USE OF OSTRACODES AS PALEOENVIRONMENTAL TOOLS IN THE INTERPRETATION OF ANCIENT LACUSTRINE RECORDS

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ABSTRACT

Lacustrine ostracodes have been studied during the last three decades because of their apparent utility in reconstructing aquatic paleoenvironments. These microcrustaceans are ideal for paleoenvironmental analysis because: 1) they are cosmopolitan and abundant lacustrine inhabitants; 2) they show high diversity; 3) they are sensitive to climate-related limnological variations; 4) their valves incorporate some trace elements from host waters that may provide information on paleolimnologic conditions; and 5) valve calcification appears to be in stable carbon and oxygen isotope equilibrium with the host water.

The purpose here is to compare the recent advances in these various approaches, as well as their limitations in paleolimnologic reconstructions. It is evident that our current knowledge is far from complete, but it is also true that the progress achieved has established a basis for quantitative paleoenvironmental reconstructions using nonmarine ostracodes.

Keywords: **Continental ostracodes, paleoenvironments, paleoecology, paleoclimate, hydroclimate, local atmospheric climate, regional climate, trace elements, stable isotopes.**

RESUMEN

Los ostrácodos lacustres han sido objeto de estudio durante las últimas tres décadas por su aparente utilidad en la reconstrucción de paleoambientes acuáticos. Estos microcrustáceos son ideales para análisis paleoambientales por las siguientes razones: 1) son cosmopolitas y abundantes en aguas continentales; 2) muestran gran diversidad; 3) son sensibles a variaciones limnológicas relacionadas con el clima; 4) sus valvas incorporan algunos elementos traza derivados del agua en que habitan, que pueden proporcionar información sobre las condiciones paleolimnológicas, y 5) la calcificación de las valvas parece ocurrir en equilibrio isotópico con el oxígeno y carbono del agua en la que viven.

El propósito de este trabajo es comparar los avances recientes y las limitaciones interpretativas de las reconstrucciones paleolimnológicas mediante el uso de ostrácodos. Es evidente que aún queda mucho por hacer en este campo antes de establecer conclusiones definitivas, pero también es claro que los progresos alcanzados han sentado las bases para reconstrucciones paleoambientes cuantitativas confiables usando ostrácodos continentales.

Palabras clave: **Ostrácodos continentales, paleoambientes, paleoecología, paleoclima, hidroclima, clima atmosférico local, clima regional, elementos traza, isótopos estables.**

INTRODUCTION

Until about 1960 most ostracode scientists focused their research on the taxonomic features of the numerous marine and nonmarine species. During the 1960's some workers became interested on the environmental utility of continental ostracodes and developed experimental and field studies to understand the relationship between these organisms and their environment (Benson, 1959; Löffler, 1961; Delorme, 1969, 1978; Turpen and Angell, 1971; Cadot and Kaesler, 1977; Bodergat, 1985; Forester, 1983, 1986, 1991a; De Deckker, 1981, 1983, Cohen et al., 1983, Cohen, 1986; Anadón et al., 1986; Carbonel et al., 1988). During the 1980's and there after, many researchers have used fossil ostracodes to reconstruct the history of ancient lakes either by means of their paleoecologic assemblages and occurrence patterns or with geochemical techniques (Chivas et al., 1983; 1985, 1986a, b; De Deckker et al., 1988a, b; Lister, 1988a, b, 1989; Anadón and Juliá, 1990; Benson et al., 1991; Engstrom and Nelson, 1991; Holmes et al., 1992; Palacios-Fest et al., 1993; Anadón et al., in press).

This paper reviews the current use and significance of nonmarine ostracodes as paleoenvironmental indicators in light of current progress, and highlights both the potential utility and the pitfalls of the various analytical methods now in use.

OSTRACODES IN THE LACUSTRINE REALM: AN ECOLOGIC PERSPECTIVE

Ostracodes are bivalved crustaceans equipped with a low Mg-calcite carapace attached by a dorsal hinge

and a ligament (Pokorný, 1978). Continental ostracodes are widely distributed in fresh and saline waters, normally under well oxygenated conditions. They occur in lakes, ponds, springs and streams. A knowledge of modern ostracode response to physico-chemical and biotic environment is critical to interpret the paleoecology of these organisms in the geologic record. Many ostracode species are benthic, crawling on the substrate, moving interstitially between sediment grains or swimming just over the sediment surface or around subaquatic vegetation. A few nektonic lacustrine species also occur. Most ostracode species subdivide a broad range of lake environments, from freshwater to hypersaline, from subpolar to tropical climates and from shallow nearshore to deep water into well-defined habitats. Under such circumstances, a number of factors affect ostracode occurrence, distribution and productivity. The best documented of these factors are temperature, ionic composition and concentration, oxygen content of the water, substrate and food resources. In addition, the size, depth, energy level, turbidity and permanence of the water body as well as predation can be significant limiting factors for ostracode species (Holmes, 1992).

Environmental Controls on Ostracodes Within Lakes

Figure 1 synthesizes some of the most significant factors controlling ostracode distribution in limnic environments. The nature of the water body and substrate exert considerable control over ostracode populations.

Ostracodes are likely to respond directly to depth correlated factors such as temperature, light penetration (affecting vegetation) or sediment texture (affecting the ability of bottom crawlers to move; see for example: Kotzian, 1974; Keen, 1975; Danielopol et al., 1985; Cohen, 1986 and Mourguiart et al., 1986) rather than depth itself.

Substrate is an important control on ostracode distribution in a lake and several species appear to be restricted to fine sediments (e.g. some species of the genus Candona; Holmes, 1992). Lacustrine ostracodes usually have a smooth carapace; however, it is not uncommon to find some species ornamented or equipped with "stabilizers" (particularly among surface crawlers). Populations of some species adapted to coarse sediments or hard substrate have robust carapaces (e.g. Cypridopsis vidua; Henderson, 1990). However, valve thickness may also be driven by other factors, such as water chemistry (ecophenotypic) and predation (selective). Zonation related to lateral differences in substrate have been suggested to occur in several lakes (Carbonel et al., 1988; Holmes, 1992).

Wave energy levels are also important factors in the environmental zonation of lacustrine ostracodes. The usually fragile nature of ostracode valves makes wave energy a restrictive factor to ostracode populations since most of these organisms cannot withstand the wave shock of the surf zone in large lakes. Although growth aquatic plants, may somehow atenuate this effect in certain lakes (i.e. Lake Titicaca; Carbonel, pers. comm., 1994). Furthermore, turbidity and food supply are directly affected by wave energy. Although most ostracode spe-
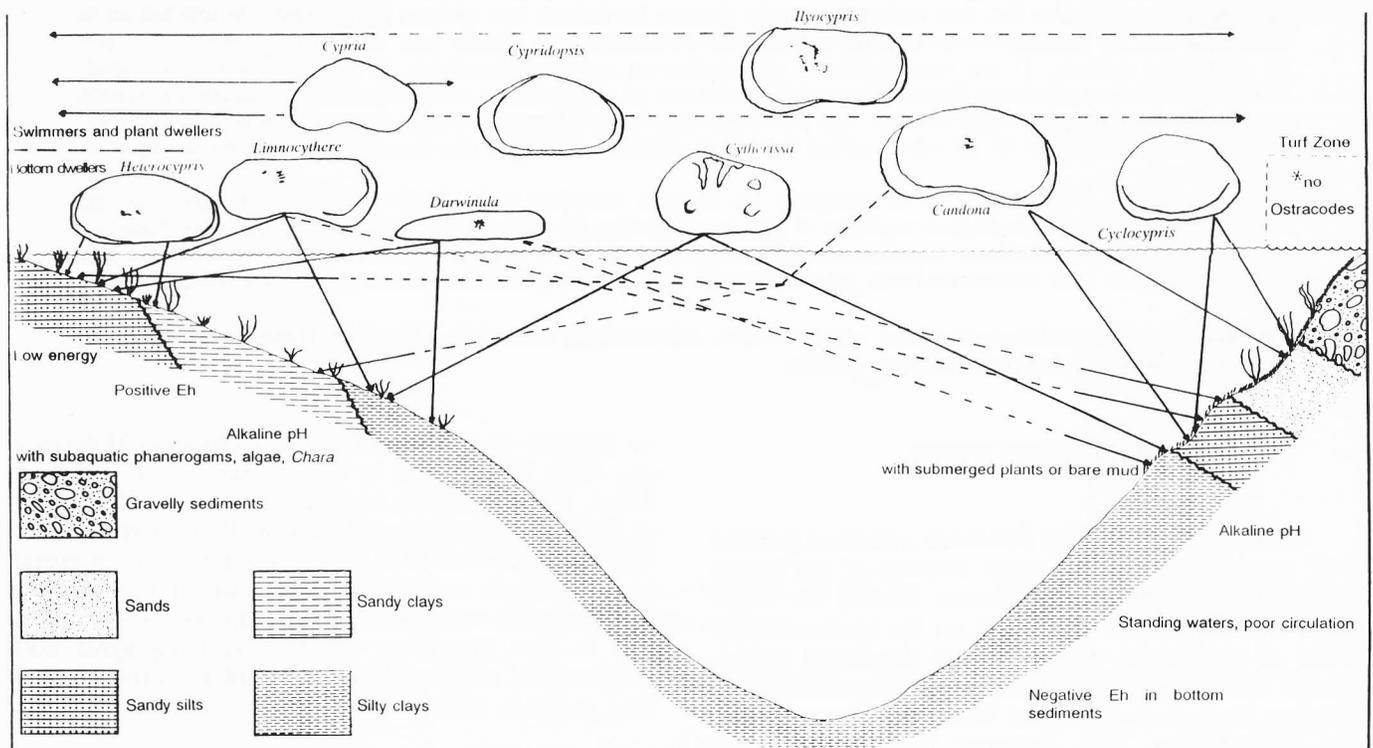

Figure 1. Occurrence of nonmarine ostracodes in a hypothetical North American lake in response to physical and biological parameters (such as substrate, light penetration, depth, wave energy and vegetation). Notice that genera shown in this diagram are only examples chosen to illustrate organisms preferences. Solid lines (→) indicate occurrence range recorded in several lakes in Canada and Northern United States. Dashed lines (----) do not necessarily indicate that the group lives in that area, it only suggests its occurrence in the shoal and steep side of a half-graben basin. *Although usually no ostracodes occur in the turf zone a few interstitial species may live here, however, their valves commonly do not get preserved in the fossil record. (Genera compiled from Delorme, 1969, 1978; and Delorme and Zoltai, 1984).

cies prefer to live in quiet slow moving waters, a few genera are represented in agitated flows near drainage inlets or outlets, for example, *Ilyocypris, Psychrodromus, Heterocypris* and *Potamocypris* (Henderson, 1990). Wave action is important in ostracode valve accumulation. Saucer-stack arrangement of ostracode valves are common in shallow waters affected by lapping (cf. Guernet and Lethiers, 1989).

River discharge points also provide appropriate conditions for certain ostracodes and it is possible to recognize mixed river/lake assemblages, or variations in saline tolerant vs. freshwater species (Vargas, 1982; Carbonel *et al.*, 1988; Fig. 2). Some ostracodes are also closely associated with groundwater discharge zones like *Cypridopsis, Cavernocypris* and *Chlamydotheca* (Forester, pers. comm, 1989, 1991a).

Biotic factors such as food supply and predation are also significant in controlling ostracode distribution in a lake. Most ostracode species are herbivores, including in their diet diatoms, filamentous algae and subaquatic phanerogams (Henderson, 1990). Detritivores, scavengers and predaceous species also occur. Predators, such as the nektonic ostracodes in Australian salt lakes (De Deckker, 1983) or species in British lakes (Henderson, 1990), feed on desmids, protozoans, rotifers and other small organisms (including small ostracodes). Although ostracodes are rarely a primary food item they are subject to regular predation by fish (e.g., gut contents of Pyramid Lake chubs filled with ostracodes). Where fish occur (mostly in permanent water bodies) large, and hence conspicuous, ostracode species may be excluded. However, ephemeral basins commonly deprived of fish, provide the ideal environment for a number

of species. Taylor (1992) has shown that some ostracode species are very sensitive (both negatively and positively) to human disturbance. *Cypridopsis okeechobei* for example, increases in abundance in more disturbed environments where diverse pollutants or modification of the land use contribute to changes in the water chemistry. Cohen *et al.* (1993) have shown that ostracode diversity is significantly reduced in Lake Tanganyika in areas where excessive quantities of sediment have been discharged into the littoral zone as a result of deforestation and erosion. Thus, ostracode response to human disturbance is characterized by decreasing diversity and increasing abundance of those species adapted to such an environment.

Environmental Controls on Ostracodes Between Lakes and Over Time

Among the environmental factors controlling ostracode occurrence and geographic distribution, water chemistry and temperature are probably the two most important factors constraining the occurrence patterns of ostracodes between lakes or over time within a lake. Because fluctuations in water temperature and chemistry are often closely coupled to climate, these factors have received the most attention by paleoecologists. Variations in regional climate will produce corresponding changes in the lake water and its ostracode fauna. Thus, understanding the thermal and hydrochemical preferences of individual species is fundamental to the use of ostracodes as paleoenvironmental indicators of climatic change.
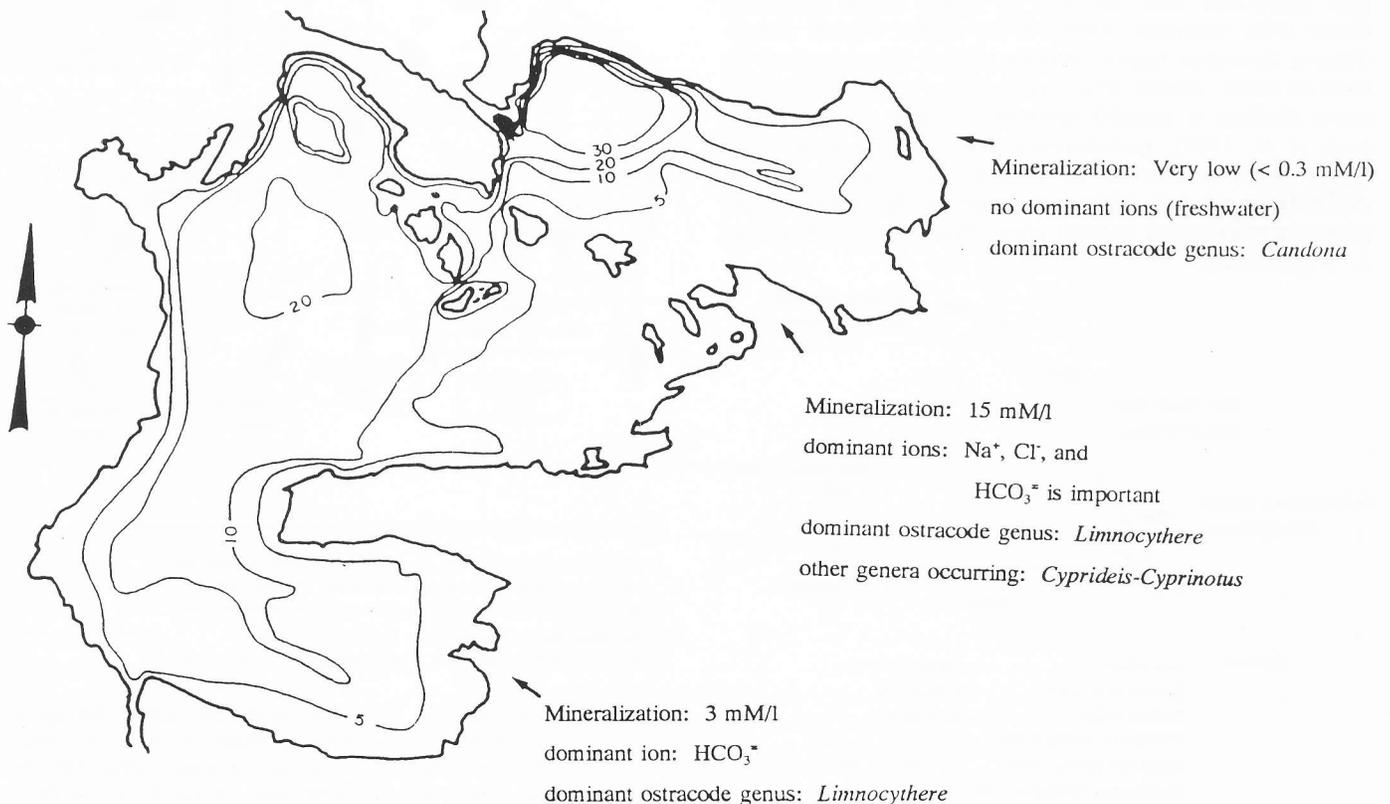

Mineralization: Very low (< 0.3 mM/l)

no dominant ions (freshwater)

dominant ostracode genus: *Candona*

Mineralization: 15 mM/l

dominant ions: Na^+, Cl^-, and

$HCO_3^=$ is important

dominant ostracode genus: *Limnocythere*

other genera occurring: *Cyprideis-Cyprinotus*

Mineralization: 3 mM/l

dominant ion: HCO_3^-

dominant ostracode genus: *Limnocythere*

Figure 2. Influence of tributary water discharge chemistry on ostracode fauna of Lake Titicaca. (Simplified from Carbonel *et al.*, 1988).

The latitudinal distribution of many ostracode species throughout the world suggests that temperature is a major biogeographic control. Many species are highly sensitive to temperature, which regulates both their ability to survive and to reproduce (Delorme and Zoltai, 1984; Forester, 1987; De Deckker and Forester, 1988). For example, *Cytherissa lacustris*, a species limited to temperatures under 23° C, is a common inhabitant of temperate to subpolar region lakes (i.e. in subalpine lakes *C. lacustris* today lives only in the "profound" zone where temperature is *quasi* unvariable and cold; Carbonel, pers. comm., 1994), whereas *Limnocythere bradburyi* is restricted to lakes with higher temperatures and occurs in low to mid latitude lakes (Delorme, 1978; Danielopol *et al.*, 1985; Forester, 1985). However some species, like *Candona rawsoni*, are eurythermic, occurring in almost all temperature regimes (Sohn, 1987). Globally, knowledge of temperature preferences for individual species is quite limited, although in some areas an extensive database of temperature ranges has been compiled (Delorme, 1970a-d, 1971a-c; Delorme and Zoltai 1984; Delorme *et al.*, 1977).

Ostracodes display great sensitivity to variations in water chemistry (both composition and concentration). The modern salinity tolerances of a number of ostracode species may be useful for paleosalinity reconstructions based on the coexistence of two or more species with limited or overlapping salinity tolerances (Anadón *et al.*, 1986; see also Holmes, 1992 for details). Several euryhaline ostracodes (e.g. *Cyprideis torosa* and possibly *Limnocythere ceriotuberosa*) reflect their sensitivity to salinity variations by changes in carapace thickness, structure, ornamentation and size. *Cyprideis torosa* an estuarine ostracode that can live in saline lakes including those with salinities under 6‰, under which conditions it develops heavy ornamentation characterized by four to seven nodes, whereas in more saline waters the valve surface is usually smooth (Vesper, 1972; Athersuch *et al.*, 1989). *Limnocythere ceriotuberosa* in western North America occurs in alkaline, euryhaline waters; under freshwater conditions this species develops a thick, posteriorly-oriented ventral wing (this form is known as *L. platyforma*).
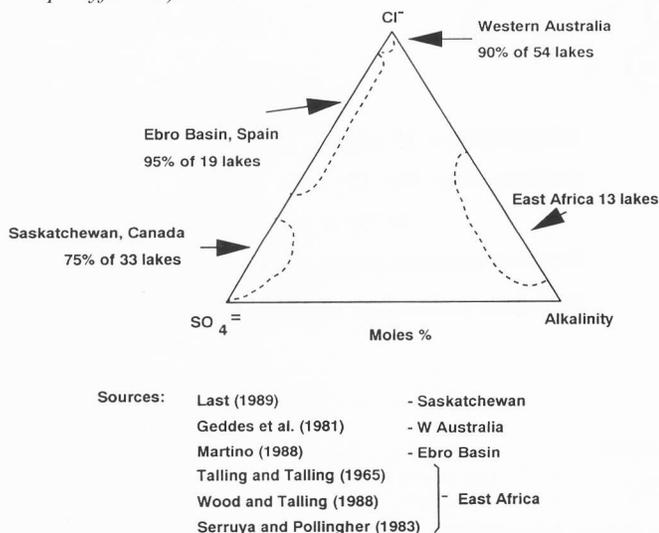
Major changes in ostracode faunas and lake conditions correspond to regionally recognized indications of climate change. As can be seen from Fig. 3 (Anadón, unpublished data), lakes within specific regions tend to have well defined compositions along particular pathways as a result of similarities in bedrock geology and climate. For example, lakes in Saskatchewan are dominated by $SO_4^=$ because of the high contribution of ions from rock and soil weathering and hydrothermal sources in the surrounding areas, whereas southwestern Australian lakes are Cl^--dominated as a result of the high evaporation rates characteristic of that semi-arid region. Gorham *et al.* (1982) showed that the chemical composition of North American lakes changes from alkali-dominated waters in the humid forests east of the Mississippi to $SO_4^=$-dominated waters that precipitate calcium carbonate in the more arid prairie regions of the west.

A considerable body of data exists which suggests that water composition and concentration pathways within basins and regions over time are important parameters in affecting ostracode response to the environment (Chivas *et al.*, 1985, 1986a, 1986b; De Deckker *et al.* 1988a, b; Anadón and Juliá, 1990; Holmes *et al.*, 1992). Although water composition and concentration
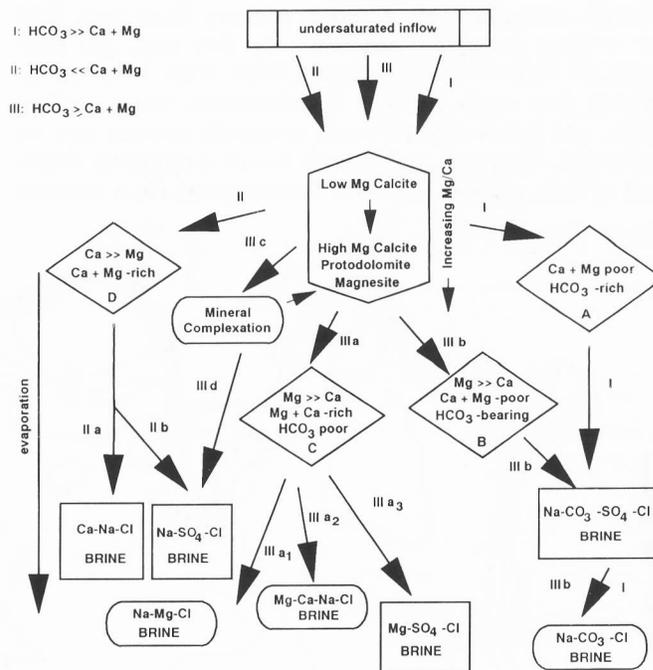
Examples of modern lakes by hydrochemical pathway and occurrence of ostracodes:

A: Lake Turkana, East African Rift - *Gomphocythere angulata* (Cohen, 1982)
   Lake Texcoco, Mexico - *Limnocythere sappaensis* (Forester, 1983)
B: Devils Lake, N.D. USA - *Candona rawsoni* (Engstrom and Nelson, 1991)
C: Ebro Basin, Spain - *Eucypris inflata* (Baltanas *et al.*, 1990)
D: Wanacut Lake, Washington, USA - *Limnocythere staplini* (Forester, 1983)

Figure 4. Flow diagram for brine evolution. Large hexagon represents initial saturation stage prior to pathway evolution; diamonds are typical water compositions with examples of lakes and common ostracodes. Final brine types usually contain no ostracodes. For a detailed explanation see Eugster and Hardie, 1978. (Modified from Eugster and Hardie, 1978).

Figure 3. Trilinear diagram of lake anion compositions for lakes in different regions of the world. (Anadón, unpublished data).

in lakes are both frequently coupled to climate since waters undergo predictable "pathways" of change in both composition and concentration as evaporation occurs (as shown in Fig. 4), detailed studies to test this hypothesis are yet to be conducted (Eugster and Hardie, 1978; Forester, 1983; De Deckker and Forester, 1988). In wet climates where precipitation exceeds evaporation, waters are typically very dilute. In temperate areas they are typically rich in both Ca^{2+} and $CO_3^=$, with increasing evaporation these waters may become either depleted in Ca^{2+} or depleted in carbonates (HCO_3^- + $CO_3^=$) depending on the initial concentrations of these ions prior to early calcite precipitation (Forester, 1987). In tropical lakes Na^+, Mg^{2+}, and Cl^- may all also be important because of these ions solubility (with Na^+ and Cl^- being the more soluble ions). Ostracodes respond to the changes in the solute composition pathways, through changes in abundance, total species diversity and individual species occurrence. Some species are restricted to specific types of waters or concentrations within a pathway. In nature many ostracode species occur in saturated or supersaturated waters with respect to calcium carbonate but diversity decreases significantly in undersaturated conditions. De Deckker and Forester (1988) have suggested that lakes dominated by Ca^{2+} and HCO_3^- but undersaturated in $CO_3^=$ (under the calcite branchpoint of Eugster and Hardie, 1978), usually contain fewer than five species and a low abundance of individuals. Species diversity rises up to 20-30 species and remains constant as water becomes saturated with respect to calcite (calcite branchpoint). Once depletion takes place in either direction (Ca^{2+} or HCO_3^-) and salinity increases, ostracode diversity decreases again to less than five species but abundance often increases significantly particularly in alkaline lakes where TDS is often strongly correlated with productivity.

Forester and Brouwers (1985) found that ostracode distribution is not only controlled by salinity variations but also by the solute composition of estuaries where these organisms live. Solute composition is primarily driven by climate (temperature and evaporation/precipitation rates). Baltanás et al. (1990) also found a direct correlation between water ionic composition and ostracode occurrences. They concluded that lake chemistry played a key role in the occurrence of saline lake ostracodes in several Spanish ephemeral lake basins. Cl^--dominated waters are preferred by Eucypris mareotica whereas Heterocypris barbara inermis prefers $SO_4^=$-dominated waters, but Eucypris aragonica only lives in Cl^--dominated but $SO_4^=$-rich waters.

Smith (1993) demonstrated how lacustrine ostracode abundances and distribution are related to ionic composition of the waters they inhabit in the northcentral United States. She concluded that ostracode species may define hydrochemical fields. For example, as shown graphically by Forester (1986), Limnocythere staplini occurs more commonly in HCO_3^--depleted, $SO_4^=$-dominated waters, whereas Limnocythere sappaensis prefers HCO_3^--enriched, $SO_4^=$-dominated waters. Eurytopic species, such as Candona rawsoni, live in both HCO_3^--enriched and HCO_3^--depleted, $SO_4^=$-dominated waters but stenotopic species, such as Candona ohioensis restricted to fresh waters, are limited by the environment. Anion composition of the host water also affects ostracode occurren-

ce patterns as shown by Carbonel (1983), Forester (1983, 1986) and Carbonel et al. (1988). Forester (1983, 1986) has shown the close relationship kept between anionic composition and ostracode occurrence. Two species of Limnocythere which he studied, L. sappaensis and L. staplini, have different anionic requirements although their pH and salinity tolerances are similar. L. sappaensis occurs in waters enriched in HCO_3^-, whereas L. staplini is limited to Ca^{2+}-dominated and $SO_4^=$-enriched waters. Trilinear plots of anionic tolerances for the two species suggest that their occurrences are mutually exclusive. However, under specific circumstances in which both Ca^{2+} and $CO_3^=$ are in equilibrium in a $SO_4^=$-rich environment, these species may coexist (Forester, pers. comm., 1993). For example, one of us (MP, unpublished data, 1992) has recently found L. sappaensis and L. staplini co-occurring in the late Pleistocene Laguna Diablo (Baja California, México).

Forester (1986) has also shown that the absolute salinity tolerance ranges of ostracodes are often dependent on the specific ions present. For example, the Candona rawsoni group can survive in alkaline waters of low salinity, but its maximum salinity tolerance increases dramatically in HCO_3^--depleted waters. Limnocythere sappaensis, L. staplini and L. ceriotuberosa are also subject to a relationship between salinity and the anionic composition and concentration of the host waters (Fig. 5). Similarly, Cohen et al. (1983) found that ostracode distribution in modern Eastern Africa lakes respond to the ionic composition and concentration of the
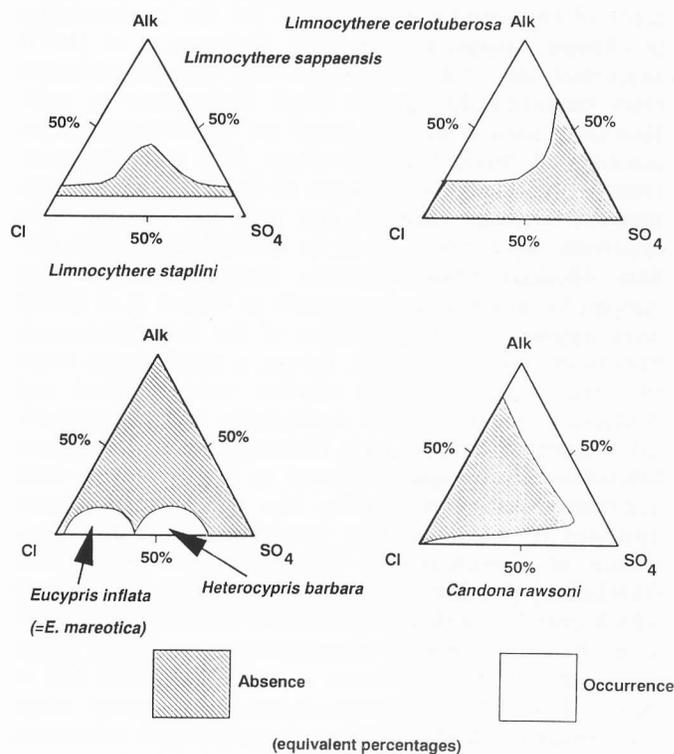

Figure 5. Trilinear diagrams for ostracode occurrences in Spain and North America. Eucypris inflata (=E. mareatica) and Heterocypris barbara occur in Spain (Baltanás et al., 1990). Limnocythere ceriotuberosa, L. sappaensis, L. staplini and Candona rawsoni are widespread species in North America (Forester, 1986). (Simplified from Baltanás et al., 1990; and Forester, 1986).

host waters. For example, they suggested that ostracode assemblages in East African lakes vary uniformly along concentration gradients of Na⁺, Cl⁻.

Furthermore, De Deckker and Geddes (1980) arrived at similar conclusions with respect to Australian lake ostracodes. In this study they determined ostracode salinity tolerance based on the presence/absence and replacement of species with changing salinity. De Deckker (1981) concluded that most ostracode species present in Australian salt lakes are halobionts, an adaptation which probably evolved in response to extreme aridity during the Pleistocene. In these lakes the total dissolved solids (TDS) range from 30 to 400 ‰, with Na⁺ and Cl⁻ accounting for more than 70 % of the equivalent percentage of ions (De Deckker and Geddes, 1980).

APPLICATION OF ECOLOGICAL DATA FROM OSTRACODES TO PALEOECOLOGICAL PROBLEMS

QUATERNARY RECORD

Recognition that modern ostracodes respond to various ecological parameters in lakes, and particularly to changes in water chemistry lead Delorme (1969) to first develop detailed models based on paleoecological associations of fossil ostracodes and the occurrence patterns of the same extant species for the interpretation of climate change. For example, Delorme et al. (1977) suggested that higher temperatures and precipitation rates occurred during the latest Pleistocene to mid-Holocene than at present based on the statistical interpolation of modern meteorologic data and the occurrence and relative abundance of fossil ostracodes with modern analogs through the geologic record. This approach has been followed in several subsequent studies. Modern water chemistry ranges for many East African ostracode taxa determined by Cohen et al. (1983) were applied to reconstruction of the late Quaternary history of Lake Elmenteita, Kenya, a small closed basin rift lake, which is highly alkaline today (Cohen and Nielsen, 1986). Ostracode stratigraphy and paleochemical interpretations from Lake Elmenteita, from the known tolerances of the species found as fossils in lake core sediments, indicated that the lake underwent alternate episodes of water dilution (associated with the occurrence of *Gomphocythere obtusata*) and concentration (marked by the dominance of *Limnocythere michaelseni*) which correlate well with periods of shrinkage or expansion. Paleolimnological interpretations matched those from other lines of evidence at Lake Elmenteita and at nearby Lake Nakuru (the two lakes are connected when lake levels are high). These ostracode-based inferences agree closely with regionally documented changes in precipitation/evaporation during the late Quaternary based on shore-line and sensitivity-analysis studies (Washbourn-Kamau, 1970 and Hamilton, 1982; in Cohen and Nielsen, 1986).

Forester et al. (1989) interpreted the ostracode stratigraphic record of Kepler Lake (Alaska) in terms of

limnologic and climate change during the late Holocene. The alternating occurrence of *Cyclocypris ampla, Candona protzi* and *Candona rectangulata* and the occasional appearance of *Cypridopsis vidua* and *Cyclocypris ovum* suggested that this lake underwent significant seasonal variation. Salinity probably decreased to values under 300 mg/l when *C. protzi* occurred.

Ostracode data may provide highly quantitative records of lake histories (Delorme, 1989). When large data set on modern distribution patterns allow for closest fit analogies between a fossil assemblage and its closest modern lake counterpart fauna, it is possible to develop transfer functions to describe matches between fossil assemblages and a given set of limnological conditions. The application of transfer functions can be established by multiple regression analysis from current observed hydroclimate or climate data (independent variable) and coupling them to interpreted derived climate data (dependent variable, ostracode relative abundance). Transfer functions represent a highly deterministic approach to inferring climate, the application of which assumes that ecosystem structure in ancient communities closely resembles that of the modern. Their use therefore is most appropriate with very recent records for time periods when this assumption is a reasonable one (Fig. 6). The appropriate equation is chosen based on the climatic parameter selected, correlation coefficient, and the species relative abundance. The selection is based on the highest correlation coefficient derived from the stepwise multiple regression of the species dependant files.
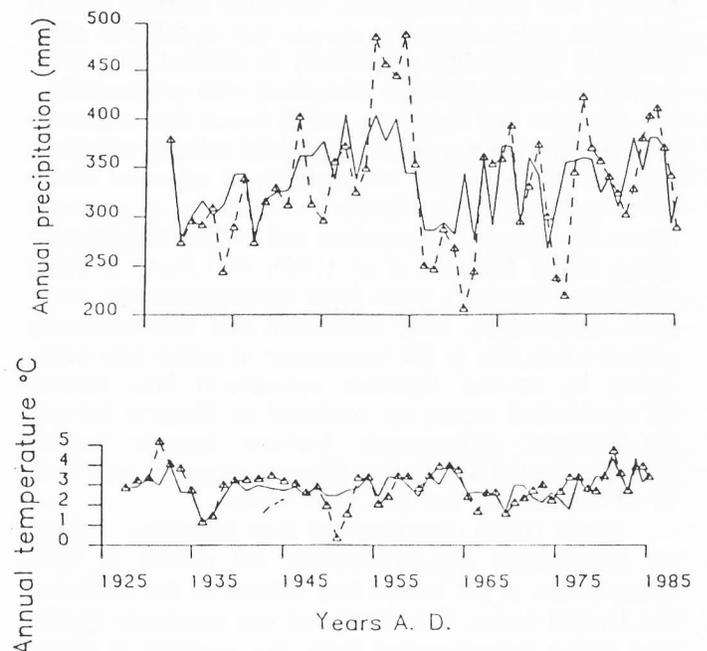

Figure 6. Mean annual precipitation and temperature profiles based on observed (weather station) and inferred (transfer functions from fossil ostracodes) records. Dashed lines with open triangles show revised-observed values and solid lines and triangles show interpreted values for the last 60 years of sediment deposition in Clearwater Lake, Saskatchewan, Canada. (Simplified from Delorme, 1989).

Smith *et al.* (1992) used two statistical methods to reconstruct the solute history of Elk Lake, Clearwater County, Minnesota from a Holocene core based on the ostracode record. They concluded that Elk Lake remained a freshwater lake through most of its history, with only minor variations between 8800 and 4000 years B.P, and that the lake was probably buffered by groundwater input. In contrast, the pollen records showed episodes of prairie expansion which the ostracode faunal composition should record as greater changes in total dissolved solids.

PRE-QUATERNARY RECORD

The level of detail of paleoenvironmental inference that can be derived from fossil ostracode assemblage data depends on both the extent to which the fossil species under study can be analogized with modern ones and the amount of information available on the modern species analogs. For pre-Quaternary faunas, ostracode workers have had to focus on alternative methods of inferring paleoecology from ostracode assemblages that are invariably more qualitative than the methods discussed earlier.

For example, a general application of paleochemical analysis is justified for genera with restricted ecological tolerance ranges. Forester (1991b) suggested that at a generic level, ostracode faunal composition may be useful for inferring annual water body variability in the pre-Quaternary geologic record (Fig. 7). Some workers have used ostracodes to reconstruct paleoenvironments in ways which are not dependent on detailed knowledge of the modern distribution of species but which rely on more general principles of shell morphology, taphonomy and shell geochemistry (Carbonel *et al.*, 1988).

Carapace Ornamentation and "Exotic" Structures

Many species of ostracodes display considerable ecophenotypic variety in carapace ornamentation, which some authors believe can be exploited for paleoecologic information. Peypouquet *et al.* (1980) and Carbonel *et al.* (1988) have suggested that valve ornamentation may be tied to Mg/Ca ratios in water (and thereby indirectly to concentrations in most lakes with calcareous biotas). Carbonel and Peypouquet (1979) and Carbonel *et al.* (1988) have applied this principle to both Quaternary and pre-Quaternary lake beds.

Carapace shape (subrectangular, elongate and slightly subtriangular or with pointed posterior ends, dorsally arched, highly triangular, and trapezoidal) appears to be commonly related to specific lake conditions (Carbonel *et al.*, 1988). For example, unstable water bodies are

characterized by subrectangular to elongate, slightly subtriangular ostracode species, whereas permanent, stable basins or springfed areas tend to be inhabited by highly triangular, trapezoidal or elongate species with pointed posteriors. The occurrence of "exotic" carapace morphologies (often marine convergent) has been related to extreme conditions of lake stability where the evolution of biologically accommodated adaptations has strong selective value (Cohen and Johnston, 1987). These features include valve thickening and the development of strong spine, flange or alae structures. Such features are well known from living ostracodes of Lake Baikal and Lake Tanganyika, as well as fossils from Pliocene "Lake Idaho", the Cretaceous rift lakes of Brazil and the early Tertiary lakes of north China (Swain, 1986; Moura, 1988; Forester, 1991b; Martens, 1993; and Kozhova and Erbaeva, 1993).

Taphonomy

The quality of paleoenvironmental reconstructions is highly dependent on the taphonomic history of the fossil assemblage under study and a failure to analyze taphonomic features of an ostracode assemblage can lead to serious interpretative errors. However, taphonomy can be put to use in a positive sense as well, *sensu* Behrensmeyer (1987), aside from its role as an information filter. Taphonomic features are useful indicators of transport, currents and post-mortem sorting. De Deckker (1988) defined the most useful taphonomic characteristics: breakage, fungal/bacterial degradation, carapace/valve ratios, bedding plane alignment and adult/juvenile ratios. Comparisons should always be made strictly within species, as transport and breakage patterns vary greatly between taxa. Evidence of transport or reworking is of primary significance in distinguishing autochthonous from allochthonous fossils. However, the worker must first define the nature of the paleoenvironmental problem being investigated before deciding whether a given level of post-mortem transport in a fossil assemblage is acceptable or not. An autochthonous fossil in one context (e.g. a study of a whole lake history, or comparison with other basins) would be allochthonous in another (i.e. comparing subenvironments within a lake). Whatley (1988) has discussed the criteria for recognizing *in situ* from transported ostracodes. Since ostracodes grow by molting, the size, weight, and shape of the different stages will respond differently to the hydrodynamic characteristics of the environment. Adult/juvenile ratios, for example, allow the inference of degrees of post-mortem reworking.

Taphonomic and true biological signals can be confounded in fossil ostracode populations. For example, the absence of either adult or juvenile ostracode specimens in a population may be indicative of post-mortem sorting or environmental stress during life. Reproductive and maturation success are dependent on water being stable for sufficient time for the species to undergo a complete life cycle. By analogy comparing the adult/juvenile ratio histories of two or more species, the investigator may be able to not only differentiate between taphonomic and ecologic controls on population structure but also infer useful data on water body permanence (Palacios-Fest, 1994).
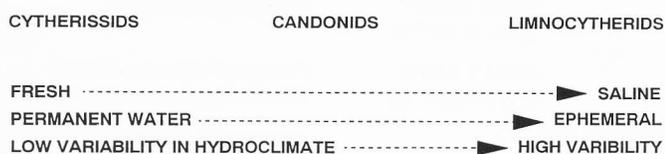
CYTHERISSIDS	CANDONIDS	LIMNOCYTHERIDS

FRESH --➤ SALINE

PERMANENT WATER -------------------------------➤ EPHEMERAL

LOW VARIABILITY IN HYDROCLIMATE --------------➤ HIGH VARIBILITY

Figure 7. Ostracode ecologic replacement in response to salinity, water body permanence and hydroclimate. (Derived from Forester, 1991b).

Valve/carapace ratios are useful in determining environmental stress as well. During molting, ostracode carapaces commonly disarticulate, producing two valves. The occurrence of large numbers of juvenile carapaces within a sample is symptomatic of large-scale infant mortality suggesting the rapid advent of adverse conditions to the species (Whatley, 1988). However, Brouwers (1988) and Forester (pers. comm., 1993) suggests that most juvenile only assemblages are the product of mechanical enrichment and depletion processes owing to the different hydrological equivalence of instars versus adults. In addition, the large number of carapaces may also indicate rapid sedimentation rates or low-energy conditions (Holmes, 1992). However, as stated by Whatley (1988) the application of this criterion requires further information such as the articulatory efficiency (i.e. the strength and complexity of the dorsal hinge mechanism and the extent to which one valve overlaps the other) of the species concerned on the ostracode assemblage before coming to final conclusions.

The degree of valve overlap, the type of hinge and the state of the adductor muscles at the time of death all affect the probability of disarticulation. Therefore, these data should only be compared within species; though trends between species may be usefully compared (Whatley, 1988).

The abundance of broken valves within a sample may reflect the degree of post-mortem disturbance and, hence, energy level (Holmes, 1992). It is important to note, however, that breakage may also result from sampling or disaggregation techniques (De Deckker, 1988). Thus, one must be cautious in using this approach. Abrasion, is a more reliable feature for assessing post-mortem transport. Coatings and encrustations on ostracode valves are also useful in inferring paleoenvironments. The extent and uniformity of oolitic coating in hardwater lakes may be indicative of nearshore deposition where ostracodes have been continuously reworked back and forth.

Encrustations may be related to either environmental conditions or post-burial effects. In supersaturated environments evaporative mineral crystals grow from valves or carapaces suggesting desiccating conditions in the basin. Pyrite or other reducing minerals may also precipitate over previously sedimented valves indicating the anoxic nature of the depositional environment or post-mortem paradiagenetic alteration. However, one must be aware that pyrite may form in places where subbottom sediments are anoxic but where the sediment/water interface is oxygenated. Ostracode valves which are slightly stained reddish or black have experienced variable redox conditions where the valves were deposited.

Family (Subfamily)	Genus	Strontium K_p [Sr]	Magnesium K_p [Mg]	Source of data
Cypridae				
Cyprinae	Ilyocypris gibba	0.1655 ± 0.0072 F		De Deckker (in: Holmes, 1992)
	Cyprinotus edwardi	0.176 ± 0.014 F, n = 10		Chivas et al., 1986 b
	Cypridopsis vidua	0.142 ± 0.009 F, n = 7	0.0098 ± 0.0004 F, n = 7 (22 °C)	Palacios-Fest, unpublished Montezuma Well, Arizona
	Cypretta	0.290 ± 0.009 F, n = 6	0.0091 ± 0.0006 F, n = 6 (30 °C)	Holmes, 1992
	Australocypris/Mytilocypris	0.208 ± 0.048 L, n = 32		Chivas et al., 1986 b
	Diacypris	0.212 ± 0.020 F, n = 10		Chivas et al., 1986 b
	Reticypris	0.237 ± 0.027 F, n = 7		Chivas et al., 1986 b
Candoninae	Candona rawsoni	0.406 L	0.0024 L (25 °C)	Engstrom and Nelson, 1991
Darwinulidae	Darwinula stevensoni	0.175 ± 0.006 F, n = 6	0.0101 ± 0.0003 F, n = 6 (22 °C)	Palacios-Fest, unpublished Montezuma Well, Arizona
Cytheridae	Cyprideis	0.474 ± 0.061 F, n = 37	0.0046 ± 0.0007 L, n = 15 (25 °C)	Chivas et al., 1986 b
	Limnocythere sappaensis	0.348 ± 0.013 F, n = 7	0.008 ± 0.0015 F, n = 7 (25° C)	Palacios-Fest, unpublished Willcox Playa, Arizona
	Limnocythere	0.350 ± 0.058 L, n = 16		Chivas et al., 1986 b

Table 1. Partition coefficients for strontium and magnesium from various species of ostracodes. Data compiled from research on field (F) collected and laboratory (L) cultured specimens by various authors.

GEOCHEMICAL APPROACHES TO INTERPRETING PALEOLIMNOLOGIC AND PALEOCLIMATOLOGIC HISTORIES FROM OSTRACODES

TRACE ELEMENT ANALYSES

The ostracode carapace dominantly consists of low-Mg calcite, but numerous other ions occur in the form of trace elements, most notably Mg, Sr, K, Na, Si, Al and Ba (Sohn, 1958; Cadot and Kaesler, 1977; Bodergat, 1979, 1985). In experiments on solute uptake using ^{45}Ca, as a tracer, Turpen and Angell (1971) showed that ostracodes do not absorb calcium before molting or once the carapace is fully calcified. Such experiments suggest that solutes come from ambient water and not from the organism's metabolism; thus, shell chemistry is inherited at time of valve calcification, which in turn is fixed more or less in one hour.

Magnesium is the most common trace element present in ostracode valves. With the advent of sophisticated analytical tools like the inductively coupled plasma atomic emission spectrometer (ICP-AES), more precise measurements of trace elements have been possible. In 1983, Chivas et al. proposed that Mg^{2+} uptake in ostracode valves is dependent on both the temperature and Mg^{2+} content of the host fluid, whereas Sr^{2+} uptake was exclusively dependent on the Sr^{2+} concentration in the water (no temperature dependence) on the basis of a series of in vivo culturing experiments. This work demonstrated the potentials of using Mg/Ca and Sr/Ca ratio data in fossil nonmarine ostracodes as a tool in paleolimnologic reconstructions.

Based on numerous measurements these authors developed *partition coefficients* (K_p) for Mg^{2+} and Sr^{2+} for several species of ostracodes (Chivas et al., 1983, referred to these as distribution coefficients, but strictly speaking they are partition coefficients, because they are empirically derived, and not thermodynamic equilibrium constructs):

$$K_p \ (Me) = (Me/Ca)_v \ / \ (Me/Ca)_w$$

where Me = either Mg^{2+} or Sr^{2+}, v = valve and w = water.

Different K_p values were obtained for different species. Table 1 summarizes K_p values for several species collected from natural lakes in Australia, North America and Pakistan as well as from laboratory culture experiments (Chivas et al., 1986a, b; Engstrom and Nelson, 1991; Holmes et al., 1992; Palacios-Fest, in prep.). Chivas et al. (1986a) found that ostracode species belonging to phylogenetically-closely related genera or within the same genus have similar partitioning coefficient for Mg^{2+} and Sr^{2+}, whereas unrelated species have very different K_p's. This suggests that these uptakes of trace elements are genetically programmed. The plesiomorphic character state among ostracodes appears to be having a K_p equivalent to that of inorganic calcite, whereas K_p values closer to high Mg-calcite appear to be the derived state (De Deckker and Forester, 1988).

Applications of ostracode trace element analyses to paleoenvironmental reconstructions

Chivas and co-workers (1986a) showed that poorly calcified juvenile valves precipitate high-Mg calcite as a consequence of higher precipitation rates. As the organisms approach maturity the Mg^{2+} content decreases; the lowest Mg^{2+} concentrations are found in the adult carapace and reflect more accurately the ambient aqueous environment. Chivas et al. (1985, 1986a and 1986b) used Mg/Ca ratios as potential paleothermometers based on the thermo-dependence of Mg^{2+} uptake, whereas they used the Sr/Ca ratios of ostracode valves as paleosalinometers. For example, De Deckker et al. (1988b) calculated the temperature effect on the uptake of Mg^{2+} in *Cyprideis*, a cosmopolitan genus.

These paleothermometers and paleosalinometers can be useful in inferring ancient conditions in hydrologically simple lakes (Chivas et al., 1986a). De Deckker and Forester (1988) have shown how trace element based inferences can be used in a hypothetical lake model (Fig. 8). Clustered values, within a stratigraphic horizon, are likely to represent stable or low variability conditions whereas widespread data, in the same plane, suggest highly variable environments (De Deckker and Forester, 1988; Palacios-Fest et al., 1993).

Since Chivas et al.'s, (1983) early work a number of similar studies have been conducted, both in Quaternary and pre-Quaternary ostracodes. Quaternary Lake Keilambete in Victoria, Australia is a small maar lake in which the water balance is primarily controlled by precipitation and evaporation (Chivas et al., 1985, 1986a). Chivas et al., (1985, 1986a) generated a paleosalinity curve from Sr/Ca and Mg/Ca which showed good agreement with previous curves constructed from particle-size analysis. They found that at certain intervals the Sr/Ca and Mg/Ca trends did not parallel to each other, suggesting that temperature changes were also significant.

De Deckker et al. (1988b) interpreted the environmental history of the last ~ 40000 years B.P. of the Gulf of Carpentaria, Australia based on Sr/Ca and Mg/Ca determinations on *Cyprideis*. During that time, the Gulf was often isolated from the ocean in response to sea-level fluctuations. Their study suggests that "Lake Carpentaria" fluctuated from fresh to saline waters prior to sea level rise in the Holocene. This study also provided information for distinguishing lacustrine from marine influences from both trace element ratios (Fig. 9).

Cyprideis has become a popular ostracode for trace element analyses because of its ubiquitous distribution and eurytopic characteristics. De Deckker et al. (1988a) reconstructed salinity variations for the Messinian Mediterranean "Lago Mare". These authors used the K_p values for Mg^{2+} and Sr^{2+} previously determined for *Cyprideis* in the Gulf of Carpentaria, Australia. From this study, De Deckker and co-workers concluded that "Lago Mare" did not have a marine connection while *Cyprideis* inhabited the basin. Furthermore, they showed that "Lago Mare" was isolated from other Mediterranean basins during this time.

Candona, Ilyocypris, Cypridopsis, Limnocythere or *Darwinula* were used in other studies. Engstrom and Nelson (1991) calculated K_p values for *Candona rawsoni* (Table 1) and used this data to reconstruct the recent

history of Devils Lake, North Dakota. They obtained a good correlation between the ostracode-constructed versus historically measured salinities from this lake.

Holmes *et al.* (1992) measured the Mg^{2+} and Sr^{2+} content of *Ilyocypris bradyi* and calculated salinity variations of Quaternary lacustrine deposits (Karewa Formation) of Kashmir, India, using K_p values generated by De Deckker (unpublished data, 1989 in: Holmes *et al.*, 1992; Table 1). Trace metal contents from ostracodes from Karewa Formation suggested that the water body in which these ostracodes lived, was even more dilute than today. Through their study they were able to show that tectonic rather than climatic events drove the lake to desiccation.

Palacios-Fest (1994) determined the Mg/Ca and Sr/Ca ratios of three ostracode species present in pre-historic irrigation canals in south- central Arizona. Palacios-Fest analyzed valves of *Limnocythere staplini*, *Cypridopsis vidua* and *Candona patzcuaro* (a member of the *C. rawsoni*

group) and compared these data to reconstruct paleohydrochemistry of the canals. All three species generated very similar trends confirming that synoptic environmental trends were responsible for variations in trace element uptake. More recent experimental data (Palacios-Fest, in prep.) suggest that the covariance between Mg/Ca and Sr/Ca is temperature related.

Recently, one of us (Palacios-Fest; unpublished data) has applied trace element analysis in ostracodes to industrial minerals exploration. Trace element trends have allowed Palacios-Fest to reconstruct the evaporitic evolution of a small, alkaline basin in northern Mexico and to suggest the best horizons to search for zeolites. Sr^{2+} uptake by *Limnocythere ceriotuberosa* and *Limnocythere sappaensis* systematically showed increasing values as shown by the Sr/Ca ratios (from 0.001 to 0.01) until a level where all ostracodes disappeared but subaquatic conditions prevailed. Independent evidence indicated that precipitation of lacustrine evaporitic minerals com-
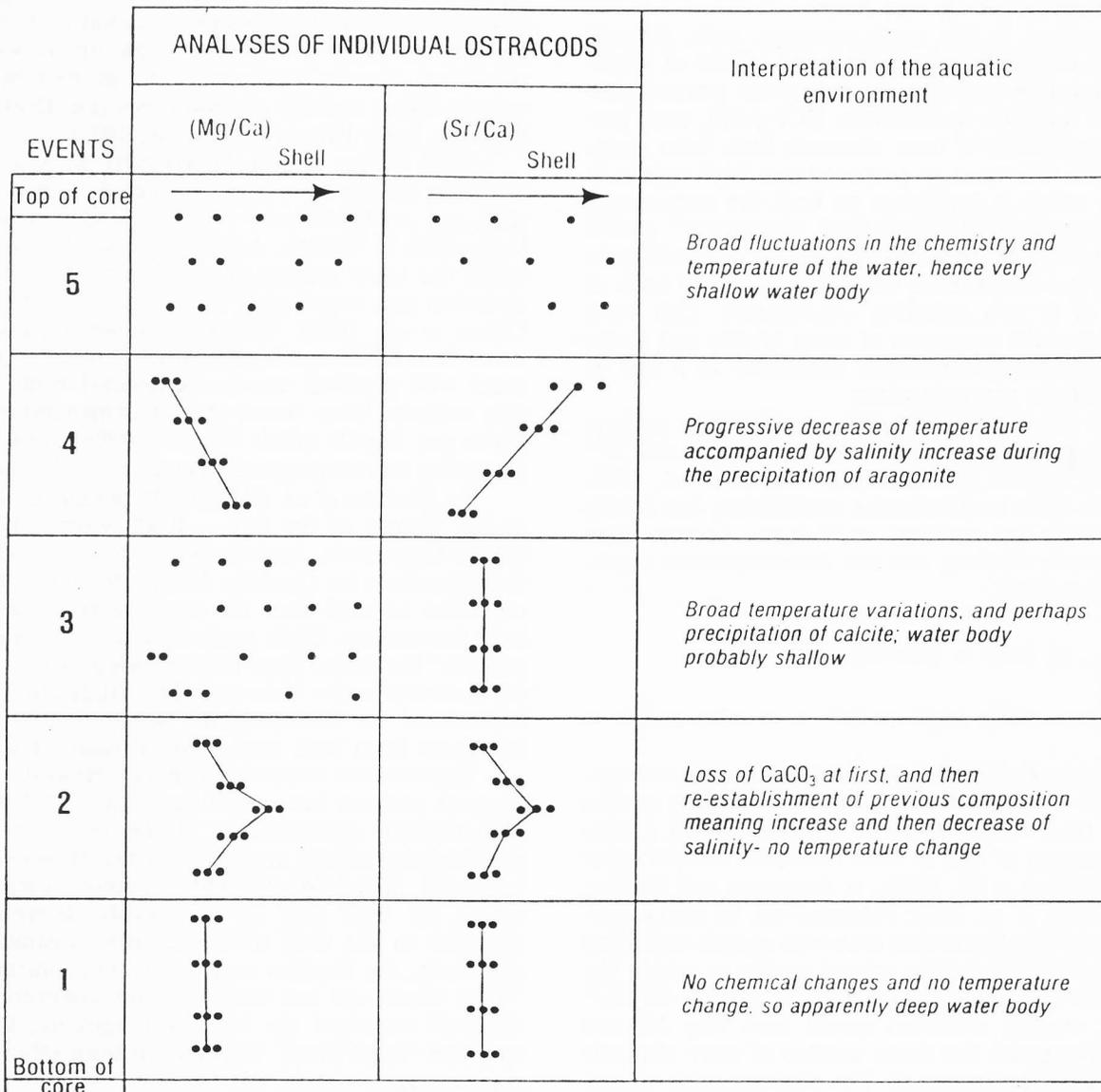

Figure 8. Summary diagram showing the types of aquatic environments reconstructed from Mg/Ca and Sr/Ca analyses of individual ostracode valves obtained from various horizons sampled from a core. Dots represent analyses of individual valves and lines connect points of mean values for each horizon. (Source: De Deckker and Forester, 1988).

menced soon after the ostracodes had vanished. Howe-
ver, if other anions like $SO_4^=$ had been present sulfate
mineral complexation may have disrupted the signal
recorded by ostracode valves.

Limitations to trace element methodology

Because the number of workers currently studying
ostracode geochemistry is small, very few *in vivo* deter-
minations of K_p in ostracode species have been made to
date. Experiments are tedious, time consuming and the
success rate for molting under strictly controlled (i.e.
geochemically invariant) conditions is low (< 40 %), due
to the severely stressing experimental conditions. But
without such experiments, paleoenvironmental work using
trace element ratios will remain highly inferential.

Among the major problems for the use of ostraco-
des as paleoenvironmental indicators are breakage and
abrasion during sampling or laboratory preparation. The
use of corrosive surfactants (e.g. calgon; discussed in
Kontrovitz *et al.*, 1991) or even diluted hot chemicals
(e.g. 5 % H_2O_2 at 85° C; used by Engstrom *et al.*, 1993)
may damage fragile ostracode valves and alter original
Mg/Ca and Sr/Ca ratios. Until gentler, non-reactive
techniques are developed to clean ostracode valves, it

remains an assumption that ionic composition is uni-
formly modified by surfactants between species and
samples.

Of more concern theoretically are the findings of
some studies which do not uniformly corroborate Chi-
vas *et al.*'s (1983, 1985) original findings. Palacios-Fest
(in prep.) found that for *L. staplini*, Mg^{2+} uptake is
controlled by temperature rather than water chemistry,
making the calculation of K_p for [Mg] impossible. Also,
Fig. 10 shows the non-zero "y" intercept for the K_p
[Mg] found by Engstrom and Nelson (1991). This non-
zero "y" intercept strongly suggests that ostracodes have
a different uptake rate at low Mg/Ca ratios. Furthermo-
re, ostracode valves show an average excess of Sr^{2+} over
that of Mg^{2+} which does not match with predicted
thermodynamic considerations alone (Morse and Ben-
der, 1990; Engstrom and Nelson, 1991).

Morse and Bender (1990) suggest that experimental
investigations have revealed more complexities to trace
element analysis because of the increasing number of
parameters that can exert a major influence on partition
coefficients, including temperature, reaction rate and
solution and solid composition. Thus, in certain lakes
salinity may not be accurately derived from Sr/Ca but
more readily from Mg/Ca despite its temperature effect,
since the solubility of Sr^{2+} is a complex function of its
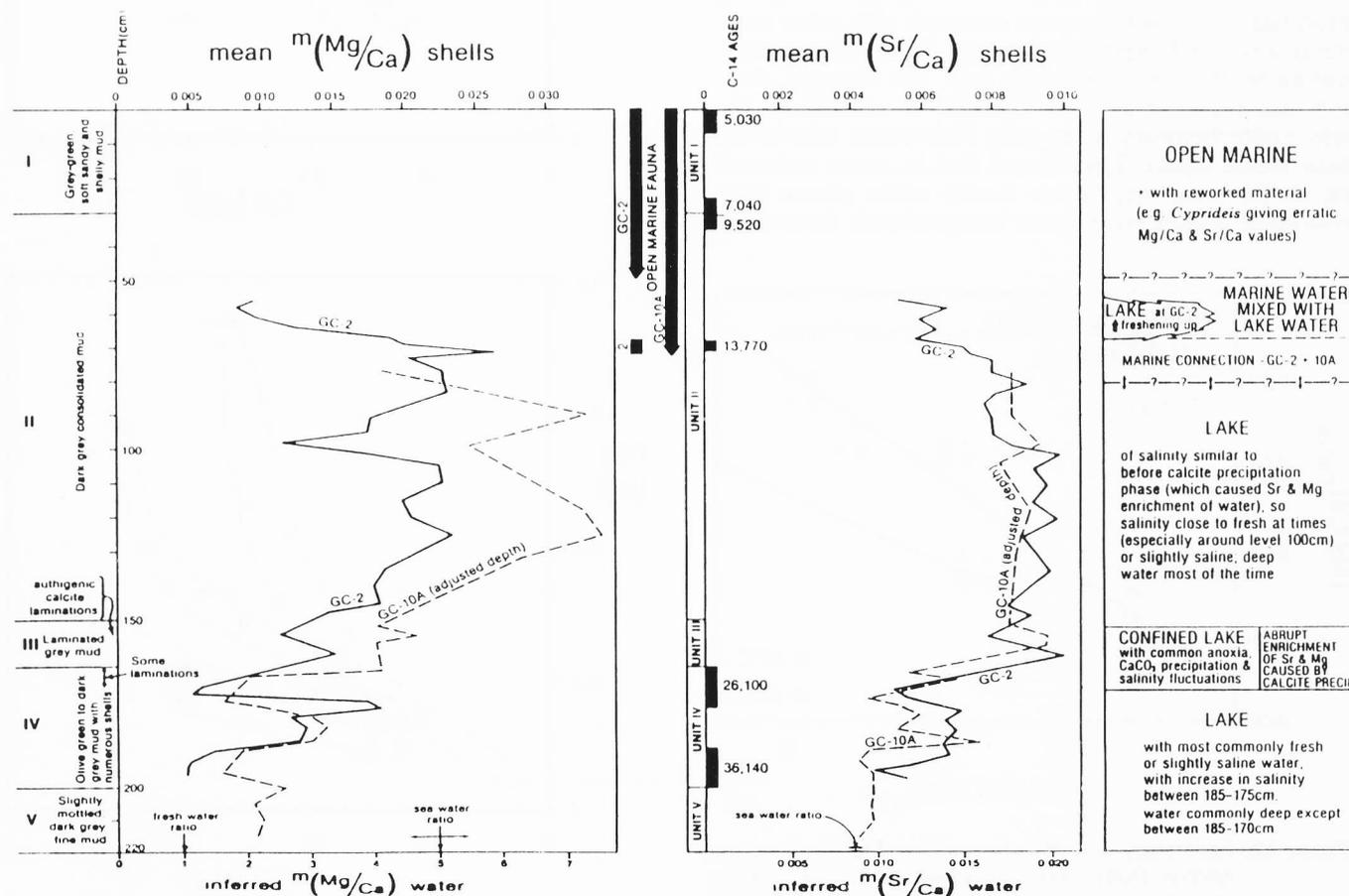uptake in several carbonate phases.

Figure 9. Paleoenvironmental reconstruction of the Gulf of Carpentaria based on Mg/Ca and Sr/Ca mean values from *Cyprideis*
valves (upper horizontal scale). The inferred trace element ratios (lower horizontal scale) were derived from the modern
K_D values of modern *Cyprideis*. (Simplified from De Deckker *et al.*, 1988).

True thermodynamic equilibrium is rarely obtained in laboratory experiments or natural systems. Vital effects of organisms and kinetic influences must play a role in the uptake of trace elements. As shown by Chivas *et al.* (1986a) uptake rates for Mg^{2+} (but not for Sr^{2+}) may be dependent on growth processes since concentrations in the valves are not constant with respect to the size of ostracodes grown under the same conditions. Since ostracode growth rates vary as the organisms reach maturity, the magnesium content in their shells decreases because during the pre-adult stages ostracodes precipitate Mg-enriched calcite but in the pre-adult/adult transition they precipitate low-Mg calcite (Fig. 11).

Furthermore, some data suggest that kinetic effects are likely to be important in Sr^{2+} uptake. In addition, Mg^{2+} uptake may be highly influenced by biological processes. Ohde and Kitano (1984) have shown that partition coefficients for Sr^{2+} are dependent on Mg^{2+} content in biogenic calcite. For natural systems in which significant Sr^{2+} or Mg^{2+} precipitation occurs inorganically (for example in aragonite or strontianite), no simple relationship will exist between salinity and Sr/Ca in water (Chivas *et al.*, 1986b). In these types of lakes, trace element analysis would not be warranted for paleosalinity estimations. All the above considerations suggest that trace element ratio data in ostracodes must be used cautiously, and preferably in conjunction with other lines of independent data.

Several studies of ancient lake deposits comparing interpretations based on trace elements with other independent methods highlight the need for caution in interpreting Mg/Ca and Sr/Ca ratio data. For example, Anadón and Julià (1990) used *Cyprideis* to reconstruct the paleohydrochemistry of an early Pleistocene lake in the Baza Basin, Spain. They found that in some instances the Sr/Ca ratios were lower during saline phases than freshwater phases (as inferred independently from other

evidence). The Sr^{2+} and Mg^{2+} content of *Cyprideis* valves in the Baza Basin reflect the Sr/Ca and Mg/Ca of the waters they lived in, but these ratios in turn are not necessarily direct indicators of salinity (Anadón and Julià, 1990; Anadón *et al.*, in press).

Because of the remaining uncertainties surrounding the controls on trace element uptake and the interpretation of trace element data, it is critical that more experimental studies be undertaken to understand how uptake proceeds in other species and how such factors as uptake, growth rates and synergetic interactions between Mg^{2+} and Sr^{2+} influence trace element uptake with temperature and hydrochemical ranges. Par-
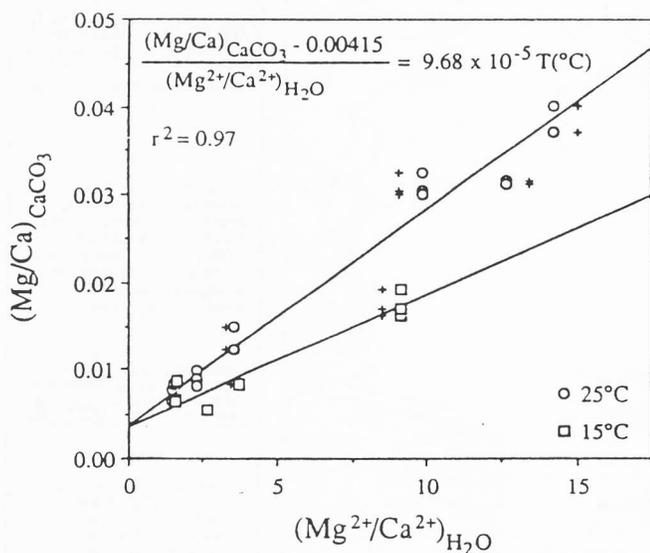

Figure 10. Laboratory determination of K_D [Mg] for *Candona rawsoni* from valves of individuals grown in water of different free-molar (uncomplexed) Mg^{2+}/Ca^{2+} at two controlled temperatures: + symbols indicate total-molar $(Mg/Ca)_{water}$ (where different from free-molar ratios). (Source: Engstrom and Nelson, 1991).
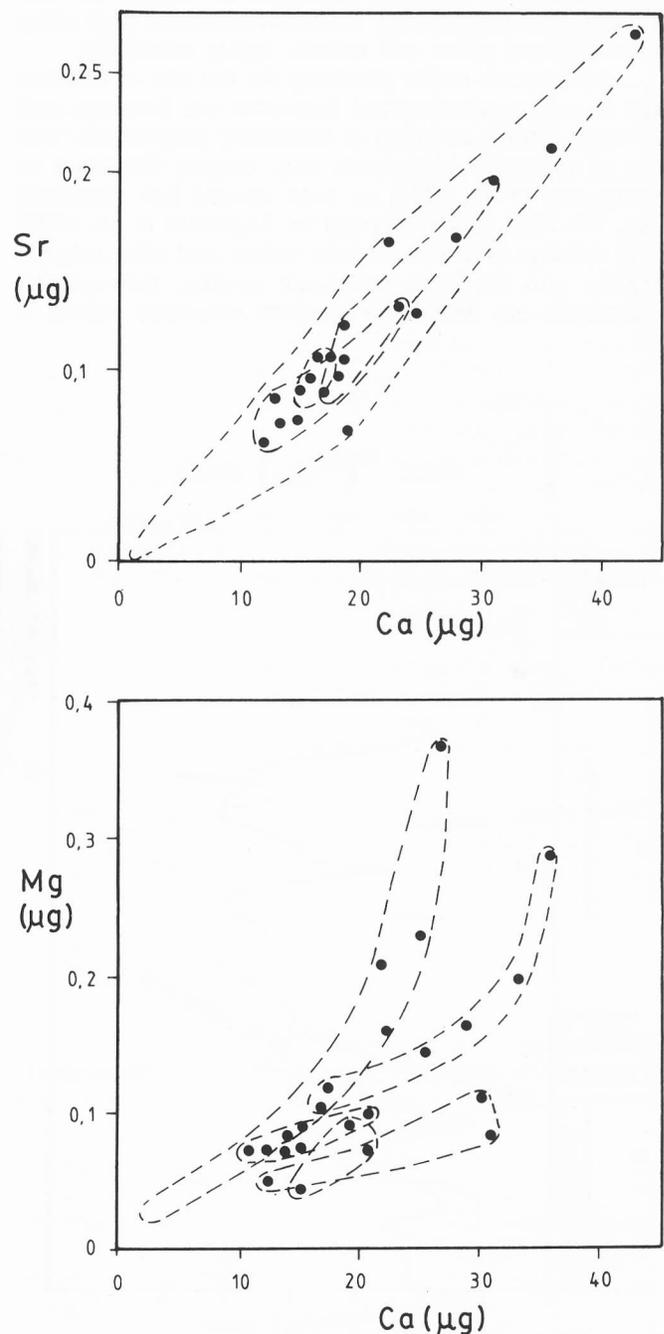
$$\frac{(Mg/Ca)_{CaCO_3} - 0.00415}{(Mg^{2+}/Ca^{2+})_{H_2O}} = 9.68 \times 10^{-5}\, T(°C)$$

$r^2 = 0.97$

Figure 11. Mg/Ca and Sr/Ca ratios as a function of body size in single populations of *Candona* sp. (Anadón, unpublished data).

ticular attention is also required to determine ecophysiological controls on precipitation rate and how these vary between species.

STABLE ISOTOPE ANALYSES

Carbon and oxygen isotopic analyses from primary carbonates from lacustrine systems have proven extremely useful in reconstructing paleoenvironments and paleoclimates (e.g. Talbot and Kelts, 1986, 1990; Kelts and Talbot, 1989; Talbot and Livingstone, 1989; Talbot, 1990). Because their calcite carapaces are calcified from ions in the ambient lake water, it is a reasonable assumption that fossil ostracodes are useful sources of carbon and oxygen isotopes for measurement. However, one must be aware of vital effects which may influence stable isotope signature. The use of stable isotopes in paleoenvironmental studies of continental waters is based on the observation that the $^{18}O/^{16}O$ ratio of rainfall (the main source of lake waters) depends on the regional evaporation/precipitation rate (associated with climate, and particularly with temperature). The $^{18}O/^{16}O$ ratios of water, bicarbonate and carbonate are related by equilibrium constants that are functions of temperature (Siegenthaler and Eicher, 1986). However, it is unrealistic to determine lake water temperatures from the $^{18}O/^{16}O$ measured because their variations are not identical to those from the original water as a result of the evaporation/condensation effect. The $^{13}C/^{12}C$ ratio of authigenic lake carbonates are a function of local processes. In general, carbon isotopes are more complex to interpret than oxygen isotope ratios because of local effects but under certain circumstances they provide some information on the lake's productivity (Siegenthaler and Eicher, 1986).

The covariance of $\delta^{13}C$ values with the $\delta^{18}O$ is characteristic of primary carbonates formed in closed lakes (Talbot, 1990). Covariant trends of $\delta^{18}O$ and $\delta^{13}C$ in ostracode shells have been reported from a Pleistocene sequence of the Baza Basin, Spain (Anadón et al., in press) and from a Pleistocene sequence of the Summer Lake, Oregon (Palacios-Fest et al., 1993). The covariant trends provide additional evidences for the evolution of the respective lake waters within a hydrologically closed basin.

Applications of ostracode stable isotope analyses to paleoenvironmental reconstructions

Durazzi (1975, 1977) carried out the first systematic analysis of stable isotopes from modern marine ostracodes. Durazzi concluded that water temperature is a major factor in controlling oxygen isotope uptake in ostracode valves but that vital effects are also significant. Carbon isotope uptake appeared to be independent from both water temperature and salinity but, a biokinetic signature was important among different species.

Fritz et al. (1975) made the first oxygen and carbon isotope measurements on modern and fossil lacustrine ostracodes. Their study of Lake Erie, Ontario showed that at ~ 13 000 B.P. ostracode $\delta^{18}O$ values were much lighter than those from other materials analyzed from younger intervals, although the $\delta^{13}C$ are somehow high with respect to other carbonates. They concluded that during the time ostracodes were abundant, Lake Erie received a great input of $\delta^{18}O$-depleted meltwater and $\delta^{13}C$ was in, or close to, isotopic equilibrium with atmospheric CO_2.

After the Fritz et al. (1975) study, lacustrine ostracode isotopic analyses remained dormant for more than a decade. However, with the advent of more powerful mass spectrometers these studies have re-emerged. Lister (1988a, 1988b) measured the oxygen and carbon isotope contents of late Pleistocene (~ 15 000 to ~ 12 400 years B.P.) fossil Candona candida and Cytherissa lacustris from Lake Zürich (Switzerland), a deep, thermally stratified lake. Lister concluded that temporal shifts in $\delta^{18}O$ values resulted from shifts in the isotopic character of the net lake inflow, whereas changes in $\delta^{13}C$ values were responding to biological productivity which was low during the late Pleistocene but increased during the Holocene. First use of isotopic record from ostracodes for reconstruction of past mean annual air temperatures was provided by Lister (1989).

Niessen and Kelts (1989) used isotopic analysis of valves from benthic deep water ostracodes for paleoclimatic reconstructions of the deglaciation in Lake Lugano. They used two species (Candona candida and Limnocythere inopinata) that are present in two different stratigraphic intervals. The $\delta^{18}O$ stratigraphy shows a clear difference of 3 ‰, between samples of one interval in comparison to the other. They interpret this change as produced by a change in isotopic composition of inflow waters.

Lister et al. (1991) analyzed the isotopic contents of Limnocythere inopinata and Eucypris inflata from Lake Qinghai (China), a large, dimictic and brackish-water alkaline lake in the Tibet-Qinghai Plateau. Their results indicated that $\delta^{18}O$ values shifted in response to the evaporation/precipitation rates governing the paleolake levels for Lake Qinghai, which reflect the changing intensity of the south Asian monsoon during the late Pleistocene to the Holocene. Carbonel found a similar response of $\delta^{18}O$ values in African Saharan paleolakes (pers. comm., 1994).

Benson et al. (1991) measured $\delta^{18}O$ and $\delta^{13}C$ from late Holocene specimens of Limnocythere ceriotuberosa from Walker Lake, Nevada. Their study demonstrated that the oxygen isotope content in these ostracodes shifted in response to the isotopic composition of the waters they inhabited and was consistent with the lake level changes recorded by independent evidence. However, Benson and co-workers found that several factors may have influenced the final oxygen isotope concentration (i.e. site of precipitation, carbonate chemistry, biokinetics and recrystanization). With respect to the carbon isotope, their findings suggest little or no correlation with TIC values. Hodell and co-workers (1991) reconstructed the latest Pleistocene and Holocene paleolimnology of Lake Mirangoane, a small, deep lake in Haiti, using the $\delta^{18}O$ values obtained from Candona sp.

It is a reasonable assumptioll that analyses of single ostracode valves could produce better constrained data sets than bulk analyses. Multiple analyses of valves from a single horizon can be used to determine within-horizon variance in environmental conditions, below

the level of stratigraphic resolution, something that cannot be inferred from bulk analyses. However, the small size of most ostracodes (average 10-50 μg) coupled with the detection capabilities of most mass spectrometers has impeded this type of study. The first attempt to obtain isotopic measurements from individual ostracode valves was undertaken by Eyles and Schwarcz (1991). Eyles and Schwarcz analyzed valves of *Candona subtriangulata* and *C. caudata* from late Pleistocene Lake Ontario deposits. The secular trend shown by both species is consistent with the glacial meltwater contribution to the basin. Also, the consistent differences in isotope values for the two species suggest an isotopically stratified lake (today these species are ecologically stratified). This study provides a strong caution against using multiple species of ostracodes which although accumulating together as fossils, may have originally inhabited very different environments (with attendant differences in oxygen and carbon isotopic compositions).

Grafenstein *et al.* (1992) analyzed the stable isotopes of benthic ostracodes from two different Bavarian lakes (Lake Starnberg and Lake Amersee). *Candona* sp. and *Cytherissa lacustris* showed evidence of vital effects; once vital effects were accounted for these authors were able to estimate and reconstruct the mean annual air temperature of southern Germany for the past 14000 years.

Because of the large number of steps which link climate and the isotopic composition of the original host water to the final stable isotope ratios in a fossil it is critical that several conditions be met (at a minimum) before an analysis is attempted (Siegenthaler and Eicher, 1986): 1) the investigator should be certain that what is actually being analyzed is original carbonate from an autochthonous ostracode, 2) organic matter must be removed to avoid interference and, 3) as with trace elemellt studies, curves should be established using single species.

As is evident from the previous examples it must be assumed when using stable isotope data from ostracodes (or any other sources) that the carbonates have been precipitated in isotopic equilibrium with lake water and that the $\delta^{13}C$ and $\delta^{18}O$ contents of the carbonates analyzed reflect environmental conditions existing in the area where the carbonates accumulated. In cases where the investigator has reason to doubt either of these caveats, isotopic analysis of ostracodes for paleoenvironmental purposes is unwarranted.

Turpen and Angell (1971) found that ambient water was the direct source for the new shell material during
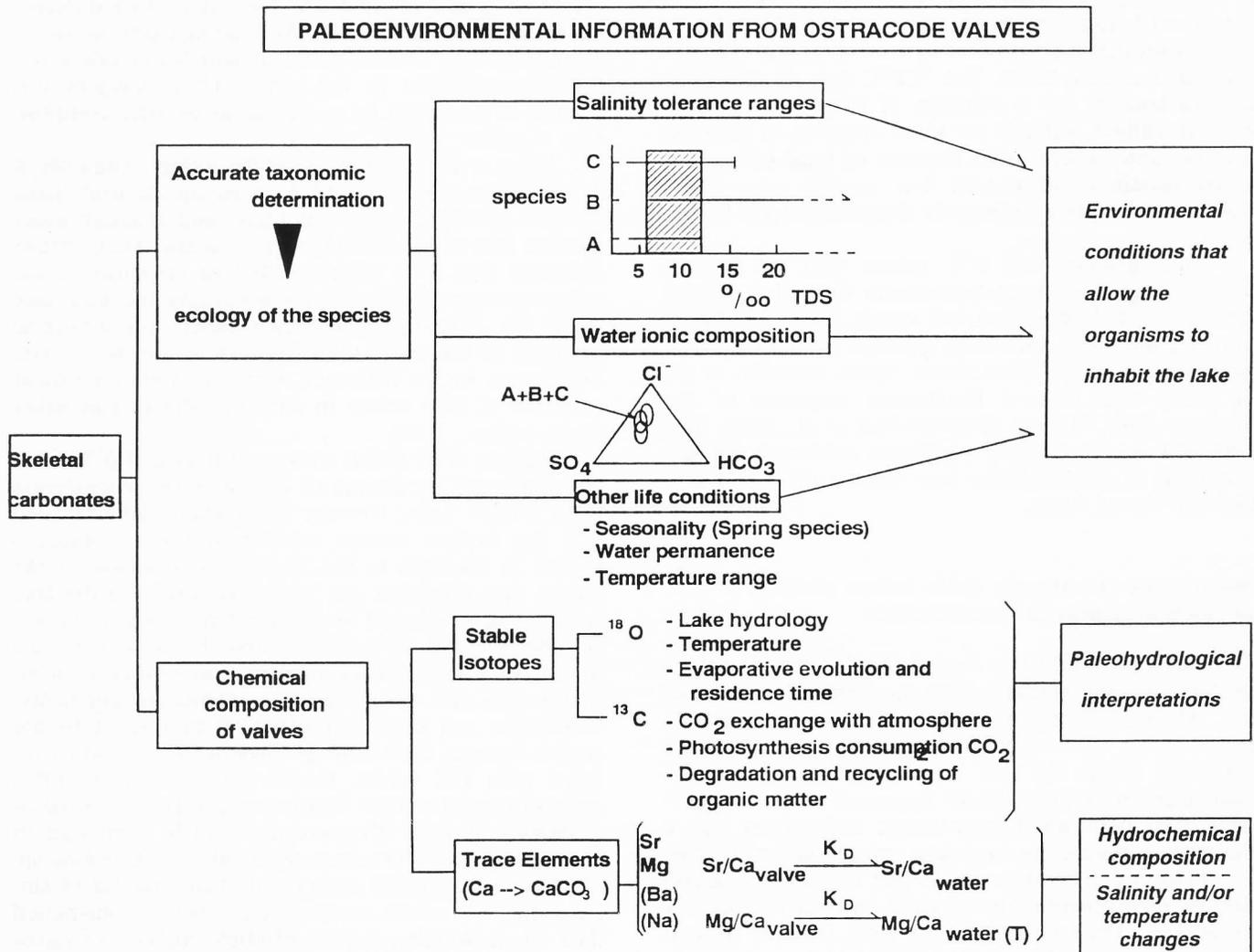

Figure 12. Flow diagram suggesting the stepwise combination of paleoenvironmental information derived from ostracode data.

the ostracode moulting process. Nevertheless, no information has been provided about the non-equilibrium isotopic fractionation during shell calcification. Fritz *et al.* (1975), and many subsequent authors, assume that the ostracode valves were deposited in isotopic equilibrium with the lake water and therefore reflect the composition of the water at the time of growth of the ostracodes. Several authors have recognized differences in $\delta^{18}O$ in as much as 1.3 ‰ from different species of the same sample (Fritz *et al.*, 1975; Durazzi, 1977; Lister, 1988b; Lister *et al.*, 1991; Benson *et al.*, 1991; von Grafenstein *et al.*, 1992). Some authors have argued that differences may result from non-equilibrium isotopic fractionation during shell formation (different vital effect) or simply reflect different seasonal growth preferences of the different taxa. However, variation in the isotopic values of ostracode valves from a single species in a core, reflect primarily the temporal changes in the environmental conditions in the lake where the shell formed.

COMBINED FAUNAL AND PALEOGEOCHEMICAL ANALYSES

Given the limitations attendant to each method of paleoenvironmental analysis using ostracodes to solve paleolimnologic problems, it seems clear that the best alternative is to combine paleontologic and paleoecologic information with geochemical techniques. By using these different approaches together it will be possible to draw more realistic and complete paleoenvironmental reconstructions (Fig. 12).

Since $\delta^{18}O$ values increase with increasing salinity or increasing concentration of waters but decrease with a temperature rise, it is possible to detect temperature and salinity changes from the analyses of ostracode valves. A combination of $\delta^{18}O$ and Mg/Ca and Sr/Ca analyses of the same monospecific ostracode individuals (from the same horizon) provide useful information of the past conditions operating in aquatic environments. The $\delta^{13}C$ values may also yield additional information, however, the meaning of the $\delta^{13}C$ signal remains controversial (see, e.g. De Deckker and Forester, 1988).

The first attempt to combine faunal and geochemical (trace elements and stable isotopes) analyses was that of Palacios-Fest *et al.* (1991a, b; 1992; 1993). These authors have shown the utility of combining paleoecologic with trace element and stable isotope data in a study of Lake Chewaucan, a pluvial paleolake which formed in the northwestern Great Basin (USA) and which has a long and well dated record. These authors measured the total and relative species abundances, taphonomic indicators (e.g. fragmentation, abrasion, coating), and adult/juvenile and valve/carapace ratios. They used their species data to generate a salinity index, based on known tolerance ranges. Geochemical analyses were performed after selecting whole carapaces and splitting the valves. They analyzed one valve for trace elements by inductively-coupled plasma mass spectrometry (ICP-MS), and the other for stable isotopes by supermagnetic mass spectrometry.

In the Lake Chewaucan record trace element ratios were covariant. However, trace elements had only a weak concordance with the paleoecologic and isotopic records; there was no evidence of Sr-bearing minerals in the cores. Covariant isotopic records and faunal composition present in lake sediments strongly suggest that the lake remained a hydrologically closed basin through most, if not all, of its history.

The combined record presents evidence for the end of strong aridification during the late part of oxygen isotope stage 5, that in Lake Chewaucan is marked by an unconformity. In a regional context, effective precipitation gradually increased prior to ~ 75000 years B.P. and reached a maximum about that time intelval. This process most likely triggered increasing runoff input as well, and contributed to increase the lake's volume. Fluctuations may be related to displacement of jet stream as a response to ice cap advances during the Wisconsin (Würm). Further studies by Palacios-Fest *et al.* (1992) showed a good agreement between Ice Age palynologic data and the faunal and geochemical records (Fig. 13).

Anadón *et al.* (in press) have reconstructed the lacustrine paleoenvironmental record during the Early Pleistocene for a shallow lacustrine sequence of the Baza Basin (Southern Spain), based on faunai assemblages and the shell chemistry of two ostracode species (*Candona* sp. and *Cyprideis torosa*). The faunal assemblages from a lacustrine sequence, up to 10 m thick, record alternating phases of 1) slightly saline, bicarbonate-rich waters, when fresh water organisms predominated, and 2) saline, NaCl-dominant water in which marine like organisms lived. The ostracode valves from intervals with saline fauna show higher $\delta^{18}O$ values than those from intervals with fresh water fauna as would be expected for a gain in TDS by evaporation. This feature corresponds to a parallel alternation of positive and negative hydrologic balances. The isotopic trends show a better correlation with the inferences from faunal assemblages than either does with trace element trends. The trace element data, although occasionally fitting well with the isotope and faunal interpretations, suggest overall that trace element contents in ostracodes are not consistent indicators of salinity and/or temperature valiations, but depend on a set of complex factors, which may not be easily deciphered.

Chivas *et al.* (1993) have recently developed a techllique to analyze both trace elements and stable isotopes from the same valves. The advantage of this technique over splitting valves is that it allows smaller specimens to be analyzed and avoids sample loss through mechanical splitting of valves. As a result, more accurate geochemical analyses from ostracode valves are warranted, but more importantly, it will allow to determine what kind of a relationship, if any, exists between stable isotopes and trace elements.

CONCLUSIONS

Ostracodes respond through greater or lesser success in reproduction to their hydroclimate (i.e. lake water characteristics). These are at least one step remo-
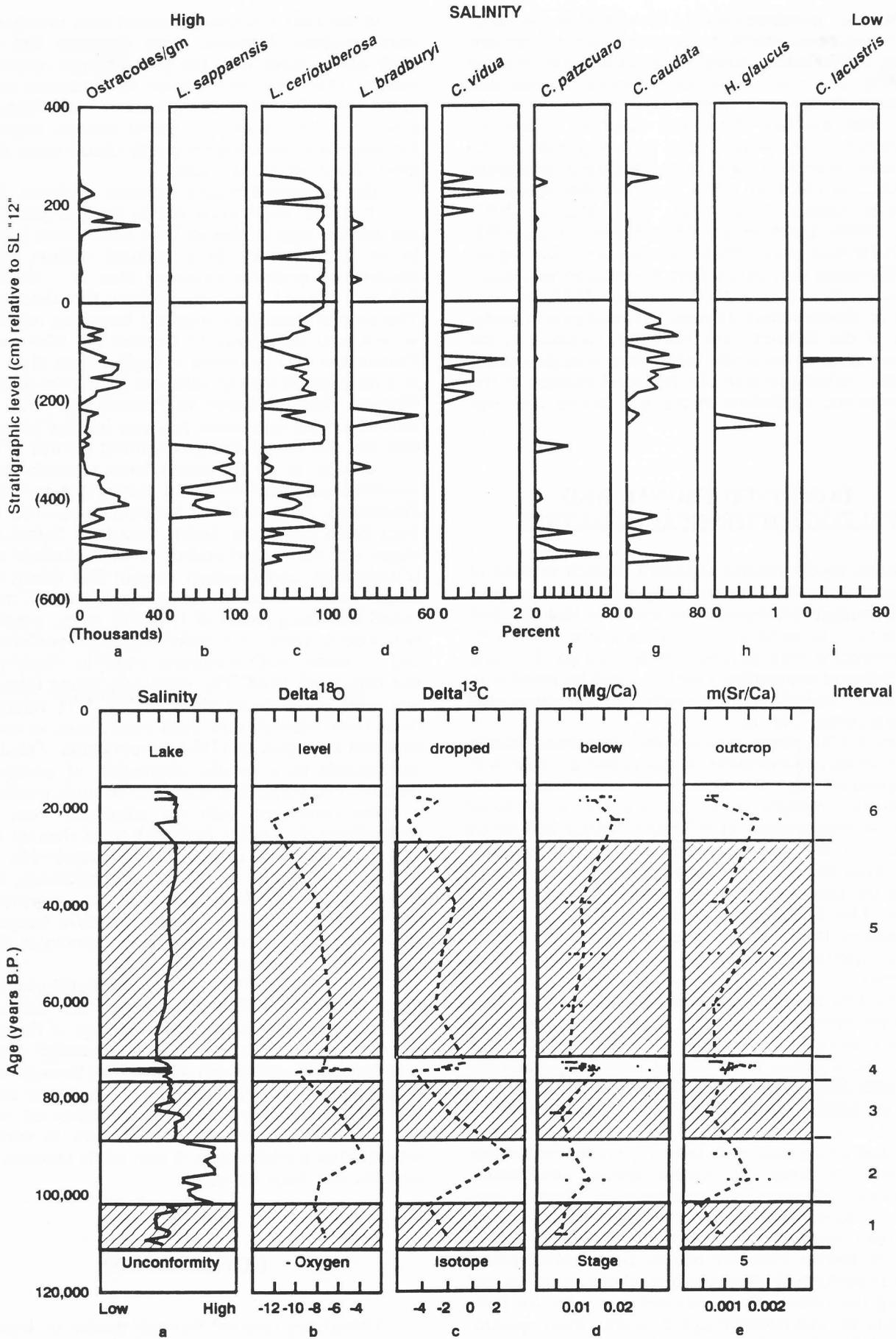
Figure 13. Ostracode stratigraphy and paleoenvironmental trends in pluvial Lake Chewaucan, south-central Oregon, USA. (Source: Palacios- Fest *et al.*, 1993).

ved from local atmospheric climate and several steps away from regional climate. Yet it is the latter which is most often of greatest interest to investigators. Since the ostracode paleoecology and hydroclimate is a complex relationship it is always advisable to be cautious in interpretations involving regional climate.

Ostracodes are one of the few groups of lacustrine organisms (along with diatoms) which have proven to be useful as fossils in limnological studies based on their environmental sensitivity, abundance and diversity in lake sediments and which are readily preserved in pre-Late Quaternary deposits. Water chemistry, salinity and temperature are some of the major parameters affecting ostracode occurrence and life cycles in lakes. Other factors like substrate, turbidity, depth, food supply and predators may also affect ostracode occurrence within a lake. Unlike many other lacustrine organisms ostracodes precipitate a geochemically stable calcite shell which serves as a source for isotopic and geochemical records of changing $\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$, Mg/Ca and Sr/Ca, all of which are of potential interest from a paleolimnological and paleoclimatic standpoint.

Despite the potential utility of these fossils much work needs to be done to enhance their value for interpreting lacustrine paleoenvironments. Detailed ecological data are required for more species and geographical localities and over extended periods of time at single locations. For many regions of the world little is known of the ecological controls on ostracode distributions which could be transferred to interpreting fossil assemblages. Particular attention must be given to tropical and subtropical lakes where seasonal variations in wind and precipitation may leave a specific imprint in ostracode valves (both molphologically and geochemically). Semi-arid regions, where closed basins are most common deserve more attention as well, to develop paleohydrochemical schemes which might be related to climate.

Standardization of experimental methods among ostracode specialists could contribute to the development of a more rigorous understanding of what partition coefficients (K_p) imply. Additional chemical analyses of numerous ostracode species are required to determine the temperature dependence of Mg^{2+} uptake which in turn will be useful to reconstruct paleotemperature curves from lacustrine records. However, given the linkage between Mg^{2+} with respect to aqueous chemistry and the rate term in biocalcification that must be operative for a temperature effect, the use of Mg/Ca ratios may be an impossible task because it would require to determine such values from all species present in a given lake and to repeat this process in all extant lakes before any attempt to apply the technique to the geologic record. Furthermore, the analysis of trace elements other than strontium and magnesium (e.g. iron, barium, zinc, lead and manganese) may prove useful in paleolimnological reconstructions.

Nonmarine ostracode stable isotope recolds are of major significance in reconstructing lake evaporation/precipitation records and possibly paleoproductivity. To date $\delta^{18}O$ records have proven more useful and interpretable than $\delta^{13}C$, but both should continue to receive attention. Probably the most fruitful approach with fossil ostracode studies can be achieved through the simul-taneous analysis of multiple records (faunal, trace elements, stable isotopes). Using all possible approaches together we have the best chance of quantitatively inferring climate change from fossil ostracodes.

ACKNOWLEDGMENTS

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