; goniatites including dimorphoceratids, *Reticuloceras* spp., *Hudsonoceras ornatum* and *Homoceratoides varicatus;* conodonts and fish. Conodonts, bivalves (including *Caneyella* sp.), radiolaria, sponge spicules together with bivalve and gastropod spat have been reported from comparable parts of the sequence nearby (Holdsworth, 1966; Frost & Smart, 1979). Frost & Smart (1979) recorded goniatites (*Reticuloceras*, *Hudsonoceras* and *Dimorphoceras*), bivalves *(Posidonia)* and conodonts in the concretions elsewhere in Derbyshire, but myodocopids have not been previously recorded.

PALAEOENVIRONMENTAL SETTING

The Bowland Shale Formation of central England was deposited in a series of fault controlled platforms and troughs (Fraser & Gawthorpe, 1990). The Lower Hays Farm borrow pit is located near the northern edge of one of these troughs, the Widmerpool Gulf (Fig. 1). Sedimentation was controlled by repeated glacio-eustatic changes in sea level (Trewin & Holdsworth, 1973;

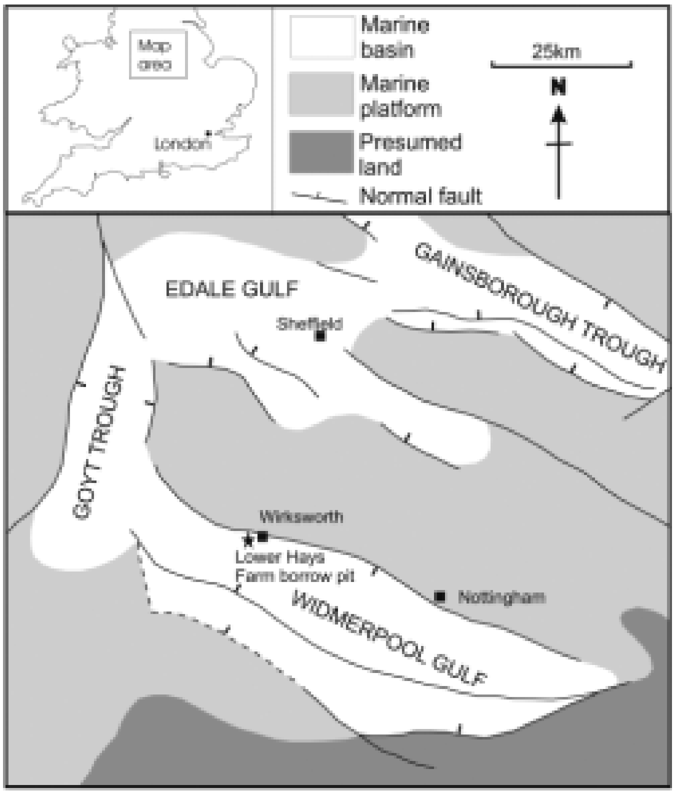

FIGURE 1–Palaeogeographical map of the English Midlands for the Namurian (modified from Ebdon *et al.*, 1990).

Collinson, 1988; Maynard & Leeder, 1992; Church & Gawthorpe, 1994). During R_{1a} and R_{1b} times, deposition of unfossiliferous mudstones took place during low-stands and thin, condensed, regionally widespread marine bands with concretions reflect sediment starvation during high-stands.

The marine bands are believed to have been deposited from suspension as soupy, poorly oxygenated substrates in water depths that probably exceeded 100m (Holdsworth, 1966; Trewin & Holdsworth, 1973; Church & Gawthorpe, 1994). The lack of bottom currents not only prevented post-mortem dispersal of the fauna, but allowed dysaerobic conditions to prevail. The low diversity, the predominance of nektonic (e.g. goniatites, nautiloids and fish) and pseudoplanktonic (e.g. sponges and *Caneyella*) taxa and the absence of burrowing indicate that the sediment surface was, for much of the time, inhospitable for benthonic colonisation. The presence of a sparse benthos may reflect periodic amelioration of conditions on the sea floor or they may have been transported in from the adjacent platform via floating plant material, which is abundant as coalified plant debris.

Bless (1973) recorded *Eocypridina radiata* (as *Radiicypridina*) from “an apparently non-marine band” in Belgium and The Netherlands. He went on to state that in Britain it is found “in association with *Geisina arcuata*, an ostracod with a preference for brackish environments. It is also known from marine bands (although not in association with other marine fossils).” This was certainly not the case in the Widmerpool Gulf. The stratigraphical position, regional palaeogeography and the associated fossil content of the concretion and enveloping strata, indicate that the myodocopes were associated with a fully marine, black-shale milieu. The palaeoenvironmental setting is similar to that described by Kesling & Ploch (1960) for the cypridinacean ostracods in the Upper Devonian Blakiston Shale of southern Indiana, from which *Eocypridina campbelli*, the type species of the genus, was recovered.

PALAEOECOLOGY

Lifestyle

Modern myodocopes have adapted to a number of lifestyles from the entirely pelagic Halocyprididae, to nektonic (e.g. cypridinids and cylindroleberids), nektobenthonic (e.g. sarsiellids and philomenids) and benthonic rutidermatids. The question arises, was *Eocypridina carsingtonensis* a pelagic species or did it have a nektobenthonic mode of life?

Siveter *et al.* (1991) and Vannier & Abe (1992) concluded that the myodocopes from the Late Silurian were the first to adopt a pelagic lifestyle. They based this conclusion on: the overall ovate valve shape; the presence of a rostral incisure; the presence of a prominent anterodorsal bulb (in the bolbozoids), which they speculated may have accommodated swimming appendages; the nature of the adductor muscles; the weak mineralisation of the carapace; and the spatial and facies distribution and faunal association of the myodocopids. In particular, they pointed out that Late Silurian myodocopids were spatially widespread and that, whereas the Early Silurian forms were associated with shelf sediments and faunas, by the Late Silurian myodocopids were associated with low-diversity, essentially pelagic outer shelf faunas and sediments suggestive of dysaerobic (or even anaerobic) conditions.

However, a number of criteria suggest that a nektobenthonic, rather than a pelagic, lifestyle is more likely for *Eocypridina carsingtonensis*. It has an ovate carapace with a well-formed rostrum and rostral notch, indicating that its frontal appendages may have protruded from the shell, possibly to aid (swimming) loco-

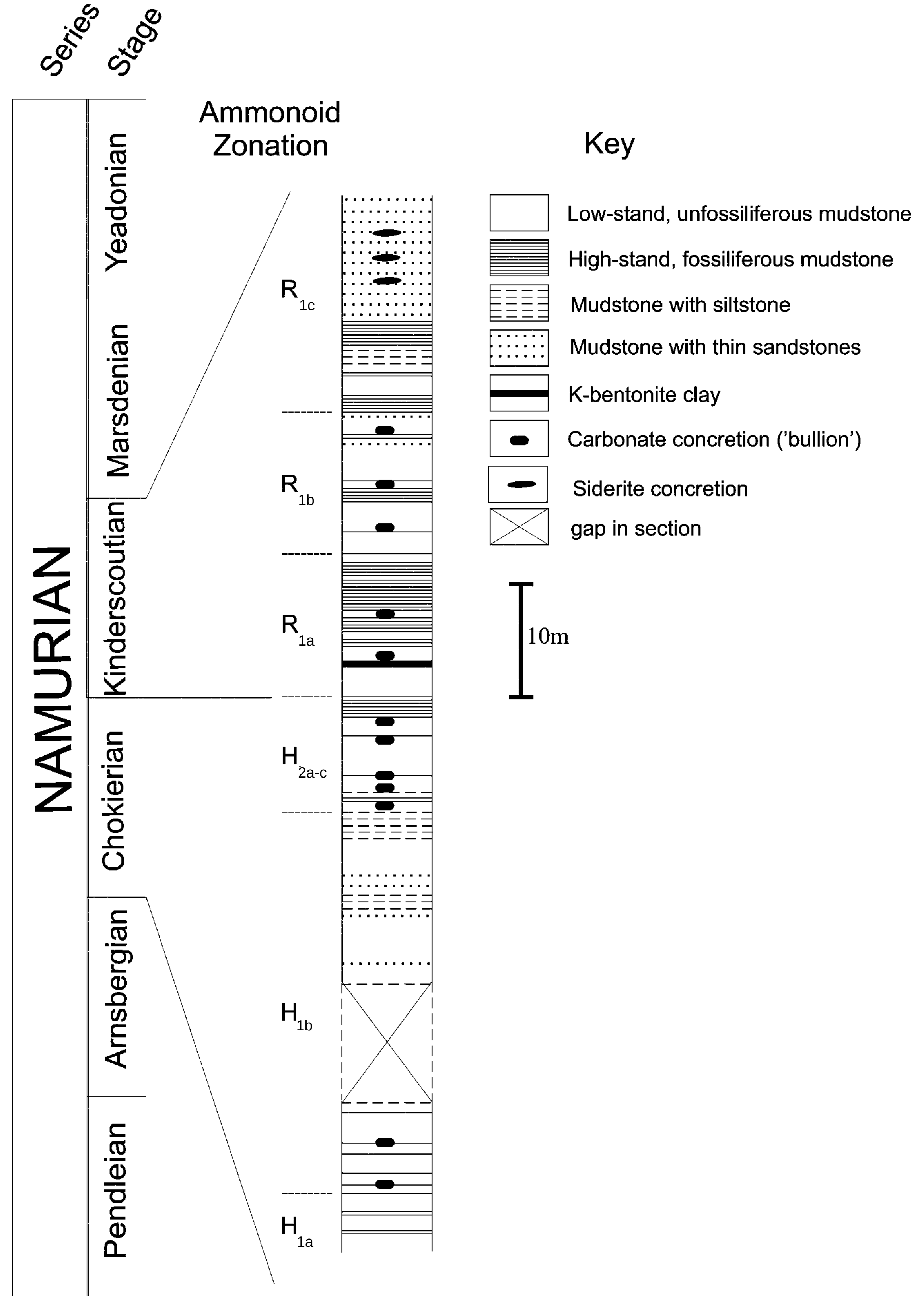

FIGURE 2–Lithological log of the Bowland Shale Formation at Lower Hays Farm borrow pit and biostratigraphy (ammonoid zones) (modified from Wilby *et al.*, in press). The ostracod-rich concretion was derived from ammonoid zone R_{1a} or R_{1b}.

motion (a rostral incisure was not observed with certainty due to preservation and the orientation of the valves in the enclosing matrix). The carapace is well mineralised, unlike the taxa described by Siveter *et al.* (1991). It is also the case that *E. carsingtonensis* was found in association with a fauna biased towards nektonic elements (a benthos was very rare) and the host-sediments appear to have accumulated in dysaerobic conditions. However, if the ostracods were nektonic, their exuviae and dead adults should also be present in the surrounding sediment rather than being confined to the shark remains. Thus, it seems likely that the ostracod population was either living on the shark at the time of its death (as parasites or scavengers), or was transported to the shark by an unknown vector (possibly floating vegetation as coalified plant material is present in the concretion). Whatever the method, once the ostracods had colonised the shark carcass, they were prevented from leaving by the surrounding dysaerobic conditions of the sea floor. If they had been strong swimmers, they would have been able to escape the eventual collapse and burial of the carcass (Wilby *et al.*, in press). Thus, *Eocypridina carsingtonensis* probably had a nektobenthonic lifestyle, similar to many modern species within Cypridinacea (e.g. the morphologically similar *Vargula hilgendorfii* (Müller), see Vannier *et al.*, 1997, Fig. 2; herein Pl. 1, Fig. 8), and the ostracods were killed by the collapse of the shark carcass.

Feeding strategy

Myodocopes in general and Cypridinidae use a variety of feeding strategies (e.g. see Vannier *et al.*, 1998). Some genera are carnivores and hunters of live prey (e.g. *Gigantocypris*), some are 'comb' feeders (e.g. *Philomedes*), whereas others are raptatory (e.g. *Cypridina castanea*). In baited trap experiments some cypridinids swarm to fish or crustacean carrion (Cohen, 1983, 1989; Stepien & Brusca, 1985; Cohen & Morin, 1986; Vannier & Abe, 1993; Keable, 1995). There is no evidence regarding the food source sought by myodocopids in general, or the Cypridinidae in particular, during the Carboniferous. However, Wilby *et al.* (in press) show that *Eocypridina carsingtonensis* crowd the upper surface of the shark, amongst its teeth and beneath flaps of its dermis, suggesting it to be, at least opportunistically, a scavenger. Indeed, the earliest evidence for a carnivorous scavenging lifestyle in ostracods is documented from myodocopids found in the late Ordovician (Ashgill Series) Soom Shale of South Africa (Siveter *et al.*, 2001; Gabbott *et al.*, in press). The scenario in the Soom Shale, in which 'cypridinid' myodoocopes were feeding on cephalopod carrion on an area of the sea floor that was elevated above the surrounding oxygen deficient substrate/water interface, closely mirrors the situation envisaged for *E. carsingtonensis*.

The intimate association of *E. carsingtonensis* with the *Orodus* carcass suggests that the ostracods may have behaved in a similar way to some Recent taxa described by Stepien & Brusca (1985) and Vannier *et al.* (1998), gaining access to internal tissues through natural openings (e.g. anus, gill chamber, genitalia, eye sockets) or lesions in the skin. It may be postulated that *E. carsingtonensis* possessed a furcal complex to allow them to anchor firmly onto carrion and dismember it, as seen in some Recent myodocopes (see Parker, 1997; Vannier *et al.*, 1998).

SYSTEMATIC PALAEONTOLOGY

All figured specimens, together with non-figured topotypic material, have been deposited in the Palaeontological Collections of the British Geological Survey, Keyworth, Nottingham (registration numbers GSM 105458 - 105522).

Order MYODOCOPIDA Sars, 1866
Suborder MYODOCOPINA Sars, 1866
Superfamily CYPRIDINACEA Baird, 1850
Family CYPRIDINIDAE Baird, 1850
Subfamily CYCLOLEBERIDINI Hartmann, 1974
Genus *Eocypridina* Kesling & Ploch, 1960
(=*Radiicypridina* Bless, 1973)

Type-Species.–*Eocypridina campbelli* Kesling & Ploch, 1960, from the Upper Devonian Blakiston Shale of southern Indiana, U.S.A.

Remarks.–*Eocypridina* is characterised by its ovate, smooth valves in lateral view, adductor muscle scars developed as a fan-like arrangement, and a circulatory system of anastomosing sinuses radiating from the adductor muscle scar area and similar to modern cypridinids such as *Vargula* (see below). The genus includes species with a wide size-range, including some specimens 11mm long.

Eocypridina carsingtonensis sp. nov.
Pl. 1, Figs. 1-7; Pl. 2, Figs. 1-2

In press *Eocypridina* sp. Wilby, Wilkinson & Riley: Figs. 2-4.

Material.–Over 250 valves (GSM 105458 - 105522). All of these are topotypes. In addition several hundred smaller fragments were present.

Holotype.–Adult left valve, GSM 105459 (Pl. 1, Fig. 2).

Dimensions.–Valves are 3.2-8.6 mm long, representing possibly as many as six growth stages and the adult.

Diagnosis.–Eocypridina with a large carapace (adults over 8mm long), hook-like rostrum and well-formed, rounded antero-ventral margin protruding below the broad rostral notch. Adductor muscle scars fan-like, disposed in two linear groups: posterior group arcuate, anterior group straight uniting with the posterior group at approximately their mid-point.

Description.–Large (up to 8.6 mm long and 6.2 mm high) and smooth valves, which in lateral outline are ovate. In lateral view the gently arching dorsal margin merges into a broadly rounded posterior which, in turn, blends imperceptibly with the convex ventral margin. Antero-ventral margin rounded, protruding as far as the rostrum. Hook-like rostrum situated antero-dorsally with a broad rostral sinus. Rib-like thickening on the anterior margin, within and below the rostral sinus. Rostral incisure not observed.

Muscle scars fan-like, disposed in two linear groups: a subvertical, somewhat arcuate, posterior group of nine scars, the two ventral scars comprising an imperfectly formed inverted V-shape; and an anterior group comprising a diagonally disposed series of five elongate scars. The two groups unite at about the mid-point of the subvertical posterior group. Hinge adont. An anastomosing pattern of sinuses radiates from the adductor muscle area and is preserved as a positive impression on internal moulds. Sex-dimorphism uncertain, though the range of length: height ratios suggests it may be developed. Soft anatomy unknown.

Remarks.–A detailed understanding of the early phylogeny of cypridinids requires knowledge of their soft anatomy, but there are no instances of such preservation in Carboniferous or older rocks. Thus, establishing the phylogeny of the genus *Eocypridina* remains speculative. Nevertheless, the earliest known Cypridinidae evolved within the Late Silurian (Siveter *et al.*, 1987, 1991; Siveter & Vannier, 1990; Vannier & Abe, 1995), though those taxa do not show a close relationship to *Eocypridina.*

There are few species of *Eocypridina* recorded in the British Carboniferous. The Late Asbian and early Brigantian *E. brevimentum* (Jones, Kirkby & Brady, 1874) differs from the present species in its smaller size, more rounded outline, the lack of an elongate rostral sinus, and a backward-sloping antero-ventral margin. The ovate outline of *Eocypridina radiata* (Jones, Kirkby & Brady, 1874), its smaller size and its rostral sinus below mid-height distinguishes it from the present species. Jones *et al.* (1874) stated that *E. radiata* is from “a black shale of the Airdrie Blackband Ironstone of the ‘Upper Coal Measures’ of the Glasgow district”, Scotland. In terms of modern stratigraphy this places the specimen in the Middle Coal Measures, just above the Vanderbeckei Marine Band. It was originally diagnosed by the presence of the “radiate shell structure”, a feature later shown to be of secondary origin (Sohn, 1977). The species has since been recorded from France and Greece and given the range Devonian to Permian by Kornicker & Sohn (2000), although they state that several different species may have been included within *E. radiata.* Of the two undescribed species of *Eocypridina* noted by Mason (1983, unpublished thesis), one is very large (over 11mm in length) with a less hook-like rostrum and a wide rostral sinus, whilst the other is more rounded in lateral outline and lacks the protruding antero-ventral margin.

The earliest known member of the genus, *Eocypridina campbelli*, is from the Late Devonian of

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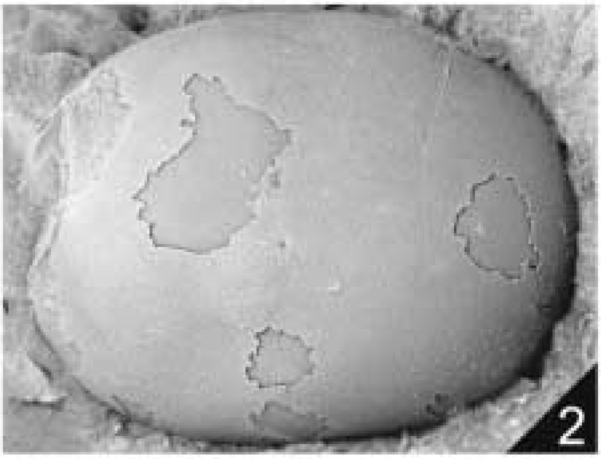
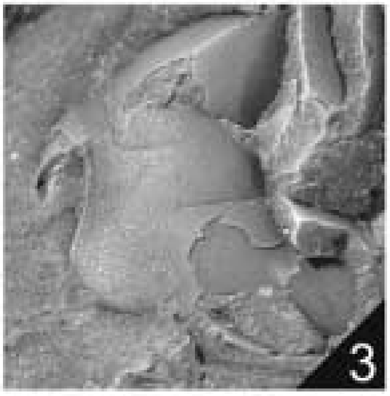
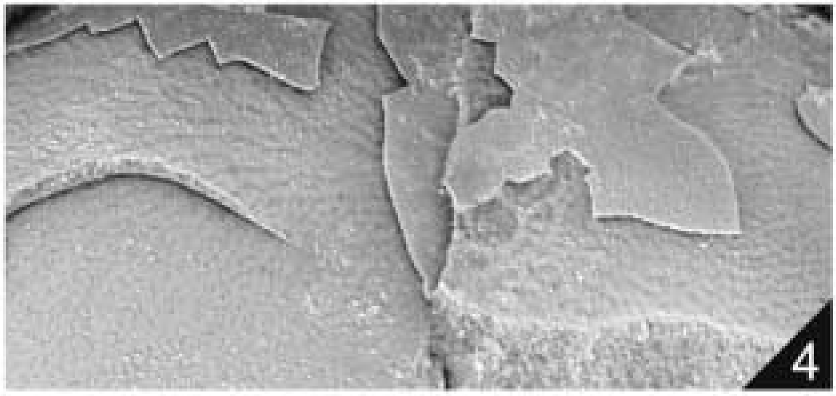
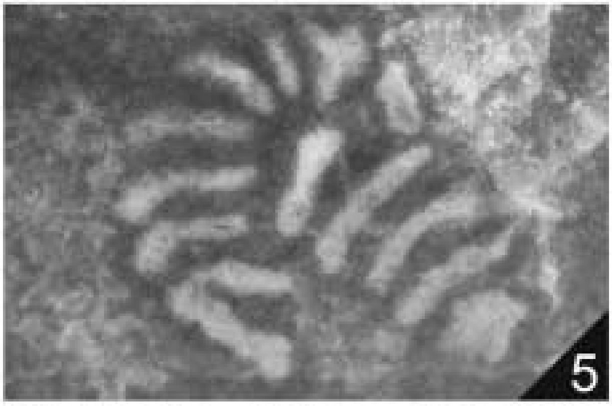
PLATE 1–*1-7, Eocypridina carsingtonensis* sp. nov. from a micritic concretion in the Namurian Bowland Shales Formation (Kinderscoutian $R_{1a\text{-}b}$) of Lower Hays Farm borrow pit, south-west of Wirksworth near Carsington, Derbyshire, England. *1*, juvenile left valve, lateral view (GSM 105484), x19, length 3.9 mm. *2*, adult left valve, lateral view, holotype (GSM 105459), x10, length 8 mm. *3*, adult left valve, lateral view, showing the hook-like rostrum and rib-like thickening on the anterior margin within and below the broad rostral sinus (GSM 105523), x10, field of view 5 mm wide. *4, 7*, the integumental circulatory system on an adult right valve (GSM105462); detail of the anastomosing sinuses that represent the afferent network of blood-vessels radiating from the partially visible adductor muscle field; *4*, x20; *7*, x11, length 0.67 mm as preserved. *5*, fan-like arrangement of the adductor muscle scars (GSM105526) (anterior towards the right), x45. *6*, adult right valve (GSM105462) with anastomosing sinuses representing the integumental circulatory system, x11, length 0.67 mm as preserved. *8*, the circulatory system of an adult male of *Vargula hilgendorfii* (Müller, 1890), a modern cypridinid from Aburatsubo Bay, Misaki, Japan,. x19, length 3.47 mm.

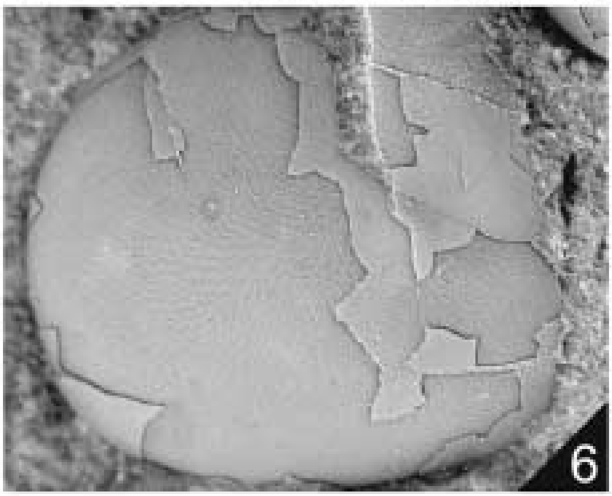
PLATE 1

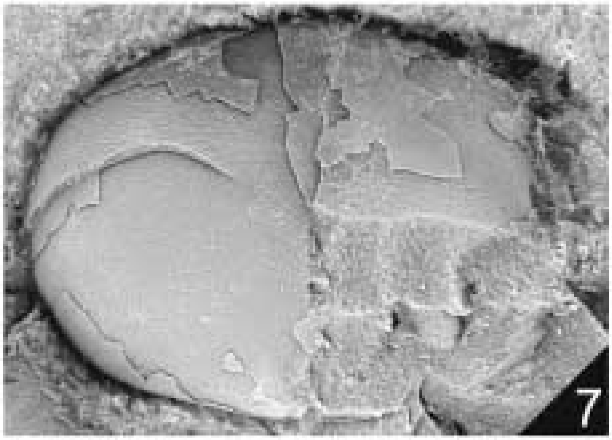


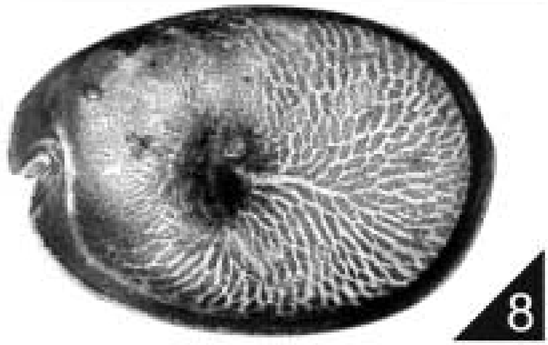












Indiana (Kesling & Ploch, 1960), is much smaller than the present species (its length is between 1.9 and 2.3 mm), almost circular in lateral outline and its adductor muscles are more rosette-like in gross morphology. *Eocypridina aciculata* (Scott & Summerson, 1943) (which includes *Radiicypridina radiata* sensu Bless, 1973, and *Cypridina radiata* sensu Scott & Summerson, 1943), from the Lower Pennsylvanian Hance Formation of southeastern Kentucky, shows a number of similarities to the present species in terms of the hook-like rostrum and muscle scar distribution, but differs in having a more highly arched dorsal margin.

Kornicker & Sohn (2000) indicate that the range of *Eocypridina* may extend through to the Late Jurassic, for they suggest that *Cycloleberis* sp. of Dzik (1978) should be included with that genus. However, there is a large gap between the Late Palaeozoic taxa and the Late Jurassic, and it is tempting to suggest that the morphological similarities are the result of similar lifestyle and environmental conditions rather than a phylogentic relationship.

MUSCLE SCARS

The disposition of the adductor muscle scars in early myodocopids is highly variable and includes a small, ill-defined reniform arrangement in the Silurian forms (Fig. 3), and a rosette and a fan-like arrangement in younger Palaeozoic forms. The scar pattern that is characteristic of *Eocypridina,* is fan-like and comprises a subvertical, generally arcuate row of scars and a diagonally disposed anterior series. This muscle scar pattern first appeared in the Devonian with *Eocypridina campbelli*. The scars of this species are almost rosette-like in gross morphology, but the reduction in size of the anterior group into a separate, arched, linear grouping had developed. Once evolved, this disposition of adductor muscles was highly successful, for although it changed in detail with time, it can be seen in a number of unrelated taxa from the Carboniferous to Recent (Fig. 3). Based on the muscle scars, the musculature of *Eocypridina* [*E. campbelli* (Kesling & Ploch, 1960) and *E. carsingtonensis*] shows a close resemblance to the Early Triassic myodocopid *Triadocypris spitzbergensis* Weitschat, 1983. The fan-shaped adductor muscle arrangement is also present during the Early Cretaceous in *Triadogigantocypris? donzei* (Neale, 1976) (originally assigned to *Philomedes*) and in a number of Recent taxa, including species of Cypridinidae and Philomedidae (Fig. 3).

EVIDENCE OF AN INTEGUMENTAL CIRCULATORY SYSTEM

Eocypridina carsingtonensis is the oldest known myodocopid to preserve incontrovertible evidence of an integumental circulatory system, although Vannier & Abe (1995, p. 863, Fig. 16) showed the external ornament of a Silurian myodocopid which they tentatively interpreted as being possible traces of a vascular system. Circulatory systems are absent in smaller ostracods (less than about 3 mm in length) such as the podocopids, intradomiciliar ventilation being accomplished by movement of the appendages and diffusion of oxygen at the uncalcified inner lamella and across the body integument (McMahon & Wilkens, 1983; Maddocks, 1992). However, this form of oxygen exchange is insufficient for larger ostracods (those in excess of 3 mm in length) and respiration is enhanced in a variety of ways. Specialised gill-like structures are used in cylindroleberid myodocopids (Kornicker, 1994; Vannier & Abe, 1995) and integumental sinuses and a heart structure occur in some myodocopids and halocyprids (Abe & Vannier, 1995; Vannier *et al.*, 1997). A circulatory system is present in several larger ostracod and ostracod-like taxa, including leperditiids, bradoriids, bolbozoids and myodocopids, as well as phyllocarids (Abe & Vannier, 1995; Vannier & Abe, 1995; Vannier *et al.*, 1997; Hou *et al.*, 2002, fig. 22a).

Internal moulds of *E. carsingtonensis* (Pl. 1, Figs. 4, 6, 7) preserve clear evidence of a complex anastomozing system that is interpreted as comparable to the integumental circulatory system of modern cypridinids such as *Vargula* (Pl. 1, Fig. 8). In *E. carsingtonensis* this comprises a series of anastomosing sinuses, representing the afferent network of blood-vessels that

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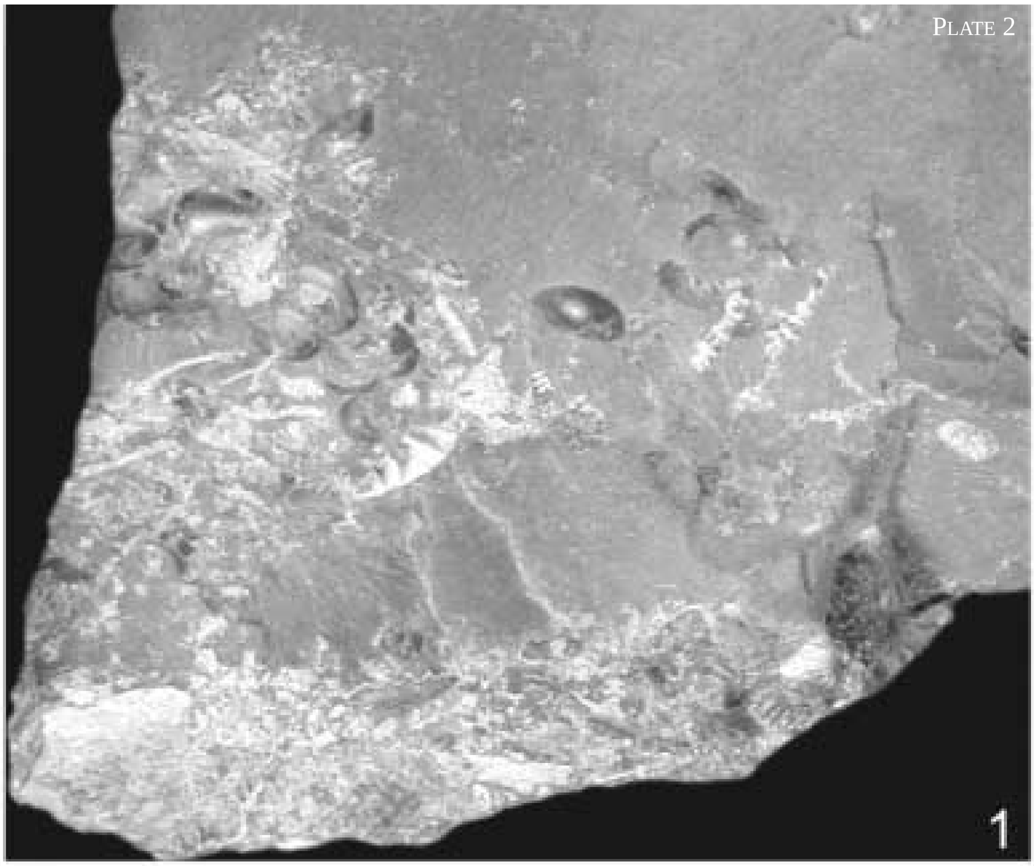
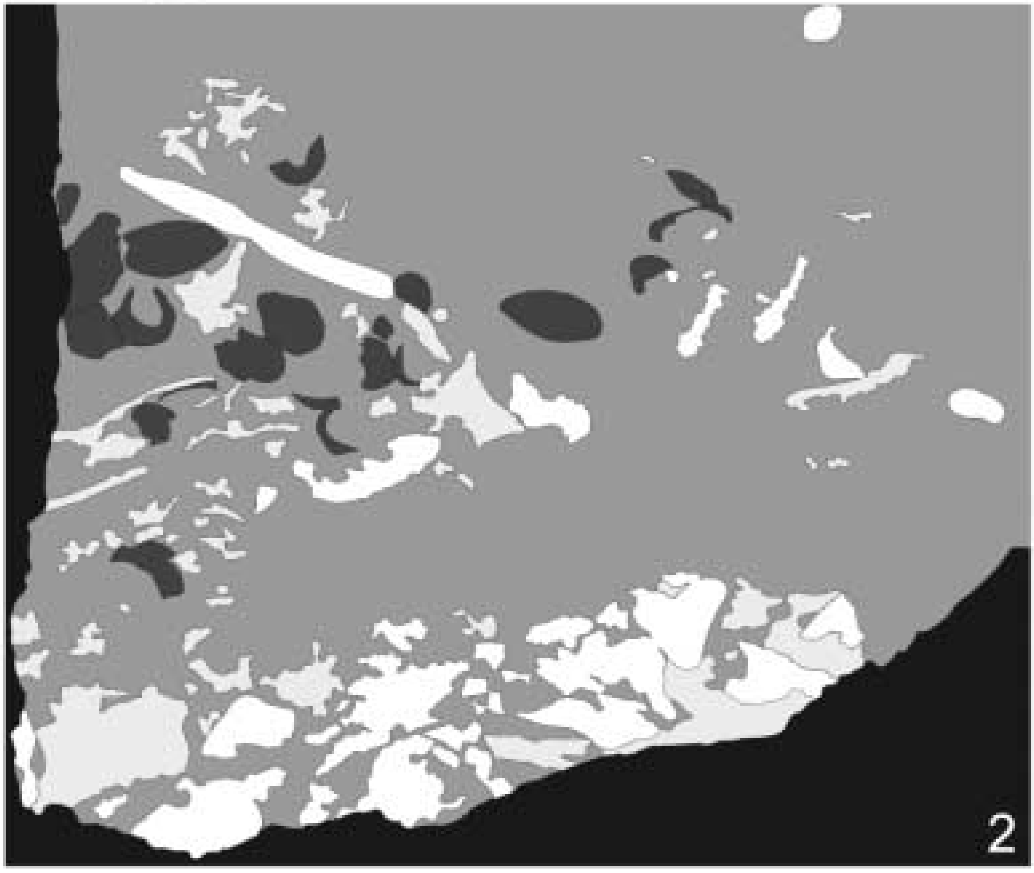
PLATE 2–*Eocypridina carsingtonensis* sp. nov. (Namurian, Kinderscoutian, $R_{1a\text{-}b}$) associated with the teeth and dermis of the shark, *Orodus* sp. *1,* a fragment of the concretion (GSM105525) showing the close relationship between the ostracods and part of the shark carcass (width of view 7.6 cm). *2,* A simplified camera lucida drawing of figure 1 highlighting the ostracods (black) and the dermis (light grey) and dentition (white) of the shark in a micrite matrix (mid grey).

PLATE 2





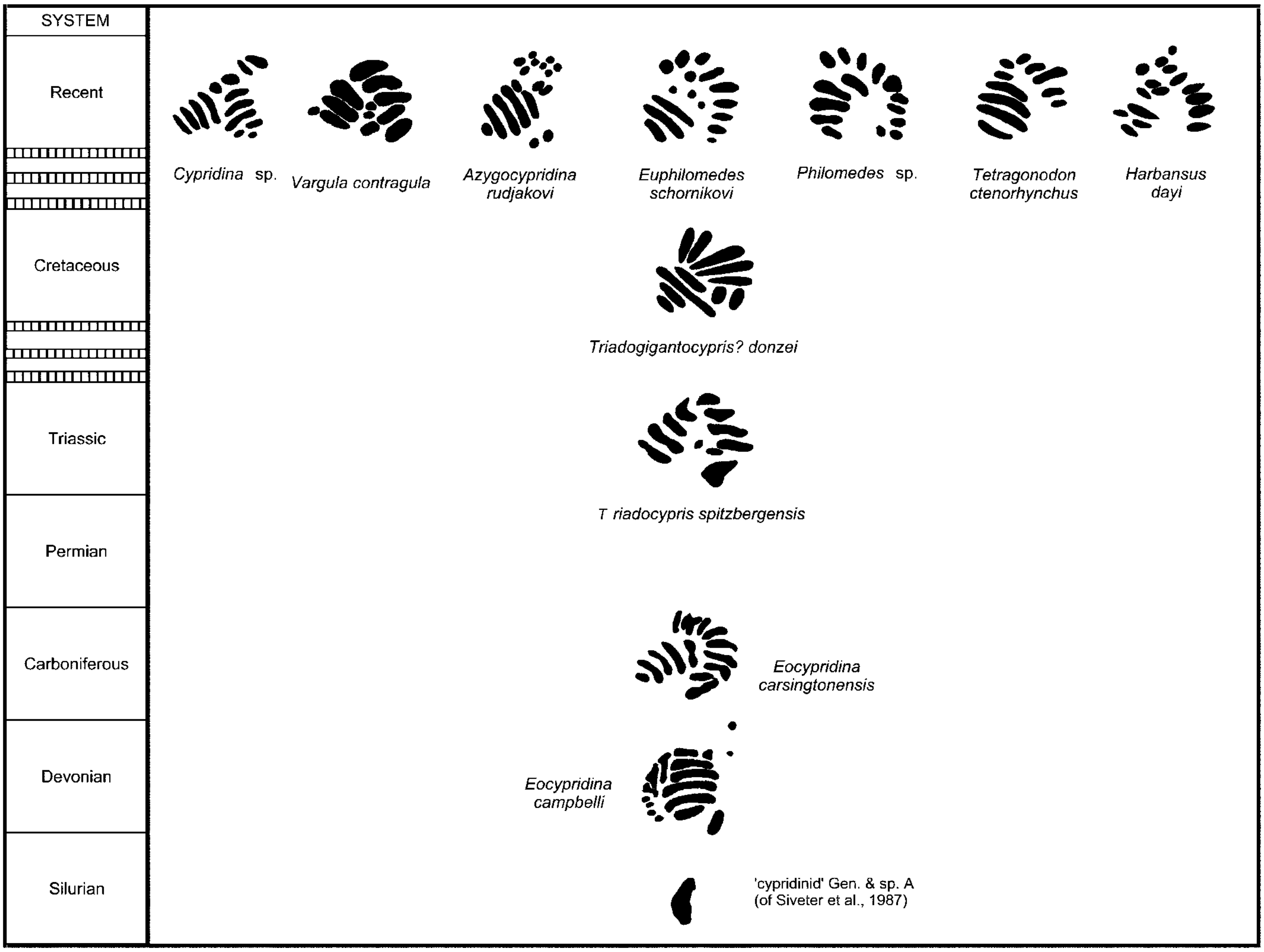


FIGURE 3–The distribution of fan-like adductor muscle scar patterns in selected myodocopids (fan-shaped muscle scars have not been described in myodocopids from the Jurassic and Tertiary).

radiate from the adductor muscle scar. In life, these structures were situated between the inner cuticle and outer lamella of the ostracod carapace. The inner cuticle, which separates the sinuses from seawater, is thin enough in modern forms (1.5-2 µm) to allow rapid gaseous perfusion over its entire area and thus acts as a preferential site for oxygen uptake. A similar mode of respiration was clearly developed in *Eocypridina* and this pattern is typical of all cypridinid myodocopes (see Vannier *et al.*, 1997, p. 174).

ONTOGENY

Although over 250 identifiable specimens were observed, the preservation of the majority was such that accurate measurement of dimensions was not possible. It is difficult to identify the individual moult stages, although perhaps six juvenile instars are present (the smallest valves are about 3.2 mm in length). It is very difficult to determine any possible sexual dimorphs in this assemblage. However, of the adults that were measurable, the length:height ratio fell between 8.6:6.2 mm and 8.6:4.9 mm. The difference in height is sufficient to speculate that dimorphism is present within the population, but insufficient measurements were possible to prove it beyond doubt.

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IN MEMORIAM HUW IDWAL GRIFFITHS (LOUTH, 14 MAY 1958 – HULL, 12 JUNE 2002)

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Picture of Huw during the post-conference excursion to Škocjanske jame Cave, Exploratory Workshop “Pattern and Process in the Balkan Biodiversity” (September 2001) along with his autograph.

BIOGRAPHIC REMARKS

Huw Griffiths was a good friend and a respected colleague, who was an internationally-recognised ostracodologist and mammalogist. At just 44 years old, he died before his time of oesophageal cancer, which caught him just as he was thoroughly enjoying his recently-achieved fatherhood and marriage, and a senior lectureship in the University of Hull. It is not the aim of this obituary to give a detailed description of Huw’s short but intense life. I intend simply to highlight his outstanding contribution to science in general and freshwater ostracod research in particular, and to provide a brief insight into his character, from my own experience of years of collaboration and friendship. Huw’s close friend and mammal specialist Prof. Boris Kryštufek (2002a, 2002b, 2002c) has reviewed in more detail his life and work, giving special focus to his line of research on mammals.

I first contacted Huw by letter in 1994, nearly ten years ago. At that time I was just starting to study ostracods. Huw was working as a Research Associate in the Department of Genetics of the University of Leeds, and at the same time trying to finish his PhD. Thesis on "*The application of freshwater Ostracoda to the reconstruction of Late Quaternary Palaeoenvironments in North-western Europe*" (Griffiths, 1995). He presented his thesis at the University of Wales, College of Cardiff, the same university where he obtained a BSc (first class) degree in Zoology in 1988, and an MPhil. on "*The conservation status of the Eurasian badger (Meles meles L., 1758) (Carnivora, Mustelidae) in western Europe*" (Griffiths, 1992). After studying Zoology, Huw worked as a Research Technician (1988-1989) in the School of Pure and Applied Biology and a Research Assistant (1989-1992) in the School of History & Archaeology of the University of Wales, where he developed most of the work for his PhD thesis under the supervision of the malacologist Prof. John G. Evans. Then he moved to Leeds in 1992, where he collaborated with the evolutionary biologist Roger K. Butlin. Finally, in 1995 he achieved a permanent job as a lecturer in the Department of Geography of the University of Hull, exactly the same place where another brilliant ostracodologist, John W. Neale, organised an international ostracod meeting (Neale, 1969) and worked until his retirement.

Huw's life changed very rapidly after this. A short time after his appointment, while doing fieldwork in Macedonia in 1997, he suffered a hypertension scare and had to spend several months in hospital and off work upon his return to Hull. This coincided with the break-up of his marriage, culminating in divorce the following year from Christine, to whom he had been married for more than ten years. And this was precisely the tumultuous period that I chose for visiting Huw for two months in November-December 1997! I had met Huw twice before, at a workshop organised in Madrid in 1995 by A. Baltanás and again in 1996 in Paris-Biervielle (3rd EOM), and his great sense of humour and his offer of help made me decide to apply for a grant to visit him in Hull. Despite the fact that Huw was still ill in hospital when I arrived in Hull, he managed to arrange everything for me at the university, including using his own computer, microscope, office and lab, until he was able to come back to work a few weeks later.

The last few years of Huw's life were probably his happiest years. In 1998 he started a new period, living together with his partner Jane M. Reed, a specialist in diatoms and palaeolimnology who eventually became a lecturer at the same department in the University of Hull. In 1999 they had a son, Thomas, and married soon afterwards. If you look at Thomas now, you cannot fail to be reminded of Huw - not only in the expression of his face but also in his strong, sociable personality and active behaviour.

A PASSIONATE SCIENTIST

This intense activity, common to father and son alike, made Huw's last years the most productive in his work, and resulted in his promotion to Senior Lecturer in 2000 and (posthumously) to Reader in 2002. Huw's scientific career and record of publications is impressive. It must be noted that he did not start university until he was in his late 20s, having hopped from job to job after leaving secondary school. However, once armed with a degree in Zoology he started publishing his research findings and never stopped. The year he read his PhD, just five years after his BSc, he had already published 40 works. His publication record currently stands at over 100 works and is still growing.

Some days, while I was in Hull on a second, one-year postdoctoral visit, I could imagine while looking at Huw that he was a workaholic. He so enjoyed writing, preparing projects, going sampling on fieldtrips, discussing with colleagues and teaching... However, this image of Huw as devoted completely to his job was soon modified. He also loved talking with friends for hours in the pub about all sort of topics or going on fun outings with his family, and was a very perceptive human being who loved to inspire confidence and enthusiasm in others.

Huw's PhD Thesis, as well as the list of meetings he organised or the books he wrote and edited are paradigmatic in showing his huge working capability. His doctoral research project on freshwater ostracods ranged from population ecology to parasite infection, from spatial distribution to biostratigraphy, from palaeoecology to evolution. He sampled some ponds biweekly for years, travelled to distant lakes to obtain recent samples and cores, and counted and measured thousands of ostracods.

He was also especially keen on managing databases, as can be easily recognised in his massive review of the European Quaternary freshwater ostracods (Griffiths, 1996), a work that will be of great value to all European ostracodologists for a long time to come. He was aware of the usefulness of these kinds of review for biogeographic studies, and published bibliographic lists of freshwater ostracod species from several countries: Britain, Slovenia, Turkey and Iran. However, he did not rely on reviewing other's works and putting things together in good order. He also found it exciting to hypothesise on evolutionary and ecological problems and was highly creative in discussing these problems with colleagues or in his publications. One of his last articles (Griffiths, 2001) reflects well many of Huw's ideas and interests in Quaternary freshwater ostracod biogeography. In this review article he remarks the indicator value of patterns of ostracod distribution in the past for the reconstruction of palaeobiogeographical changes during the Quaternary and for understanding processes such as ostracod migration following climatic shifts.

STRONG AND POSITIVE PERSONALITY

Huw was not only a hard worker, with a strong sense of responsibility, but he also made a great effort to keep smiling, and make others smile, including colleagues and students alike. He appreciated intelligent jokes and language, and was truly cynical. He could recognise clearly when to take things seriously, however, and did not shy away from facing up to problems and finding quick solutions. In this way he was always very honest with everybody. This confidence could be applied for example when reviewing papers in which he did not agree with the authors' opinions, or when postgraduate students did not progress adequately. He voiced his opinions loudly and clearly, including what he thought about himself. He would even explain in detail which of his papers were the worst (and he would probably use rude words for this), but at the same time liked also to recognise his best achievements. In his illness, he tried valiantly to hide his pain from all around him, and worked until two weeks before he died. He just did not want to accept it.

Reading through his working progress and writings, we can easily appreciate that Huw was actively interested in the preservation not only of biodiversity but also of cultural diversity. His research on mammal ecology and biogeography was closely related to the conservation of species, and he usually showed how ostracods are useful for understanding anthropogenic impacts on aquatic ecosystems. Some examples of his commitment to environmental issues are his involvement in IUCN groups, his appointment to the editorial board of the journal *Small Carnivore Conservation* or his various papers in journals such as *Conservation Biology*, *Aquatic Conservation: Marine and Freshwhater Ecosystems* and *Biological Conservation*. Similarly he had great respect for the cultural traits of the places he visited, and showed especial concern with Mediterranean countries with political or developing problems, particularly those in the Balkans. He took pleasure in learning some words in the language of the area, reading about its history and sampling the local cuisine and beverages.

Another side of Huw's sense of solidarity was the tremendous amount of work that he did checking the English language of many manuscripts written by non-native speakers. Regarding undergraduate and postgraduate students, he was always ready to pay attention to them and help them in any problem they had, including personal ones. Huw used to say that this was his first duty as a lecturer, but actually he loved to be of help to young students, and have fresh and interesting conversations with them. He knew well the music they liked, the jobs they had or where they came from, and correspondingly students loved him as well, as he was one of the few lecturers that really understood them.

Huw will be missed by many people. We will miss his cheerful character, his bright ideas and tireless work. We will miss his smile.

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