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On the preservation of carapaces of some limnic ostracods: An exercise in actuopalaeontology

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Abstract

The way in which the ostracod carapace decomposes through biological and physico-chemical processes is illustrated with Recent and Neogene non-marine ostracods (candonines, herpetocyprines and cytherids) from lacustrine and groundwater habitats. The degree of carapace preservation for Recent Candoninae, in the Mondsee (Austria) is shown to be dependent on the sedimentary microenvironment. The carapaces of herpetocyprines, because of their special morphological structure, decay very easily. This could explain the rare occurrrence of this ostracod group in Palaeogene deposits in Europe.

Introduction

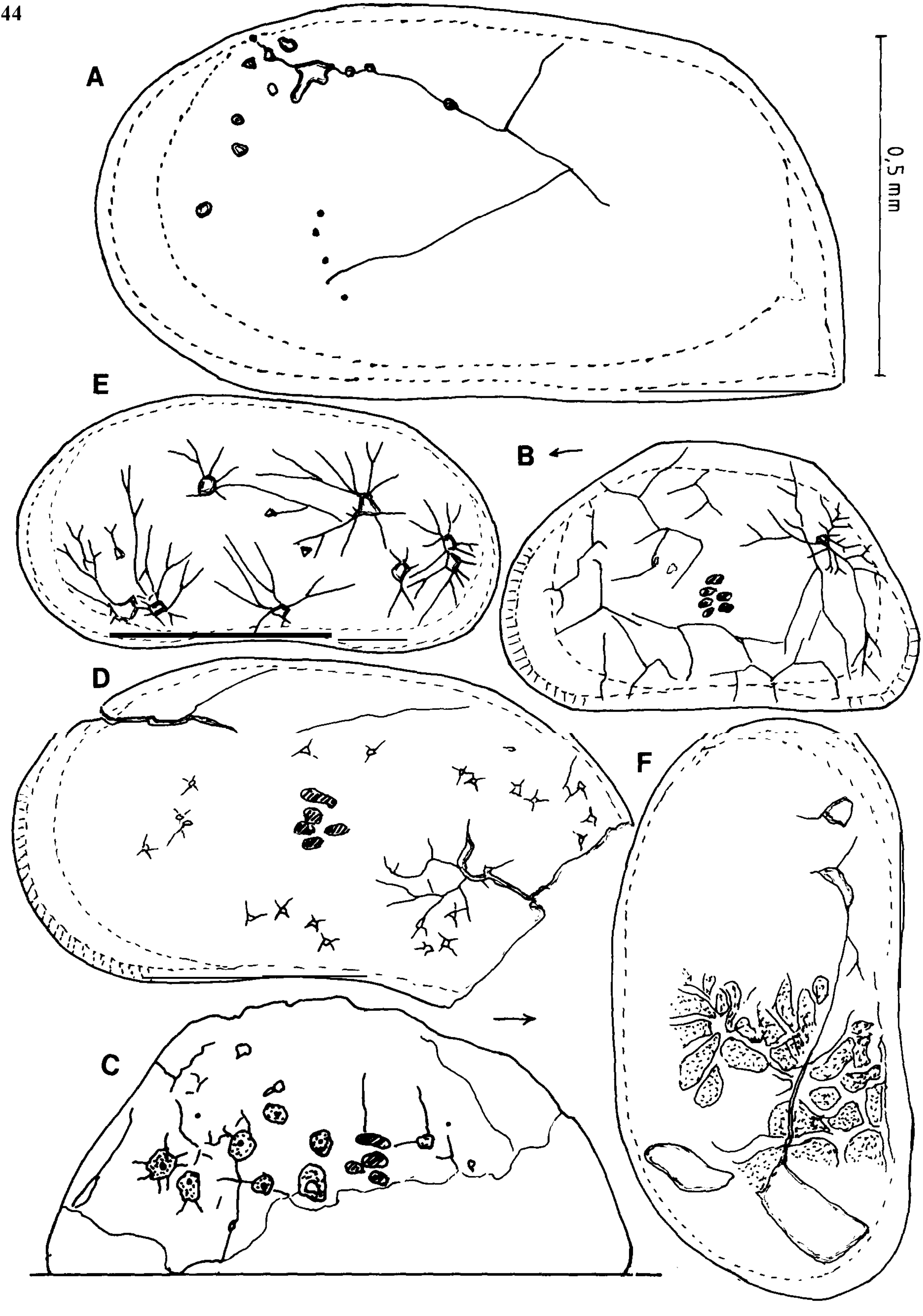
Limnic Ostracoda have a very long fossil record, ranging from Carboniferous to Recent, the consequence of the preservation of their calcareous carapaces in sedimentary deposits (McKenzie, 1971). To date, no systematic study has considered the taphonomy of limnic Ostracoda. At first glance two problems are of paramount interest in basic and applied micropalaeontological research: 1. The relationship between the degree of carapace preservation and the sediment microenvironment. 2. The causes of selective destruction of the carapaces of some ostracod groups.

For marine ostracods, Oertli (1971, 1975) documented the way in which the degree of carapace preservation can be used for palaeoecological reconstructions of the environment. Kontrovitz (1966) and more recently Whatley *et al.* (1982) showed experimentally how ostracod shells break due to physical agencies. Valuable data on the selective destruction of Holocene ostracod shells by biological and chemical agents are also reported by Frydl (1982).

In the present contribution we describe how the carapace of limnic ostracods separate from the soft parts during moulting or after death. We also show how carapaces and/or valves are corroded, first by microorganisms (bacteria and/or fungi) and later by chemical agencies (Fig. 1).

Material and methods

We studied the state of preservation of carapaces and valves from living animals, as well as carapaces and valves which are deposited on/within sediment after the moulting or death of the animal, and which are separated from the soft parts of the body. In the latter case, both Recent and fossil material were examined. In the former the material comes mainly from drinking water wells and was obtained during a survey of the groundwater ostracods of Romania carried out by the senior author during 1970–1972. *Herpetocypris* aff. *brevicaudata* Kaufm. was found in a shallow well, 4 m deep from the village of Gogosu, near Turnu-Severin; *Pseudocandona serbani* Dan. was sampled in a well from the village of Jiblea, near Rimnicu-Vilcea; *Mixtacandona* sp. aff. *chappuisi* Klie originated from a well in the village of Cuhea, in the Iza Valley (see also Danielopol, 1980, 1982); *Microdar-*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winula zimmeri (Menz.) was collected on a floating fen at Lake Caldarusani, near Bucharest.

Living and subfossil ostracods also used in this study come from the Mondsee (i.e. *Cytherissa lacustris* Sars and *Leucocythere mirabilis* Kaufm.) from site MO-7, 18 m in depth (see Danielopol et al., 1985).

The fossil material used here was collected by one of us (R.O.) mainly from outcrops in Upper Pannonian sediments at the localities of Grosi and Sintesti (between Deva and Lugoj, Banat, Romania). From these localities we studied *'Candona'* sp. aff. *lobata* (Zalany), *'Candona'* sp. aff. *lunata* (Mehes), *Bakunella dorsoarcuata* Zalany. The ostracod assemblages and the stratigraphy of the Grosi outcrops, are given in Olteanu (1971). The sediment and fauna are typical of a lacustrine phase (shallow depth and low salinity) of the Pannonian Basin (for a palaeogeographical reconstruction of the Paratethys see Rögl & Steininger, 1983). We also studied one valve of *Bakunella dorsoarcuata* collected by Dr. E. Hanganu (Bucharest) from Pliocene sediments of the Dacic Basin (Eastern Paratethys) in the Fore-Carpathians (Jud. Prahova, Romania).

Investigation of the structure of carapaces and valves was done using transmitted and stereo-light microscopes and a scanning electron microscope. The ultrastructure of the hard integument was investigated on valves which had been intentionally fractured with dissecting needles.

Observations on shell ultrastructure and on the separation of the soft body from the (hard) carapace

Bate & East (1972), Dépèche (1979, 1982), Okada (1981), inter alia, described in detail the fine structure of the carapace integument of several limnic and marine ostracods. In some of the Candoninae and Cypridinae which we studied (e.g. *Mixtacandona* sp., Fig. 2, A, B) the epicuticle appears to be undulating (thin strips of the epicuticle are not attached to the underlined calcified layer). The procuticle is built of small calcite crystals (Fig. 4, A, B, E), which are enclosed by a matrix of organic membranes. The outer lamella is traversed by pore channels belonging to the normal setae (sensilae). The nervous cell of these setae are located in an rounded space within the calcified procuticle (Fig. 4, A, B). In the case of the Herpetocypridini we noticed that vacuolar voids occur within the procuticle (Fig. 4, A) which in transmitted light resemble small dots. Some of these voids are pyriform (Fig. 4A), others are rounded (Dépèche, pers. comm.). In the case of *Herpetocypris* aff. *brevicaudata, Candona neglecta* and *Microdarwinula zimmeri,* where the valves are transparent, the crystals of the outer lamella are tightly packed and oriented with the flat side parallel to the lateral side of the valve. Those areas where the wall is spongeous (i.e. where voids occur between the calcitic layer) appear opaque in transmitted light. For example see the central muscle scars of *Microdarwinula zimmeri* (Fig. 2, C, D) or the vacuolar voids in the case of the previously mentioned herpetocyprines.

Most podocopid ostracods moult eight times. During each moult the calcified carapace separates from the soft body. Those carapaces with poorly developed hinge structures, such as the Cypridacea, Darwinulacea and most limnic Cytheracea, readily disarticulate after each moult, which explains why mainly separate juvenile valves of these groups are found. Only in the case of a catastrophic mortality will the number of juvenile carapaces be higher than those of the separate valves. We call this latter situation the 'Whatley effect' after the author who first discussed the taphonomical implications of this process (Whatley, 1983). The 'Whatley effect' can be observed in the case of a sudden desiccation of shallow water bodies (we observed this among ostracods in karstic pools and channels in several caves in France and Romania, as well as in tem-

Fig. 1. Various types of preservation of fossil and subfossil ostracod valves. A – *'Candona'* sp., aff. *lobata* (Zalany), adult (Sintesti, Upper Pannonian), left valve with holes and fractures; B – *'Candona'* sp., aff. *lunata* (Méhès), juvenile (Grosi, Upper Pannonian), left valve with superficial microborings and holes; C – *'Candona'* sp., adult? (Sintesti, Upper Pannonian), right valve (broken) with holes, fractures, superficial microborings and opaque areas around the pore canals; D–F–*Candona neglecta* Sars, juveniles (Mondsee, 47 m depth, Recent); D – left valve (broken) with holes, and with superficial microborings; F – right valve with holes and fractures, etched in glycerine (pH-5.3).

porary pools, in the wetlands, formed during the spring).

Danielopol (1980) showed, that during the last part of the life of an adult ostracod (i.e. when the sexual activity usually stops), the animal moves slowly, especially with its limbs being hardly retracted within the carapace, even when physical and/or biological disturbances occur. At the end of

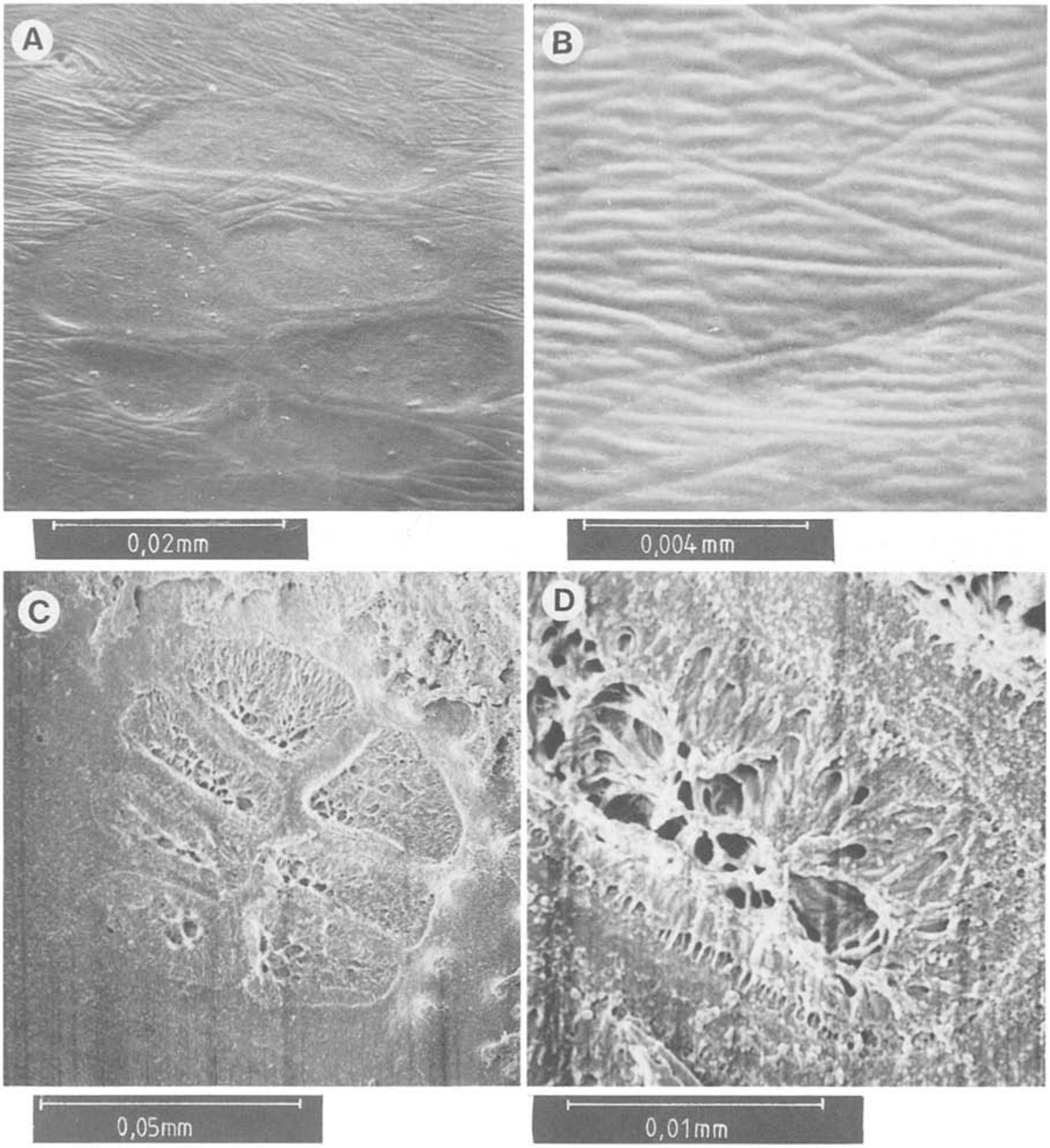


Fig. 2. Details of the outer and inner sides of the valve surface A, B – *Mixtacandona* sp., aff. *chappuisi* Klie, adult, living (Cuhea, Recent), right valve, outer surface in the central muscle scar area; A – The adductor muscle scars and the surrounding undulated epicuticle; B – detail of the epicuticle shape; C, D – *Microdarwinula zimmeri* (Menz), adult, living specimen (Caldarusani, Recent), right valve, inner surface in the central muscle scars area; C – the central adductor muscle scars with their inner spongeous structure, general view, D – detail of a muscle scars from C.

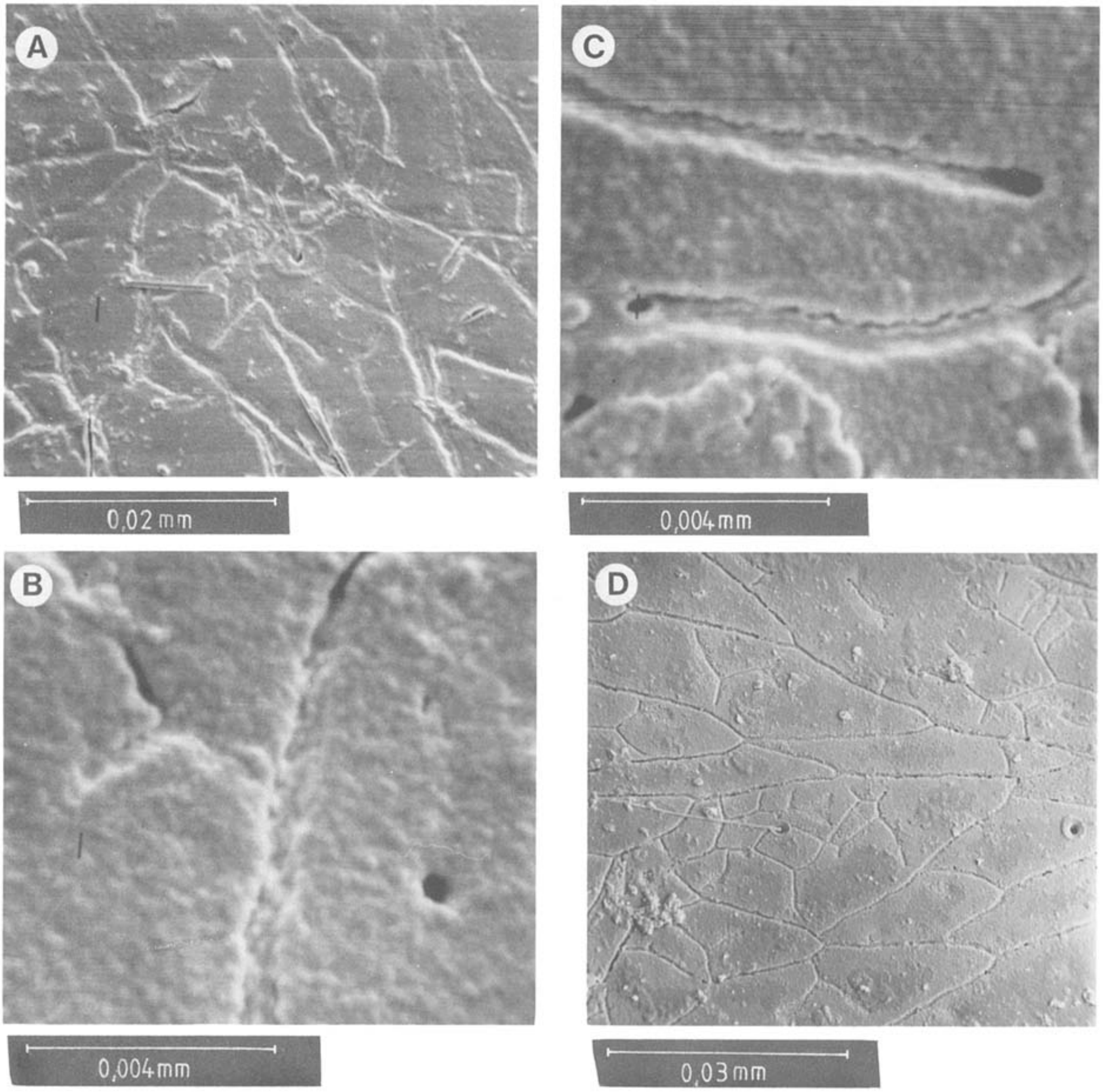
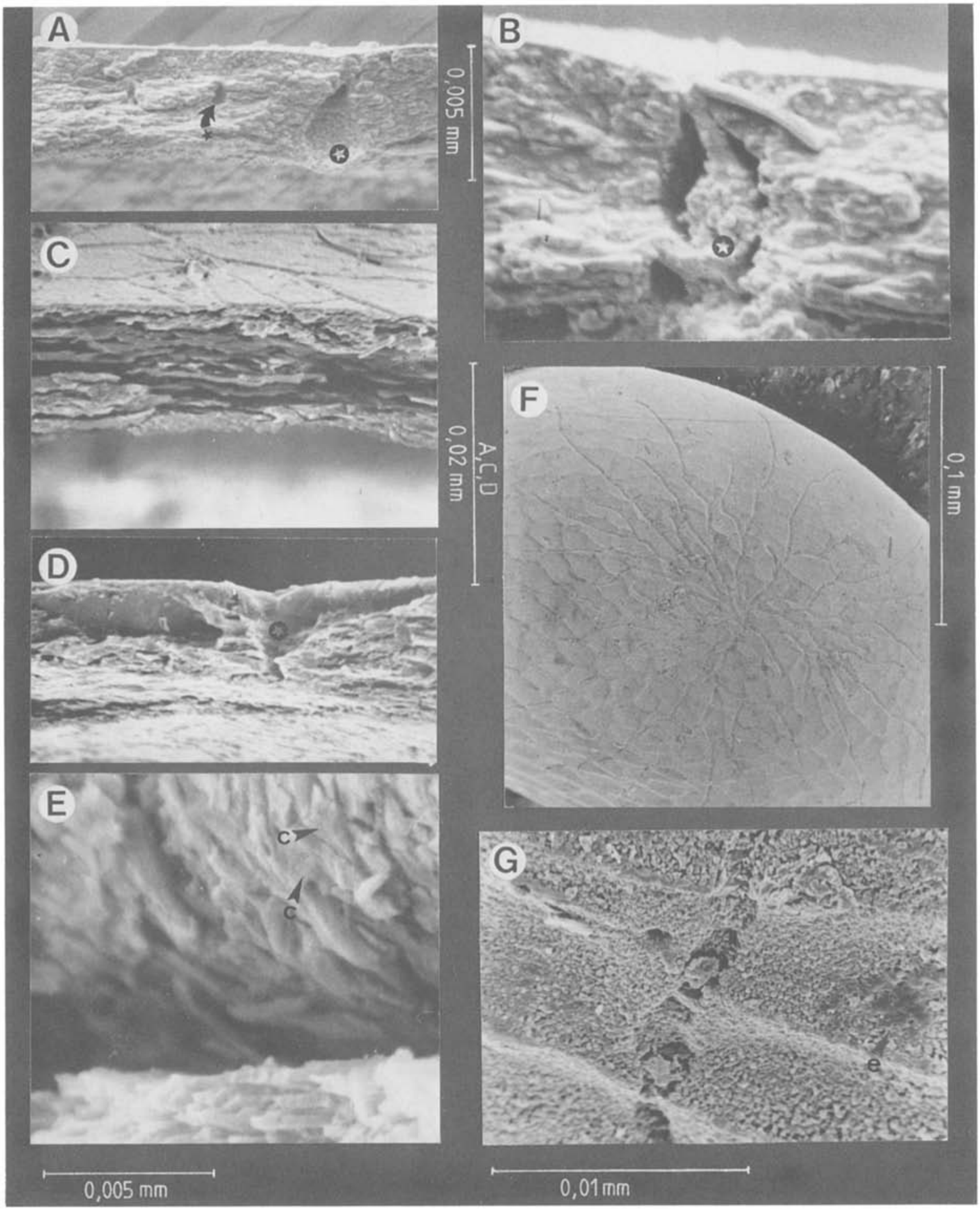


Fig. 3. Details of the superficial microborings on the outer side of the carapace; A – C – *Herpetocypris* sp., aff. *brevicaudata* Kaufm. (Gogosu, Recent), adult left valve; D – *Pseudocandona serbani* Dan. (Jiblea, Recent), juvenile, right valve.

this senile phase, the animal dies with, in most cases, its carapace open. Also, when living in waters of low oxygen or on substrates rich in organic matter and with high densities of epizoic microorganisms (bacteria, fungi, Protozoa) the ostracod will also die with its carapace open. During adverse life conditions, some ostracods can enter a torpid phase (i.e. they remain for longer periods of time with the carapace closed). Such situations occur during low temperature (Delorme & Donald, 1969) and/or poor food conditions, or during the partial desiccation of the sediment. In these latter instances, ostracods will die from this case with the valves remaining closed.

The soft body of those ostracods which die with the carapace open eventually decomposes due to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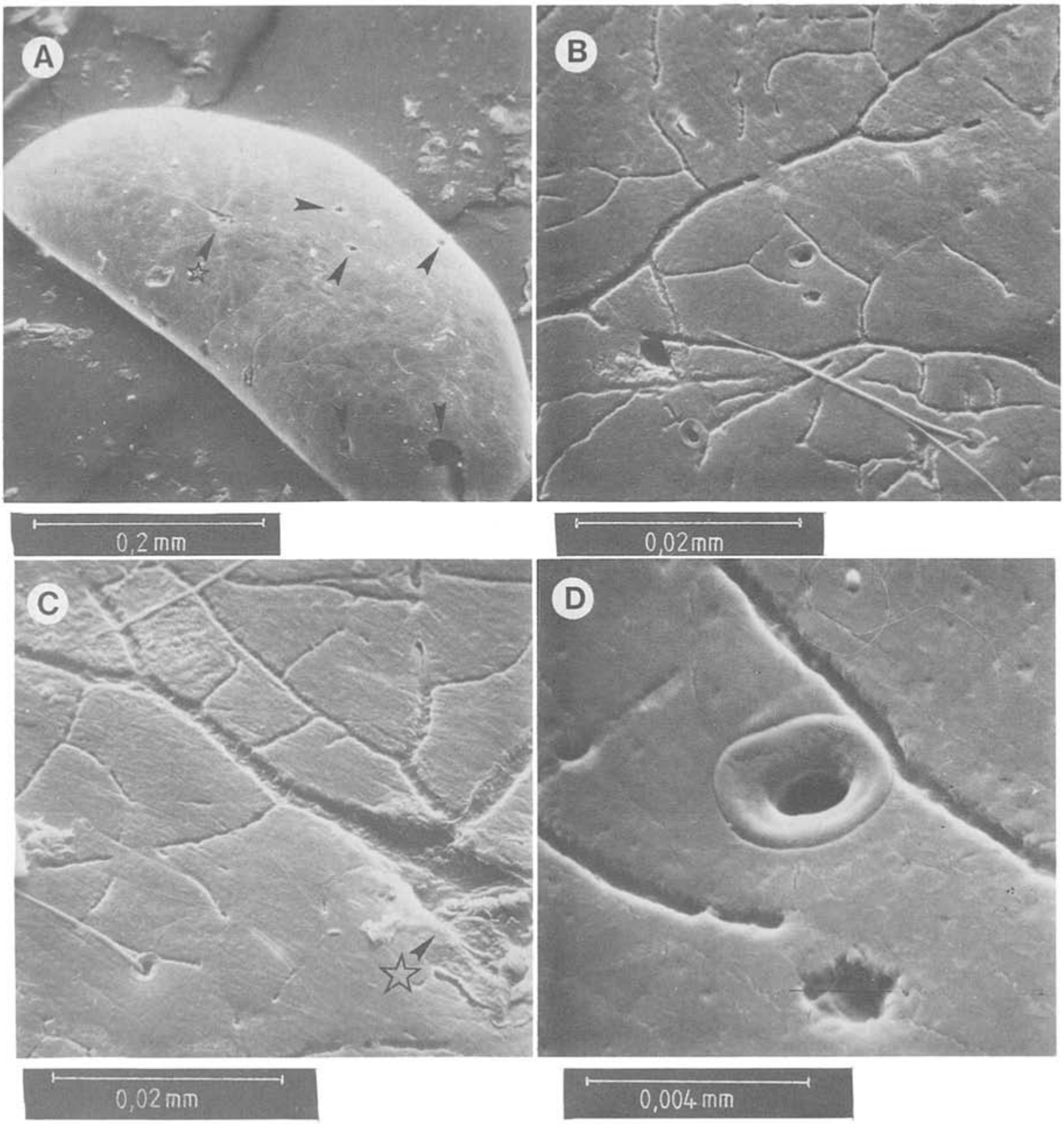

Fig. 5. Details of the superficial microborings and holes (arrows) on the outer side of a valve; *Mixtacandona* sp., aff. *chappuisi* Klie (Cuhea, Recent), adult, left 'dead' valve; A – general view; B – D – details of the microborings and holes around a normal pore opening.

tion of the calcitic layer and, therefore, the penetration of the microorganisms into the inner part of the valve.

Microborings such as those we describe from Recent ostracods (i.e. *Mixtacandona* sp., *Herpetocypris* aff. *brevicaudata, Candona neglecta, Leucocythere mirabilis*) can be also seen in fossil Neogene ostracods (*Bakunella dorsoarcuata* (Fig. 4, F, G), *'Candona'* aff. *lobata* (Fig. 1, A) and *'Candona'* aff. *lunata* (Fig. 1, B) from the Upper

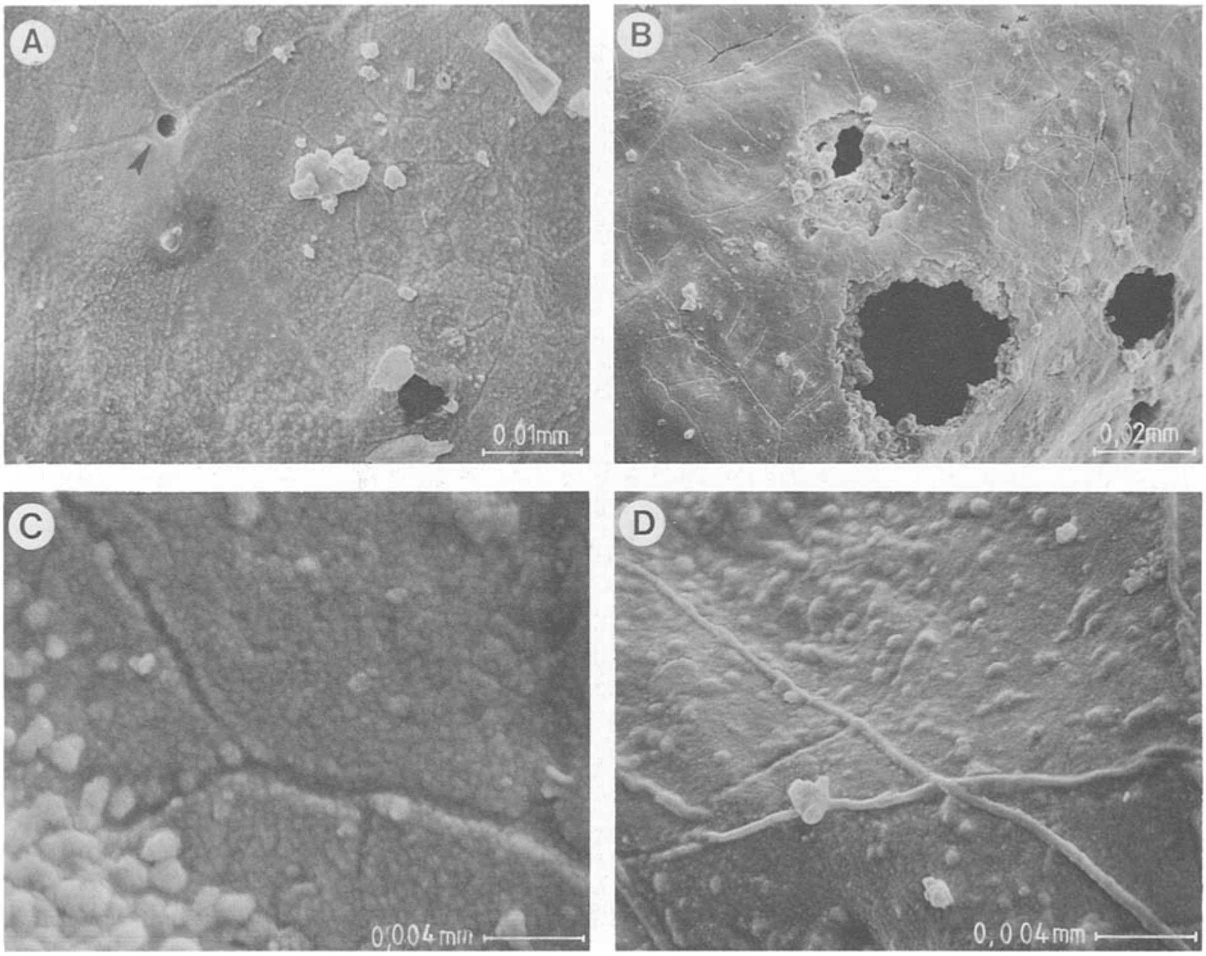

Fig. 6. Details of a 'dead' valve with microborer (bacteria or fungi), microborings and holes; *Leucocythere mirabilis* Kaufm. (Mondsee, Recent), adult, right valve. A – details of microborings around a 'normal' pore canal: B, C – details of microborings and holes; D – hyphae of a microborer.

Pannonian (Miocene) and the Pliocene of the Paratethys). Freels (1980) figured Candoninae valves from Pliocene limnic sediments of Turkey with microborings. All these data suggest that the biological corrosion of limnic ostracods by fungi and/or filamentous bacteria like Actinomycetes is a very common phenomenon and which has a history of at least 11 My years (our oldest material is Upper Miocene). It is worth mentioning that the microborings of marine ostracods differ in shape and structure (e.g. see the microborings of *Agrenocythere pliocenica* figured by Benson, 1972).

It is interesting to note that microborings have never been noticed on carapaces of living ostracods, despite the fact that fungi and/or filamentous bacteria can cover the surface of the shell (Fig. 7, E). However, Okafor (1966) found that the chitinoclastic microorganisms are inhibited by phenolic compounds. In the case of the ostracods studied here, it is likely that, only after death of the organism, a chemical alteration of the molecular structure of the epicuticle occurs, thus allowing the activity of microborers to start. Veldkamp (1955) and Warnes and Randles (1977) noted that the activity of chitinoclastic bacteria was strongly diminished under anaerobic conditions. Further, Schrader *et al.* (1983:225) noted that 'carbonate derived from Foraminifera and calcareous nan-

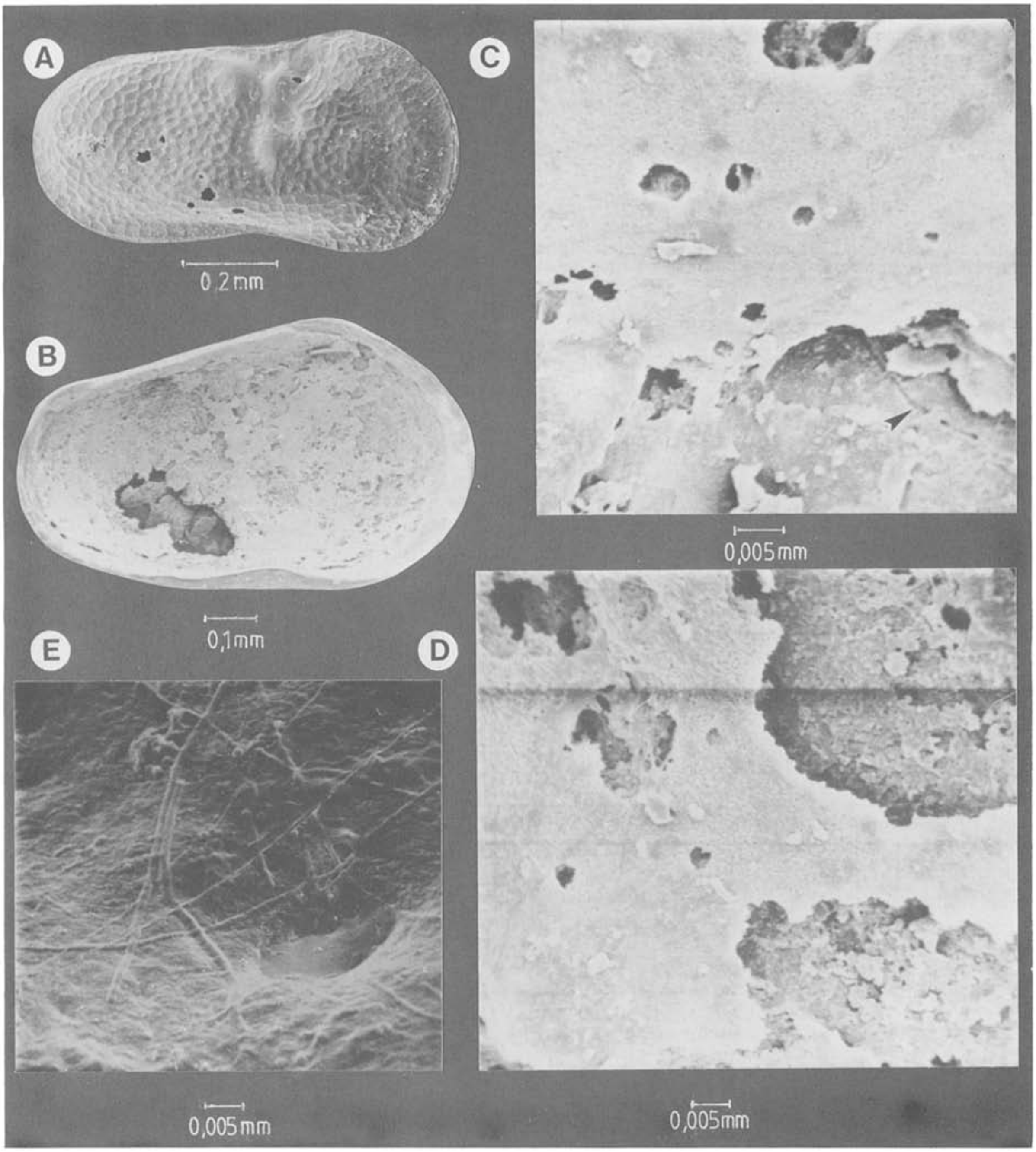

Fig. 7. 'Dead' valves after biological and chemical corrosion; A – *Leucocythere mirabilis* Kaufm. (Mondsee, Recent), adult, right valve, general view; B – E – *Cytherissa lacustris* Sars, adult, left valve (B–D); B – general view inner side; C, D – details of the corroded (calcite) procuticle; arrow indicates a deep microboring tube within the calcite layer; E – outer surface of the carapace covered with filamentous bacteria or fungi.

noplankton can occasionally be better preserved in oxygen depleted depositional environments'. In the case of the ostracods, one should expect that for the valves which remain for only a short time in contact with an oxic environment (e.g. they are rapidly burried in habitats of high sedimentation and/or the sediment becomes anoxic, the activity of microborers on them will be lower than in oxic environments and/or in habitats with a low sedimentation rate (see below).

b. Holes

Our material shows several types of holes which are caused by microborers and also which result from partial dissolution by acid water. Already noted are shallow holes most probably initiated by the sporangia of microborers. Their shape is triangular or polygonal. Other holes could be initiated by the mechanical destruction of the epicuticle which, in some places, does not tightly adhere to the procuticle (Fig. 5, D). The dissolution of the inner calcified procuticle will deepen those holes down to the perforation of the valve (Fig. 6, B). A second type of hole is caused by the enlargement of the normal pore canals and/or the vacuolar voids, through the destruction of the organic matrix and the dissolution of the calcitic structure (Fig. 1, C, 4, D, 6, A, B). The activity of 'agressive' water further dissolves the carbonate and the inner structure of the procuticle form a kind of micro-karst topography (Fig. 4, C, D). This is seen in *Herpetocypris* aff. *brevicaudata* studied here. Simple chemical corrosion can start from the inner side of the procuticle as in *Cytherissa lacustris* (Fig. 7, B–D). The presence of large inner and unstructured voids causes those areas to appear opaque and chalky; this is best seen under transmited light (e.g. Fig. 1, C). We produced similar holes by etching a valve of *Candona neglecta* (Fig. 1, C) which was kept in glycerine (pH 5,3) for a week. The shallow channels of the microborers became especially enlarged and the surrounding area became opaque. Flessa & Brown (1983) obtained similar results through experiments on bivalves. Thin valves with a spongeous central muscle scars area, like in *Leucocythere mirabilis,* are particularly exposed to perforation and hole formation.

c. Fractures

Biologically and chemically corroded carapaces/or valves become biomechanically weakened and fracture more easily (Fig. 1, A, D, F). However, we did not observe a strict correlation between the network of microborings and holes with the directions of fractures. As Whatley *et al.* (1982) observed experimentally, the fracturing of a valve or carapace is the result of the mechanical stress which forms on the whole calcified wall. A fracture can start from holes or can traverse the tracks of microborings which become paths of weakness (Fig. 1, A, D, F). The valves of limnic ostracods in high energy environments, as in littoral habitats, are already corroded and, therefore, particularly prone to perforation and fracture (see following section). Similar observations were made by Phillippon and Plaziat (1975) in their study of gastropod shells from an African mangrove area.

5. Relationships between the degree of carapace and/or valves preservation and sediment accumulation rates

Oertli (1971: 139) pointed out the interest petroleum geologists have in finding paleoecological indicators for environments with high rates of sediment accumulation and of low oxygen. He stated (op.cit.): 'A relatively rapid sedimentation rate must in effect increase the chances for hydrocarbon formation... The higher the sedimentation rate... the greater chances of a sufficiently rapid burial so that the organic matter will not be mineralized and thus retain the potential for a later, and partial, transformations into hydrocarbons.'

In order to check such a relationship between ostracod preservation and the degree of the sediment accumulation, we investigated the rate of sedimentation in the Mondsee for the last 20–30 years (Irlweck & Danielopol, 1985). Secondly, we looked in a semiquantitative fashion at the degree of ostracod preservation (of whole assemblages) at sites with various types of sediment accumulation (low rates in sub-littoral habitats to high rates in profundal deposits (D.L.D. unpubl.). Finally, one of us (L.M.C.) quantified for a single species, *Candona neglecta,* the degree of preservation at various sites of the Mondsee where the history of the sediment accumulation was already known.

Until 30 years ago the Mondsee remained a mesooligotrophic lake with well oxygenated water in the whole lake. At the time such species as *Cytherissa lacustris* were more common than today (Danielopol *et al.,* 1985). During the late fifties, and early sixties, during the construction of the adjacent Vienna-Salzburg highway, about 900000 m^3 of soil was discharged into the lake, thus dramatically increasing the sedimentation rates at least in the central part. Subsequently from the end of sixties, the lake experienced annual algal blooms as a result of increasing tourist activity, and sewage discharge into the lake. All these factors increased the rate of autochthonous sediment deposition within the lake (Schmidt *et al.,* 1985). Irlweck & Danielopol (1985) showed by using the Cs-137 and Pb-210 dating methods that in the profundal zone of the northern and central part of the Mondsee, the mean annual sedimentation rates varied between 4 and 7 mm/yr. These areas were subjected during the last years to major allochthonous and autochtonous sediment accumulation. In those areas, during the late summer and the autumn, oxygen content becomes greatly depleted. In the southern part of the lake, and on the slopes of the sublittoral zones (18 – 20 m depth), sedimentation rates are much lower i.e. 0.5 – 2.5 mm/yr. In the latter areas, good levels of oxygenation occur and delicate species such as *Cytherissa lacustris* still form abundant populations. We studied samples from site Mo-7 at a depth of 16 and 18 m, 2 – 3 cm below the water sediment interface. At that site, Irlweck & Danielopol (1985) measured annual sedimentation rates which vary between 0.5 and 2.5 mm for the last 20 – 30 years. For comparative purposes, samples from the northern part of the lake (Mo-9, 47 m depth) were also studied. There annual sedimentation rate of 6.2 mm/y were found in the upper 15 cm sediment (see Irlweck & Danielopol, 1985 and Danielopol *et al.,* 1985).

Examination of the sediment from site Mo-9 reveals that the stratigraphical sequence (Fig. 9, A) can be divided into three zones. Between depths of 30 cm and 16 the sediment is grey and more or less homogeneous; the silt fraction dominates with also a small sand fraction; between 16 and 9 cm the sediment is slightly light grey and contains a significant fraction of gravel (Fig. 9, B). This sediment most probably represents the event of discharge of the large amount of refuse during the period of the highway construction. The upper part of the sediment column is strongly laminated, with black and light coloured lamellae; this has been produced since 1968 and is the result of sedimentation of autochthonous algae which seasonally decay (Schmidt *et al.,* 1985). The black layers are due to the pyrite formation under anoxic conditions.

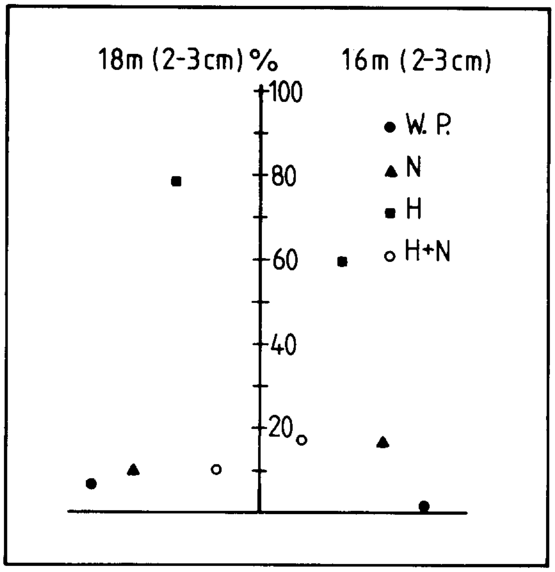

Fig. 8. Distribution of various types of valves in the sediments of the Mondsee (site MO-7, 18 m depth, 2 – 3 cm below the water sediment interface); WP – valves well preserved; N – valves with a network of microborings; H – valves with holes; NH – valves with microborings and holes; for each sample 100 valves examined.

Fig. 8 shows that for *Candona neglecta* the percentage of well preserved (WP) valves is very low at site Mo-7 at 16 and 18 m depths, and the percentage of the valves with microborings and with holes (also including fractures) is high.

Investigation of the preservation of *Candona neglecta* (Fig. 9, C, D), shows that in the lower part of the sedimentary column (which was deposited during a period of low sedimentation rates when compared with the upper half, viz. from 15 – 16 cm) the degree of well preserved valves is low, and a fairly high percentage of valves with a network of microborings occurs. The opposite is visible in the upper part of the column, where the percentage of well preserved valves increases substantially and the corroded ones decrease. In this latter zone, a higher rate of sedimentation is noticeable for the last decades; in the upper part, the sediment is also periodically anoxic. We believe that the

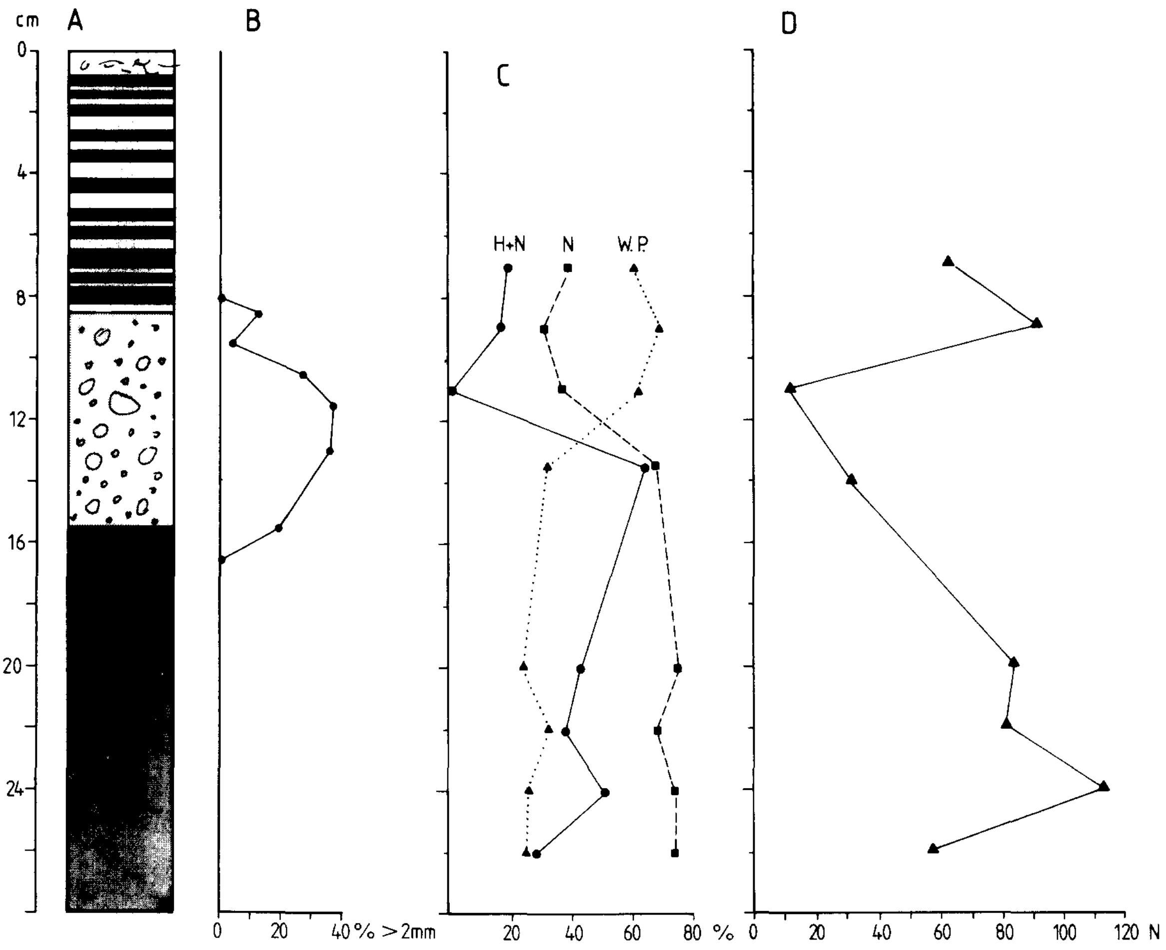

Fig. 9. Sediment core from the site MO-9, at a depth of 47 m (Mondsee) and the distribution of various types of valves of *Candona neglecta* Sars; A – Stratigraphic column; B – distribution of the gravel size fraction in the core; C – ostracod distribution; well preserved valves (WP); (N) – valves with a network of superficial microborings, (H) – valves with holes; (D) – the number of valves which have been examined for the degree of preservation.

better degree of preservation of *Candona neglecta* valves, in the latter part of the core, is due to the faster burial processes and to the shorter time during which the ostracod shells remain in contact within an oxic medium. This scenario is very similar to the one observed by Schrader *et al.* (1983) for the foraminifers and nannoplankton as mentioned previously. In conclusion, we believe that the degree of ostracod preservation can be also related to the type of sedimentation. For example, within a quiet environment and with high sedimentation rate and rapid formation of anoxic sediments, carapaces and/or valves of limnic ostracods become isolated from extensive biological and/or physico-chemical degradation. This observation surely would be of interest to the petroleum industry. Therefore, more investigations on fossil material are needed in order to test this model derived on a Recent ostracod species.

6. Why are there so few herpetocyprines in the Palaeogene of Europe?

The main genera of the tribe Herpetocypridini (Cypridinae) can easily be recognized from the morphological structures of the limbs and of the carapace (Danielopol & McKenzie, 1977). The representatives of the genera *Herpetocypris* Sars and *Psychrodromus* Dan. & McKenz. are widely distributed in cool temperate waters. On the other hand, representatives of the genera *Stenocypris* Sars, *Acocypris* Vavra, *Chrissia* Hartm., *Parastenocypris* Hartm. mainly occur in warm temperate and subtropical regions (e.g. in Africa, Asia and Central America (McKenzie, 1971). Identification of *Stenocypris* is especially easy by the structure of the carapace alone because of the radial septa which unite the external and the inner calcareous lamellae. Triebel (1953), for example, found a *Stenocypris* sp. in the Chattian (Upper Oligocene) lacustrine sediments of the Mainz Basin in Europe.

The palaeoenvironment during the Eocene and the Oligocene in Europe was subtropical to warm temperate (Pearson, 1978). Despite this similarity and the fact that lacustrine ostracods are well known from several Eocene and Oligocene deposits of England, France and Germany (see review in Keen, 1975) herpetocyprines have been seldom found (Triebel, 1953). Triebels sample consists of 30 broken valves of *Stenocypris.* We believe that the scarcity of thermophilous herpetocyprines in the fossil record in Europe could be due to the poor preservation of the carapaces and/or valves after the death of these ostracods. Following the model of the degration of the *Herpetocypris* aff. *brevicaudata* presented above, it is very likely that the thermophilous herpetocyprines, like the *Stenocypris* species, which have a high density of vacuolar voids in the procuticle, suffer corrosion under high temperatures and 'agressive' water more easily than other limnic cypridids and cytherids which benefit from a compact calcitic layer. This should explain why in so few Palaeogene herpetocyprines have been found so far.

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References

Bate, R. H. & B. A. East, 1972. The structure of the Ostracoda carapace. Lethaia 5: 177–194.

Benson, R. H., 1972. The Bradleya problem, with descriptions of two new psychrospheric Ostracoda genera, *Agrenocythere* and *Poseidonamicus* (Ostracoda: Crustacea). Smithson. Contr. Paleobiol. 12, 138 pp.

Danielopol, D. L., 1982. Nouvelles données sur les Candoninae (Ostracoda) hypogés de Roumanie et Yougoslavie. Bull. Mus. natn. Hist. nat. Paris, 4ser. 4, A: 369–396.

Danielopol, D. L. & K. G. McKenzie, 1977. *Psychrodromus* gen.n. (Crustacea, Ostracoda) with redescription of the cypridid genera Prionocypris and Ilyodromus. Zool. Scr. 6: 301–322.

Danielopol, D. L., W. Geiger, M. Tölderer-Farmer, C. P. Orellana & M.-N. Terrat, 1985. The Ostracoda of Mondsee: spatial and temporal changes during the last fifty years. In D. Danielopol, R. Schmidt & E. Schultze (eds.). Contributions to the paleolimnology of the Trumer Lakes (Salzburg) and the lakes Mondsee, Attersee and Traunsee (Upper Austria). Limnol. Inst. ÖAW, Mondsee: 99–121.

Delorme, D. & D. Donald, 1969. Torpidity of freshwater ostracodes. Can. J. Zool. 47: 997–999.

Depeche, F., 1979. Ultrastructure de la paroi externe des 'micro-Ostracodes' du Jurassique moyen normand. N. Jb. Geol. Paläont. Mh. 1979/6: 340–348.

Depeche, F., 1982. Ultrastructure of the wall of two living ostracods, *Herpetocypris chevreuxi* (Sars) and *Pontocythere elongate* (Brady), in comparison with fossil ostracods from the Middle Jurassic of Normandy. In R. H. Bate, E. Robinson & L. M. Sheppards (eds.). Fossil and Recent ostracods. Ellis Horwood Ltd., London: 61–75.

Flessa, K. W. & T. J. Brown, 1983. Selective solution of macroinvertebrate calcareous hardparts: a laboratory study. Lethaia, 16: 193–205.

Freels, D., 1980. Limnische Ostrakoden aus Jungtertiär und Quartär der Türkei. Geol. Jahrb., 39: 3–169.

Frydl, P. M., 1982. Holocene ostracods in the southern Boso

Peninsula. In: T. Hanai (ed), Studies on Japanese Ostracoda. Univ. Mus. Univ. Tokyo Bull., 20: 61–140.

Irlweck, K. & D. L. Danielopol, 1985. Caesium-137 and lead-210 dating of recent sediments from Mondsee (Austria). Hydrobiologia 128: 175–185.

Jagnow, G., 1957. Beiträge zur Ökologie der Streptomyceten. Arch. Mikrobiol., 26: 175–191.

Keen, M. C., 1975. The palaeobiology of some upper Palaeogene fresh-water ostracodes. Bull. Am. Paleont. 65: 271–283.

Kontrovitz, M., 1966. An investigation of ostracode preservation. Florida Acad. Sci. Quart. J., 29: 171–177.

McKenzie, K. G., 1971. Paleozoogeography of freshwater Ostracoda. In H. J. Oertli (ed), Paleoecologie Ostracodes. Bull. Centre Rech. Pau – SNPA, 5 suppl.: 207–238.

Oertli, H. J., 1971. The aspect of ostracode faunas – A possible new tool in petroleum sedimentology. In H. J. Oertli (ed), Paleoecologie Ostracodes. Bull. Centre Rech. Pau – SNPA, 5 suppl.: 137–151.

Oertli, H. J., 1951. The conservation of ostracode tests – Observations made under the scanning electron microscope. In F. M. Swain, L. S. Kornicker & R. F. Lundin (eds), Biology and Paleobiology of Ostracoda. Bull. Am. Paleont. 65: 549–576.

Okada, Y., 1982. Structure and cuticle formation of the reticulated carapace of the ostracode *Bicornucythere bisanensis*. Lethaia, 15: 85–101.

Okafor, N., 1966. The ecology of micro-organisms and the decomposition of insect wings in the soil. Plant Soil, 25: 211–236.

Olteanu, R., 1971. Study of ostracods within the Upper Pannonian deposits (zone E) from Grosi Locality (Banat). D. S. Inst. Geol. Bucuresti, 57: 85–101 (in romanian, english abstract).

Pearson, R., 1978. Climate and evolution. Academic Press, London, 274 pp.

Philippon, J. & J.-Cl. Plaziat, 1975. Roles respectifs de la corrosion et des Cryptrogames perforantes dans la destruction des coquilles de Mollusques des mangroves. Consequence sur la fossilisation. C.r. Acad. Sci. Paris D 281: 617–620.

Rögl, F. & F. F. Steininger, 1983. Vom Zerfall der Tethys zu Mediterran und Paratethys. Die neogene Paläogeographie und Palinspastik des zirkum-mediterranen Raumes. Ann. Naturhist. Mus. Wien 85/A: 135–163.

Schmidt, R., J. Müller & J. Froh, 1985. Laminated sediments as a record of increasing eutrophication of the Mondsee. In D. Danielopol, R. Schmidt & E. Schultze (eds), Contributions to the paleolimnology of the Trumer Lakes (Salzburg) and the lakes Mondsee, Attersee and Traunsee (Upper Austria). Limnol. Inst. ÖAW, Mondsee: 122–131.

Schrader, H., G. Cheng & R. Mahood, 1983. Preservation and dissolution of foraminiferal carbonate in an anoxic slope environment, southern gulf of California. In J.E. Meulenkamp (ed) Reconstruction of marine paleoenvironments. Utrecht Micropaleontological Bulletins: 205–227.

Triebel, E., 1953. Genotypus und Schalenmerkmale der Ostracoden-Gattung *Stenocypris*. Senckenbergiana, 34: 5–14.

Veldkamp, H., 1955. A study of the aerobic decomposition of chitin by microorganisms. Med. Landbouw. Wageningen 55: 127–174.

Warnes, C. E. & C. I. Randles, 1977. Preliminary studies on chitin decomposition in lake Erie sediments. Ohio J. Sci., 77: 224–230.

Whatley, R., 1983. The application of Ostracoda to palaeoenvironmental analysis. In R. Maddocks (ed), Applications of Ostracoda to economic and scientific problems. Univ. Houston, Houston: 51–77.

Whatley, R. C., K. Trier & P. M. Dingwall, 1982. Some preliminary observations on certain mechanical and biophysical properties of the ostracod carapace. In R. H. Bate, E. Robinson & L. M. Sheppard (eds), Fossil and Recent ostracods. Ellis Horwood Ltd., London: 76–104.

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