

Late Holocene Environmental variability in an Armenian lacustrine ecosystem based on Ostracoda from Lake Sevan

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ABSTRACT: Lake Sevan, eastern Armenia, is an ancient lake, although it has changed in morphology on several occasions. There is evidence of lacustrine conditions in the Sevan Basin since the late Miocene, but the modern lake evolved into its present form only in the Holocene. The community is dominated by extant, spatially widespread species that have been recorded throughout Europe and Asia (e.g. *Limnocythere inopinata*, *Ilyocypris bradyi*, *Cyprideis torosa*, *Candona candida* and *Candona neglecta*), although a small proportion of the association is restricted to the Caucasus (e.g. *Fabaeformiscandona caucasica* and *Limnocythere inopinata sevanensis*). The diversity of the Holocene Ostracoda communities appear to reflect the gradual increase in water depths and environmental heterogeneity during the Sub-boreal European Climatic phase (Late in the Khvalynian climatic phase of the Caspian region). Shallow water of about 6m seem likely much of the time and no more than about 20m at its deepest. None of the boreholes penetrated deeper water deposits, so that *Fabaeformiscandona dorsibiconcava*, which lives below c.40m in the modern lake, was not found. Salinity was no greater than oligohaline; and water temperatures appear to have been cool. As is the case today, there were a number of streams transporting ostracods (such as *Prionocypris zenkeri* and *Ilyocypris bradyi*) into the lake and weeds were abundant. The Holocene association of Lake Sevan is unusual in that it is one of the few in which sexual populations of *Limnocythere inopinata* occur. The first females were observed in Pliocene deposits, but males appeared in the Pleistocene and also lived in the lake during the Holocene.

Keywords: Holocene, Lake Sevan, Ostracoda, lacustrine palaeoecology

1. Introduction

Lake Sevan is situated in Gegharkounik Province, in the eastern part of Armenia (Text-Figure 1a), at an altitude of 1900 m above sea level and surrounded by peaks that rise up to 3000 m. With a maximum length of about 70 km and a maximum width of about 50 km, it is one of the largest Alpine-type lakes. The Artanish and Noraduz peninsulas reduce the width of Lake Sevan at one point, to only 7 km and the two parts of the lake have been named Greater and Little Sevan.

Although a considerable amount of data has been published on European Recent and Holocene lacustrine Ostracoda (Meisch, 2000, and references), relatively little information exists for the southern part of the former Soviet Union in general and the Caucasus in particular. Holocene ostracods from Armenia, including Lake Sevan, were briefly discussed by Bubikyan (1984), but no detailed analyses of the faunas have been published. This paper extends the data on Holocene fresh water ostracods from the well known European province into the less well known region of western Asia.

Core samples from a drilling programme into the lake bed in 1959, were available for examination. The cores penetrated through silts, sands and clays, which are believed, on the basis of sedimentation rates and geochemical evidence, to date from about 5000 years before present to Recent times (Aslanian and Sayadian, 1984; Gulakyan and Wilkinson, 2002). Data from these borehole sections were supplemented by two sections from the shore of the lake (Text-figure 1b). The first section was a cliff section on the south-western Bank of Lake Sevan, cut by the River Argichi, but samples proved barren of ostracods. The reason for this is related to facies and the environmental conditions at the time of deposition. The section cut through sands and pebble beds, which had been deposited by the river, rather than lacustrine muds and silts. Rivers in the region are fairly slow flowing through much of the year, but during April, May and June, water energy levels are high (approximately 20 m³ per second) and unsuitable for the establishment of an ostracod community. Any populations that may become established during the summer months would have been flushed out again during the following Spring. This is also the case for River Vardenik (which flows into the southern part of the lake); no ostracods were found in the river bed samples collected.

The second exposure, at the boat slipway of the village of Sevan, on the north western shore, comprised lacustrine silts that yielded a number of Holocene ostracods.

The Holocene deposits of Lake Sevan have yielded fifteen species of ostracod (Text-Figure 2) as given in the annotated systematic check list appended.

2. Geological evolution of Lake Sevan

Aslanian and Vehuni (1984) and Aslanian and Sayadian (1984) outlined the evolution of the Sevan region during the Neogene. It was during the Miocene that the environment of deposition began to change from essentially marine to non-marine. In the Sevan Trough, the globigerine and nummulite dominated foraminiferal faunas of the Eocene and Oligocene pass up into Miocene marine-lagoonal faunas with molluscs, bryozoa, smaller foraminifera and ostracods but these conditions were gradually replaced by a terrestrial environment. Bubikyan (1984) recorded several non-marine ostracods from the Miocene of the Sevan region: *Darwinula stevensoni*, *Ilyocypris bradyi*, *Ilyocypris gibba*, *Candona neglecta*, *Pseudocandona albicans* and *Cyprideis torosa* (Text-figure 3). The Pliocene of Armenia shows a complete absence of marine conditions. Damming of the River Hrazdan by volcanic material resulted in the development of the earliest known lacustrine environment in the Sevan Depression during the mid Pliocene (dated to 4.8-5.2Ma) (Aslanian and Sayadian, 1984). In addition to rare specimens of those ostracods recovered from the late Miocene (listed above), Bubikyan (1984) recorded common *Candona neglecta*, *Candona candida* (as *C. kirgizica*) and *Limnocythere inopinata* (Text-figure 3) in the Pliocene sequence of the Sevan region.

A series of volcanic episodes took place throughout the Pleistocene and into the Holocene, caused damming of the river system and further evolution of lacustrine conditions of the region (Aslanian and Sayadian, 1984). The ostracod assemblage in Lake Sevan during the Pleistocene was essentially similar to that of the Pliocene, but Bubikyan (1984) also recorded the first occurrence of *Prionocypris zenkeri* and *Limnocythere inopinata*, including males (as *L. fontinalis*).

It is unlikely that the boreholes from which Holocene samples were collected for the present study are older than the Atlantic Climatic Stage in the European sense. Radiocarbon dates are lacking, but estimates from geological and geochemical data indicate that the stratigraphically lowest samples are approximately 5000 years old, or perhaps very slightly older. This was a time when the warm and wet climatic conditions of the Atlantic European Climate phase (towards the close of the Lavlakansky phase of the Aral region) was replaced by more arid conditions throughout the eastern Mediterranean region, Turkey and Armenia (Leng et al., 2001; Eastwood et al., in press). It seems likely that this was a time of recession in Lake Sevan, for archaeological evidence indicates that by 3,500 years BP, human habitation had taken place around the shores of a much reduced lake.

It was as a consequence of the damming of the River Hrazdan by Holocene lava flows that the modern Lake formed. However, there is some evidence from Lchashen and Norashen that Lake Sevan was greatly reduced in size and depth during the Bronze Age (Aslanian and Sayadian, 1984). Archaeological evidence, revealed by the falling water level during the second half of the 20th century, indicates human habitation around the margins of the Holocene lake. Early and Late Bronze age settlements, burial sites and artifacts, including wooden chariots (giving radiocarbon dates of 3500-3630 \pm 100 years) have been recovered. Lake Sevan was in existence prior to the period of Bronze Age occupation (radiocarbon dates from lacustrine molluscs immediately below the archaeological level are 6370 \pm 110 years). Above the archaeological horizon, lacustrine sediments are again present and radiocarbon dates on the molluscs give the earliest dates for the second phase of lacustrine development as 2020 \pm 120 and 2090 \pm 70 years (Aslanian and Sayadian, 1984).

Other archaeological evidence include a stone with cuniform writing dating to the time of the Urartian King Argishti (785-760BC), which was also recovered from the lake bed near the town of Lchashen and ceramics, the youngest of which date to about 300BC.

Hence, although a lacustrine milieu has centred about the lake for a considerable period of time, the origins of Lake Sevan, in its current form, date from only about 2000 years ago.

3. Holocene Ostracods from Lake Sevan

Ostracods have been found throughout the Neogene of the region as indicated in an overview by Bubikyan (1984). Ostracod diversity during the early history of Lake Sevan region gradually increased between the late Miocene and Pleistocene, but it was during the Holocene that ostracod diversity increased to its maximum (Text-figure 3); the present study suggests that diversity was 15 species (see the appendix below). A sixteenth species, *Fabaeformiscandona dorsobiconcava* (Bronshstein), may have occurred when deeper waters had been established (it is present in the modern lake), but it was not recorded during the present study as only shallow water Holocene sands, argillaceous sands and silty sands, separated by clays, were penetrated by the boreholes (Text-Figure 4).

3.1. Transect 1 (Text-figure 4)

A single sample of clayey sand, from immediately below the lake bed, in each of borehole 903 and 933 were examined for ostracods. Borehole 903 yielded a low diversity fauna dominated by *Candona neglecta*. Borehole 933 also yielded a low diversity fauna dominated by abundant *Candona neglecta*, but with common *Fabaeformiscandona caucasica* and *Limnocythere inopinata*. *Limnocythere inopinata* was consistently frequent throughout the clays and sands of Borehole 907, where both males and females were found, but common *Cytherissa lacustris* were found only in the clay and silty sand.

Borehole 934 contained a diverse fauna, particularly in the muddy sands near the top of the sequence. Common *Candona neglecta* and *Limnocythere inopinata*, together with frequent *Ilyocypris bradyi*, were recovered from the sands at 3.5m depth and although only *Candona neglecta* maintained its dominance in the muddy sands at the top of the succession, five additional species were also present, including *Cytherissa lacustris* and *Prionocypris zenkeri*.

Borehole 939 penetrated 0.1m of silty sand and 0.25m of sand before entering 1.1m of mud. Most ostracod species are rare in the muds, although *Limnocythere*

inopinata was more frequent. There is a noticeable increase in the sands of *Candona neglecta*, *Cyprideis torosa* and, in the highest sample, *Ilyocypris bradyi*. Also of note is the fact that *Candona candida* and *Fabaeformiscandona caucasica* are present only in the sands of the top 0.4m of the borehole.

3.2. Transect 2 (text-figure 5a-d)

A low diversity fauna was recorded in Borehole 902, but one dominated by *Candona neglecta* and *Limnocythere inopinata*, particularly in the clay towards the top of the core. Borehole 914 also contains a low diversity faunas. The sand at the bottom of that borehole is dominated by *Limnocythere inopinata*, but *Candona neglecta* becomes common in the overlying clay. However, it is in the sandy silts at the top of the borehole where diversity is at its greatest with abundant *Limnocythere inopinata* and *Candona neglecta*, frequent *Ilyocypris bradyi* and several other rare species.

A thin layer of sand was also present at the top and bottom of Borehole 916, but the largest part of the sequence comprised muds. Diversity is low in the basal part of the borehole, although *Limnocythere inopinata* is consistently present. Diversity is much higher above 0.5m depth, where frequent to abundant *Limnocythere inopinata*, is accompanied by frequent to common *Ilyocypris bradyi* and *Candona neglecta*. It is only in the highest part of the borehole that *Cytherissa lacustris*, *Fabaeformiscandona caucasica*, *Ilyocypris gibba* and *Candona candida* are found, although all are rare.

A similar pattern is shown in borehole 921 where very low diversity assemblages occur in the sands at the base of the borehole, but with a marked increase in the overlying clays, including frequent *Limnocythere inopinata*. The sandy silt at the top of the borehole yielded a fauna comprising abundant *L. inopinata* and *Candona neglecta* together with frequent *Ilyocypris bradyi*, *Fabaeformiscandona caucasica*, *Candona candida*, *Cytherissa lacustris* and a number of rare species including *Limnocythere inopinata sevanensis*, *Herpetocypris chevreuxi* and *Prionocypris zenkeri*.

Borehole 924 penetrated mainly clays and muds, but with two thin sands. Abundant *Candona neglecta* and *Limnocythere inopinata* (a sexual community),

together with with frequent *Ilyocypris bradyi* dominate a diverse fauna of 12 species in the lower clay sample. The sand yielded a less diverse fauna (seven species) of rare ostracods. Borehole 925 also comprises mainly clays, but with two thin sandy silts. The lower sandy silt yielded a rare, low diversity fauna, but the higher one contained abundant *Limnocythere inopinata*, common *Candona neglecta* and frequent *Ilyocypris bradyi*, *Cypridopsis* sp, *Candona candida* and *Cyprideis torosa*. In many respects, the fauna taken from the intervening clay was similar to the higher sandy silt. In contrast, borehole 938 penetrated a sequence of sand with the exception of two thin horizons of sandy silt. Diversity is generally low in this borehole, but in the upper sandy silt, *Cyprideis torosa* and *Limnocythere inopinata* are abundant. The borehole differ from the others examined as *Darwinula stevensoni* is frequent.

Finally, a single sample from borehole 937 was taken from the muddy sand immediately below the lake surface. It yielded a diverse fauna of abundant *Limnocythere inopinata*, together with frequent *Candona neglecta* and *Ilyocypris bradyi*.

3.3. Sevan Village exposure

At the boat ramp on the side of the lake near the village of Sevan (Text-Figure 7), approximately 1m of lacustrine silts are exposed. *Candona neglecta*, *Fabaeformiscandona caucasica*, *Limnocythere inopinata* and *Cyprideis torosa* are well represented at this locality

4. Environmental controls

The ostracod assemblages recovered from the Holocene of Lake Sevan comprise extant species most having a wide geographical range. The environmental requirements of living taxa may therefore be used to draw conclusions regarding the environmental conditions prevailing during the recent past.

Four species of candoninae were found in the Holocene samples examined. Bronstein, in his monographical work on freshwater ostracods (1947), and Bubikyan (1984) recorded *Candona neglecta* from Lake Sevan. *Candona neglecta* is difficult to distinguish from *C. angulata*, but differs in having a long straight dorsal margin and

in lacking the posterior angularity of the left valve. *Candona neglecta* was found in large numbers in the present study. Meisch (2000) indicates that it shows a preference for cooler water but will survive in temperatures of about 20°C for short periods. It has been recorded in flowing streams and ponds fed by spring water and in lakes where it has been recorded from the shallows down to 311m in Lago Maggiore (Italy). It is also tolerant of low oxygenation of water (Danielopol et al., 1985, 1993) and salinities of 0.5 to 16‰. With a tolerance of a variety of environmental conditions, it is not surprising to find the species has a widespread geographical distribution throughout Europe, North Africa, Asia and North America.

Candona candida, which has a similar geographical distribution, is a common component in Pliocene to Recent faunas in Armenia. It occurs in a variety of environments from springs, streams, ponds and lakes, in both still and turbulent conditions and at a variety of water depths. However, it does not tolerate salinities much above 5.3‰ (low in the mesohaline range) (Hiller, 1972; Usskilat, 1975), particularly when these salinities are persistent, and does not tolerate summer water temperatures in excess of 18°C (Hartmann and Hiller, 1977). It is one of the more acid-tolerant species, for Fryer (1980, 1993) recorded it in pH of less than 5.0.

Pseudocandona albicans, has been found in very small numbers in the Lake Sevan boreholes, notably borehole 914. It has been recorded living in shallow water depths of ponds, pools and lakes throughout Europe, Asia and North America and shows a preference for cooler temperatures and slow moving water. Danielopol (1991) indicated that the species was found in Mondsee, only where mountain streams entered the lake.

Of the less common Holocene candoninae, *Fabaeformiscandona caucasica* is worthy of note as its distribution is restricted to the Caucasus. It is one of the few living species recorded from Lake Sevan by Bronshtein (1947), where it appears to favour water depths between 5 and 51m, although its environmental requirements remain poorly understood. Bronshtein also reported it from pools in Crimea.

Cytherissa lacustris has been found in most Holocene samples from Lake Sevan, although it is always rare. *Cytherissa lacustris* is geographically widespread

species distributed from shallow waters to profundal depths (over 200m in Lake Constance according to Meisch, 2000), although it is particularly common in waters of 20-30m (for example in Mondsee, Danielopol *et al.*, 1988), where the oxygen content and temperature of the water appear to be significant (Geiger, 1990a, 1990b, 1993). It is generally a cold stenothermic form, but is tolerant of wide temperature ranges. It favours oligo-mesotrophic lakes, but can also occur at very shallow depths. The species is adversely affected by anthropogenic eutrophication; the best documented example being Mondsee (Danielopol *et al.*, 1985, 1990a), but this has also been observed in living faunas in Lake Sevan.

Two species of the genus *Ilyocypris* colonised the Holocene Lake Sevan, *I. bradyi* and *I. gibba*. *Ilyocypris bradyi* is present in small numbers in most samples from the Holocene borehole deposits. The species is found living in slow flowing rivers, streams, ponds and lakes and appears to prefer water bodies fed by springs. In fact it has been suggested that when present in lakes, it is probably derived from nearby sources of spring water (Meisch, 2000). Although usually associated with very low salinities, it tolerates oligohaline waters up to 4.4‰ (Jaeckel, 1962; Vesper, 1975) and has also been recorded in the brackish conditions of coastal ponds in Belgium (Wouters, 1983). It is also tolerant of a wide range of Ca in the water, above 18 mg/L (Vesper, 1975), and Meisch (2000) described it as meso- to poly-titanophilic. The second species, *Ilyocypris gibba*, is also geographically widespread in shallow water and is more usually found living in small, shallow, water bodies such as ponds, streams, paddy fields and lakes. It lives in a wide range of water temperature, in both stagnant and flowing water, but has a more restricted salinity tolerance (oligohaline).

Limnocythere inopinata is one of the more common species in the Holocene of Lake Sevan. The species is ecologically very tolerant and has been recorded in a number of environmental situations throughout Europe and Asia. Its living occurrence ranges from small ponds, slow streams and rivers, through to large lakes. However, it is restricted to very shallow, littoral conditions, down to depth of about 6m (in the Mondsee) and down to 12-18m in Bothnian Bay (Savolainen and Valtonen, 1983). In Neusiedlersee, the species is particularly common on soft muds with high water content (Jungwirth, 1979).

The species is parthenogenetic throughout much of Northern Europe, although occasionally extremely small numbers of males (male:female ratio of approximately 1:500 to 1:1000) have been recorded (Horne and Martens, 1999, Meisch, 2000). In exceptional cases, bisexual populations occurred in Mid to Late Pleistocene of Germany, Poland, Austria and Croatia, but today bisexual populations are confined to southern Europe: Macedonia, Greece and Turkey (Petkovski, 1959, Martens, 1990, Griffiths and Horne, 1998; Gülen, 1985b; Horne and Martens, 1999). *Limnocythere inopinata* entered the Lake Sevan region during the Pliocene (Bubikyan, 1984), and it forms a significant part of the fauna in the modern lake assemblages. It had formed a bisexual community by the Holocene, but and this was probably also the case in the Pleistocene, when common males were recorded for the first time (as '*Limnocythere fontinensis*', Bubikyan, 1984).

Cyprideis torosa lives throughout Europe and its range extends into Asia, Northern Africa and North America. It is tolerant of a wide variety of salinities including hypersaline, marine lagoons, salt marshes and brackish marine estuaries through to fresh water ponds and lakes. *Cyprideis torosa* lives on a variety of substrates including muds, sandy muds, sands and weeds; has a wide tolerance to temperature and shows a preference for shallow waters of less than 30m. Its broad environmental tolerance has allowed it to become successful in conditions that are adverse for the majority of non-marine ostracods. The Aral Sea, for example, which has had a long history (Boomer *et al.*, 2000) is disappearing as a result of over-exploitation for irrigation and salinity has increased from 8-10‰ to 28-30‰. Of the eleven species of ostracod living in the Aral Sea in 1960, ten have gone into extinction and only *Cyprideis torosa* survives (Aladin, 1993). It is generally present in small numbers in the Holocene of Lake Sevan, but in some boreholes (e.g. borehole 938) it is abundant in the sandy silt at the top of the sequence (i.e. in sediments of about 200-300 years old).

Four species (*Darwinula stevensoni*, *Prionocypris zenkeri*, *Herpetocypris chevreuxi* and *Cyclocypris ovum*) are rare in the Holocene deposits of Lake Sevan.

Darwinula stevensoni is found living in ponds, lakes and slow running streams, and can tolerate salinities within the mesohaline range (up to 15‰ according to Hiller, 1972). However, the distribution seems to be limited by depth; it is generally found in depths less than 10-12m and it shows a preference for depths of 1 to 6m. *Prionocypris zenkeri* lives in a number of scattered localities throughout Europe, Turkey and Armenia where it shows a preference for cold water temperatures and calcium content in excess of 72mg/L and is often associated with weeds in slow flowing streams and ponds, although it also tolerates more rapidly flowing water. Occurrences in lakes are thought to be due to transportation, (Meisch, 2000). Gülen (1985a,b) has recorded males in a lake in Turkey. Although the species is found in the Holocene samples from Lake Sevan (boreholes 921, 925 and 939), males have not been recognised.

Herpetocypris chevreuxi is found in the littoral zones of lakes and slow running streams in Europe, around the Mediterranean, Turkey and Iran, Asia, South Africa and South America. It is halophilic, being found in salinities up to 3-4‰ and is tolerant of stagnant and polluted waters (Ant and Herbst, 1966; Onderíková, 1993). Despite its wide geographical range, it was found in only two boreholes in Lake Sevan (921 and 925) where it is rare. *Cyclocypris ovum*, which is another rare species in the Holocene of Lake Sevan, lives in a variety of environments such as small ponds, springs and in lakes where it has been recorded mainly from the littoral zone and only rarely rarely in deeper waters. The species is found in both still and turbulent conditions and can tolerate salinities up to 6.4‰ (Meisch, 2000).

5. Palaeoenvironmental interpretation

An idea of the environmental conditions in Lake Sevan during the Holocene can be gained by a comparison of the ostracod community with the environmental requirements of living animals.

The three most common species in the Holocene Lake Sevan (*Limnocythere inopinata*, *Candona neglecta* and *Ilyocypris bradyi*) show a preference for shallow water and it is unlikely water depths exceeded about 20 m in the sample area. The notion that water depths might have been much shallower than this (perhaps as

shallow as 6 m) is supported by the presence of species such as *Darwinula stevensoni* and *Herpetocypris chevreuxi*. Although no species restricted to profundal depths were present, a few (e.g. *Fabaeformiscandona caucasica*) can tolerate deeper waters; *Fabaeformiscandona dorsobiconcava*, which is restricted to depths in excess of about 30m in the modern lake, was not present.

Salinities during the Holocene appear to have been oligohaline. Although some species (e.g. *Cyprideis torosa*) are tolerant of a wide salinity range, the presence of *Ilyocypris bradyi* suggest salinities did not exceed about 5‰ (oligohaline) and halophilic *Herpetocypris chevreuxi* (tolerating salinities up to 3-4‰) is common at some localities.

As is the case today, numerous streams entered Lake Sevan during the Holocene and there seems to have been a large influx of spring water into the sample area. This conclusion is based on the notion that *Prionocypris zenkeri* is an inhabitant of slow flowing streams and its occurrence in lakes is said by some authors to be due to transportation. This may be supported by the presence of *Ilyocypris bradyi* which is also considered by some authors to be derived from sources of spring water. However the widespread occurrence of these species in the study area, and the occurrence of juvenile instars, may also suggest that they were living there.

It is likely that the Holocene weeds were plentiful as some species, and particularly *Prionocypris zenkeri* are often found associated with them. In fact some samples yielded charophyte oogonium, confirming this conclusion.

Although *Herpetocypris chevreuxi* is tolerant of low oxygen waters, for other species oxygen content and temperature of the water is significant. *Cytherissa lacustris* appears to have disappeared from many Alpine lakes, during the latest phases of the Pleistocene, due to dysaerobic or anoxic conditions (Danielopol et al., 1990b) and in Mondsee, Austria, it has been unfavourably affected by the periods low concentrations of O₂ (Geiger, 1993). It is not a common constituent of the Lake Sevan fauna, but its presence is interpreted as indicating that O₂ concentrations were not unduly low during the Holocene.

Prionocypris zenkeri, a rare species in the Holocene sequences, is oligothermophilic, but most of the other species recorded, are more temperature tolerant. Of the more common species, *Candona neglecta*, for example, shows a preference for cold water, but will survive in higher temperatures for short periods, and *Cytherissa lacustris* is tolerant of a fairly wide temperature range, but is generally a cold stenothermic form (Meisch, 2000). The most abundant species, *Limnocythere inopinata*, is polythermophilic, but no warm stenothermal species were recovered. Cool water temperatures appear to be indicated, rather than cold.

6. Conclusions

Lake Sevan is an ancient fresh water environment that evolved into its present morphology during the Holocene. From a biostratigraphical context, the introduction of *Fabaeformiscandona caucasica*, *Herpetocypris chevreuxi* and *Limnocythere inopinata sevanensis* into the lake during the Holocene are considered significant.

The Ostracoda recorded from the Holocene lake bed sediments appear to reflect the gradual increase in water depths and environmental heterogeneity during the Sub-boreal European Climatic phase (Late in the Khvalynian climatic phase of the Caspian region). Ostracod diversity remained low during the earliest period (latest Atlantic-early Sub-boreal), samples from the deeper boreholes rarely exceed three or four species. However, diversity increases up sequence and samples taken in the upper 2m may yield between seven and ten species of ostracod. In total fifteen species have been recorded from the late Holocene and sub-recent sediments.

The typical ostracod assemblage in the Holocene of Lake Sevan includes *Limnocythere inopinata*, *Ilyocypris bradyi*, *Candona neglecta* and *Cyprideis torosa*. Other species have a more patchy distribution, although in some boreholes they become common or abundant, presumably reflecting local microenvironmental conditions. These species are: *Fabaeformiscandona caucasica*, *Candona candida*, *Cytherissa lacustris*, *Ilyocypris gibba* and *Limnocythere inopinata sevanensis*.

The environmental conditions in the south-western part of Lake Sevan during the Holocene can be interpreted from the ostracods recovered. Shallow water of about 6m seems likely for much of the time and no more than about 20 m at its

deepest. None of the boreholes penetrated deeper water deposits, so that *Fabaeformisandona dorsibiconcava*, which lives below about 40 m in the modern lake, was not found. Salinity was no greater than oligohaline; and water temperatures appear to have been cool. As is the case today, there were a number of streams transporting ostracods (such as *Prionocypris zenkeri* and *Ilyocypris bradyi*) into the lake and weeds were abundant.

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Appendix: An annotated systematic check list of Ostracoda from Holocene deposits of Lake Sevan

All figured specimens are housed in the collections of the British Geological Survey, Nottingham, UK, together with unfigured material. Unfigured material is also held by the Geological Institute, Academy of Science of the Republic of Armenia, Yerevan.

Superfamily DARWINULINOIDEA Brady and Norman, 1889

Family Darwinulidae Brady and Norman, 1889

Genus *Darwinula* Brady and Robertson, 1885

Darwinula stevensoni (Brady and Robertson, 1870)

Darwinula stevensoni has a cosmopolitan Recent distribution and a long geological record, at least to the Oligocene and it has been recorded in deposits older than that. It has been recorded in the Miocene to Recent in Armenia.

Ecological note: thermoeuryplastic, oligorheophilic, titanoeuryplastic and mesohalophilic (Meisch, 2000).

Superfamily CYPRIDOIDEA Baird, 1845

Family Candonidae Kaufmann, 1900

Subfamily Candoninae Kaufman, 1900

Genus *Candona* Baird, 1845

Candona candida (O.F. Müller, 1776)

Common in the Pliocene to Recent in Armenia (recorded by some authors as *C. kirgizica*).

Ecological note: rheoeuryplastic, euryplastic for pH, titanoeuryplastic, oligothermophilic, and oligohalophilic (? to mesohalophilic) (Hiller, 1972; Vesper, 1975; Meisch, 2000).

The species is controlled by temperature according to Hartmann and Hiller (1977), who indicate that *C. candida* does not tolerate summer water temperatures in excess of 18°C.

Candona neglecta Sars, 1887

Range: This species has been recorded from the Miocene to Holocene in Armenia.

Ecological note: oligothermophilic, oligo- to mesorheophilic, titanoeuryplastic (Hiller, 1972; Vesper, 1975b; Hartmann and Hiller, 1977) and Meisch (2000) suggests the species is meso- and probably polyhalophilic.

Genus *Fabaeformiscandona* Krstić, 1972

Fabaeformiscandona caucasica (Bronstein, 1947)

Known only from the Holocene and Recent.

It is found living in water depths between 5 and 51m in Lake Sevan.

Candona dorsobiconcava (Bronstein, 1947)

Recorded from the Holocene and Recent of Lake Sevan.

This species is related to *F. caucasica*, but differs in the shape of the genitalia (Bronstein, 1947, page 227-228). It is a very rare species in Lake Sevan and restricted to deeper parts of the lake below about 30m (Bronstein, 1947, Friedman, 1950).

Genus *Pseudocandona* Kaufmann, 1900

Pseudocandona albicans (Brady, 1864)

Recorded in the Miocene to Holocene of Armenia by Bubikyan (1984). It is very rare in the Sevan region.

Ecological note: mesothermophilic, mesorheophilic, titanoeuryplastic, stygophilic and mesohalophilic (Hartmann and Hiller, 1977; Meisch, 2000)

Subfamily Cyclocypridinae Kaufmann, 1900

Genus *Cyclocypris* Brady and Norman, 1889

Cyclocypris ovum (Jurine, 1820)

Found only in the Holocene and Recent in Armenia, where it is very rare.

Ecological note: Thermoeuryplastic, rheoeuryplastic, and titanoeuryplastic and mesohalophilic, up to 6.4‰ (Meisch, 2000).

Genus *Cypria* Zenker, 1854

Cypria ophthalmica (Jurine, 1820)

The range of this species is Miocene to Recent, but its geological range is significantly less in the Sevan area. Rare, questionable specimens have been found in the Holocene of Lake Sevan and it has been recorded in very rare proportions (as *Cypria lacustris*) in Recent deposits (Bronshstein, 1928; Friedman, 1950).

It has a wide geographical distribution throughout Europe, Asia and America and tolerates a broad range of environmental parameters, but apparently shows a preference for more acidic waters.

Family Ilyocyprididae Kaufmann, 1900

Subfamily Ilyocypridinae Kaufmann, 1900

Genus *Ilyocypris* Brady and Norman, 1889

Ilyocypris bradyi Sars, 1890

Armenian Range: Miocene to Recent.

Ecological note: oligothermophilic and rheouryplastic (Nüchterlein, 1969); polythermophilic (occasionally found at 24°C), mesorheophilic and meso- to poly- titanophilic according to Vesper (1975b) (Meisch, 2000).

Ilyocypris gibba (Ramdohr, 1808)

Armenian range: Miocene to Recent

Ecological note: meso- to polythermophilic, rheouryplastic, titanouryplastic and oligohalophilic (Meisch, 2000).

Family Cyprididae Baird, 1845

Subfamily Eucypridinae Bronshstein, 1947

Genus *Prionocypris* Brady and Norman, 1896

Prionocypris zenkeri (Chyzer and Toth, 1858)

Common in the Pleistocene and Holocene in Armenia.

Ecological note: oligothermophilic, mesorheophilic, and polytitanophilic (Nüchterlein, 1969; Meisch, 2000).

Subfamily Herpetocypridinae Kaufmann, 1900

Genus *Herpetocypris* Brady and Norman, 1889

Herpetocypris chevreuxi (Sars, 1896)

Not common, but a typical species in the Holocene of Armenia.

Superfamily CYTHEROIDEA Baird, 1850

Family Limnocytheridae Klie, 1938

Subfamily Limnocytherinae Klie, 1938

Genus *Limnocythere* Brady, 1867

Limnocythere inopinata (Baird, 1843)

The present interpretation of the species includes those specimens from Armenia formerly assigned to *Limnocythere fontinensis* Schneider, but now considered to be the male of the species.

Fossil distribution: Pleistocene to Recent.

Ecological note: Polythermophilic, titanoeuryplastic (also occurs in Ca-poor waters), rheoeuryplastic and mesohalophilic (Vesper, 1975b; Hartmann and Hiller, 1977; Meisch, 2000).

Limnocythere inopinata sevanensis Bubikyan, 1984

Restricted to the Holocene and Sub-Recent of Lake Sevan.

Family Cytherideidae Sars, 1925

Genus *Cytherissa* Sars, 1925

Cytherissa lacustris (Sars, 1863)

Although this species has a total range of Pliocene to Recent, it is recorded only from the Holocene and Recent in Armenia.

Cytherissa lacustris has sometimes been called *Cytherissa bogatshovi* Livalent in collections from the Armenian-Azerbaijan region. This species said to differ from *Cytherissa lacustris* in size and the degree of ornamentation. However, the present authors consider that both forms fall within the limits of specific variation of *C. lacustris*.

Genus *Cyprideis* Jones, 1857

Cyprideis torosa (Jones, 1850)

This species ranges from the Miocene to Recent in the Lake Sevan region.

Both the un-noded “*Cyprideis littoralis*” and noded “*Cyprideis torosa*” morphs have been recorded in Armenia. Although the

un-noded form is the more common in the Holocene sequence of Lake Sevan, rare noded specimens have been noted.

Text-figure captions:

Figure 1a. A sketch map of Armenia showing the position of Lake Sevan. 1b. A sketch map of Lake Sevan showing the positions of the localities and boreholes mentioned in the text.

Figure 2. A generalised range chart showing the distribution of Ostracoda through the Neogene (modified from Bubikyan, 1984) and Holocene.

Figure 3. The correlation of Holocene deposits penetrated in the boreholes in south-western Lake Sevan.

(For keys to the ornament, see text-figure 5.)

Figure 4. The distribution of Ostracoda in the Holocene deposits of Transect 1 (boreholes 939, 934, 907, 933, and 903), south-western Lake Sevan.

Figure 5. The distribution of Ostracoda in the Holocene deposits of Transect 2, south-western Lake Sevan.

5a. Boreholes 938 and 937; 5b. Boreholes 925 and 924; 5c. Boreholes 921 and 914
5d. 916 and 902

(For keys to the ornament and ostracod proportions, see text-figure 4.)

Figure 6. The distribution of Ostracoda in the Holocene deposits of the Sevan Village section, north-western Lake Sevan.

(For keys to the ornament and ostracod proportions, see text-figure 4.)

Figure 7. Holocene Ostracoda from Lake Sevan, Armenia.

(A-B) *Candona neglecta* Sars, 1887: (A) right valve, lateral view, male, from Lake Sevan Borehole 939; dimensions, length 1.21mm, height 0.69mm (BGS registration no. MPK12417). (B) right valve, lateral view, female, from Lake Sevan Borehole 921; dimensions, length 1.16mm, height 0.62mm (BGS registration no. MPK12418). (C-D) *Fabaeformiscandona caucasica* Bronstein, 1947: (C) right valve, lateral view, female, from Lake Sevan Borehole 914; dimensions, length 0.83 mm, height 0.42 mm (BGS registration no. MPK12419). (D) carapace, right lateral view, male, from Lake Sevan Borehole 921; dimensions: Length 1.27mm, height 0.65mm (BGS registration no. MPK12420). (E) *Candona candida* (O.F. Muller, 1776): left valve, lateral view, from Lake Sevan Borehole 937; dimensions, length 1.06mm, height 0.64mm (BGS

registration no. MPK12421). (F) *Darwinula stevensoni* (Brady & Robertson, 1870): right valve, lateral view, from Lake Sevan Borehole 925; dimensions, length 0.66mm, height 0.45mm (BGS registration no. MPK12422). (G) *Ilyocypris bradyi* Sars, 1890: left valve, lateral view from Lake Sevan Borehole 939; dimensions, length 0.94mm, height 0.50mm (BGS registration no. MPK12423). (H) *Ilyocypris gibba* (Ramdohr, 1808): left valve, lateral view, from Lake Sevan Borehole 925; dimensions, length 0.85mm, height 0.44mm (BGS registration no. MPK12424). (I) *Cyclocypris ovum* (Jurine, 1820): carapace, left lateral view, from Lake Sevan Borehole 925; dimensions, length 0.48mm, height 0.31mm (BGS registration no. MPK12425). (J) *Herpetocypris chevreuxi* (Sars, 1896): carapace, left lateral view, from Lake Sevan Borehole 938; dimensions, length 0.64mm, height 0.33mm (BGS registration no. MPK12426).

Figure 8. Holocene Ostracoda from Lake Sevan, Armenia.

(A-B) *Prionocypris zenkeri* (Chyzer & Toth, 1858): (A) Right valve, lateral view, from Lake Sevan Borehole 921; dimensions, length 1.26mm, height 0.71mm (BGS registration no. MPK12427). (B) left valve, lateral view from Lake Sevan Borehole 939; dimensions, length 1.2mm, height 0.74mm (BGS registration no. MPK12428). (C) *Cyprideis torosa* (Jones, 1850): right valve, lateral view, male, from Lake Sevan Borehole 938; dimensions, length 0.95mm, height 0.49mm (BGS registration no. MPK12429). (D) *Cytherissa lacustris* (Sars, 1863): left valve, lateral view, female, from Lake Sevan Borehole 939; dimensions, length 0.83mm, height 0.51mm (BGS registration no. MPK12430). (E-F) *Limnocythere inopinata* (Baird, 1843): (E) left valve, lateral view, female, from Sevan Village exposure; dimensions, length 0.59mm, height 0.33mm (BGS registration no. MPK12431). (F) carapace, right lateral view, male, from Lake Sevan Borehole 925; dimensions, length 0.65mm, height 0.32mm (BGS registration no. MPK12432). (G-H) *Limnocythere inopinata sevanensis* Bubikjan, 1984: (G) right valve, lateral view, from Lake Sevan Borehole 921; dimensions, length 0.54mm, height 0.34mm (BGS registration no. MPK12433). (H) left valve, lateral view, from Lake Sevan Borehole 921; dimensions, length 0.56mm, height 0.33mm (BGS registration no. MPK12434).

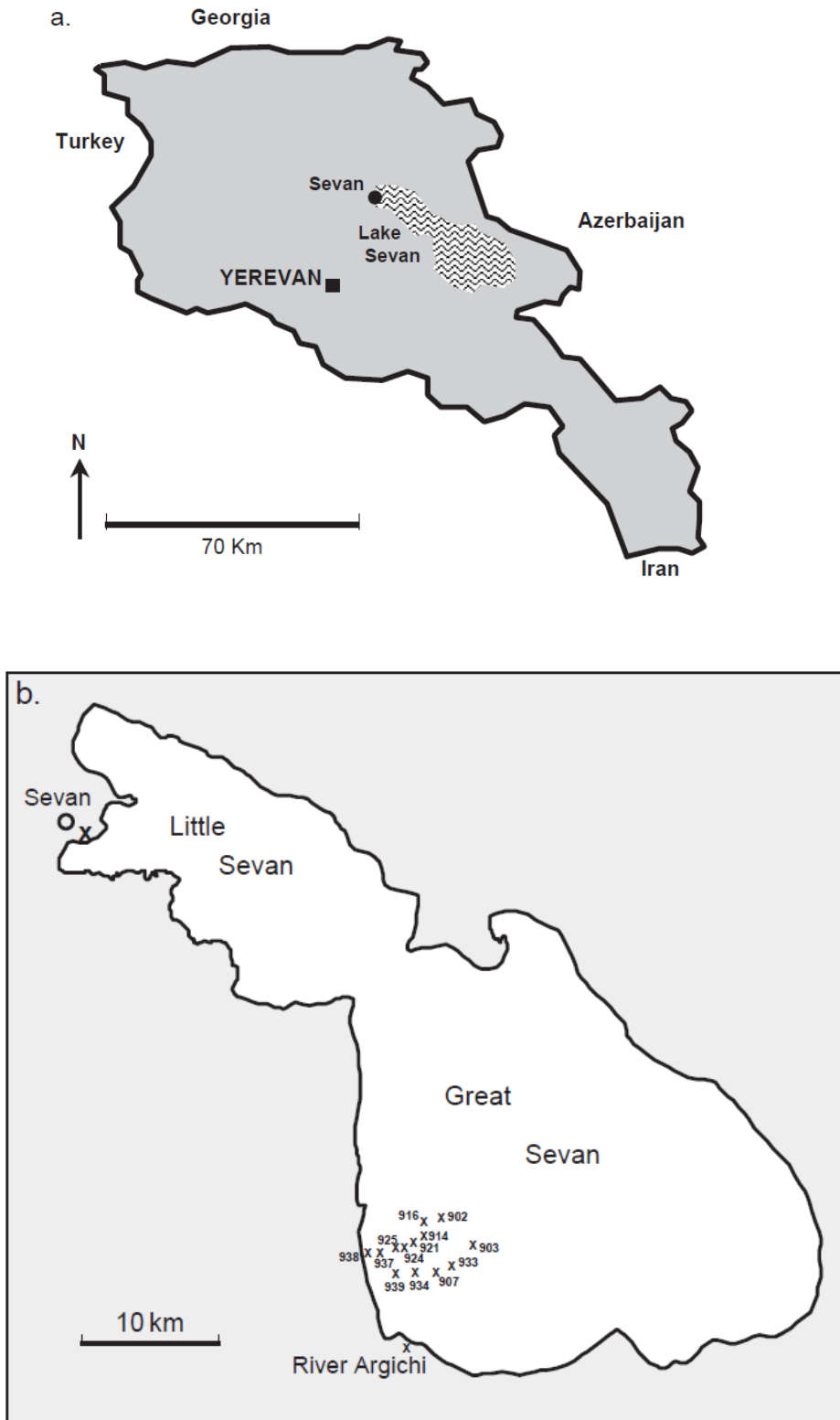


Fig. 1

	<i>Candona neglecta</i>	<i>Cyprideis torosa</i>	<i>Darwinula stevensoni</i>	<i>Ilyocypris bradyi</i>	<i>Ilyocypris gibba</i>	<i>Pseudocandona albicans</i>	<i>Limnocythere inopinata</i>	<i>Candona candida</i>	<i>Prionocypris zenkeri</i>	<i>Fabaeformiscandona? caucasica</i>	<i>Cycloocypris ovum</i>	<i>Cytherissa lacustris</i>	<i>Herpetocypris chevreuxi</i>	<i>Limnocythere sevanensis</i>	<i>Cypria ophthalmica</i>
Holocene	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
Pleistocene	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
Pliocene	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█
Late Miocene	█	█	█	█	█	█	█	█	█	█	█	█	█	█	█

Fig. 2

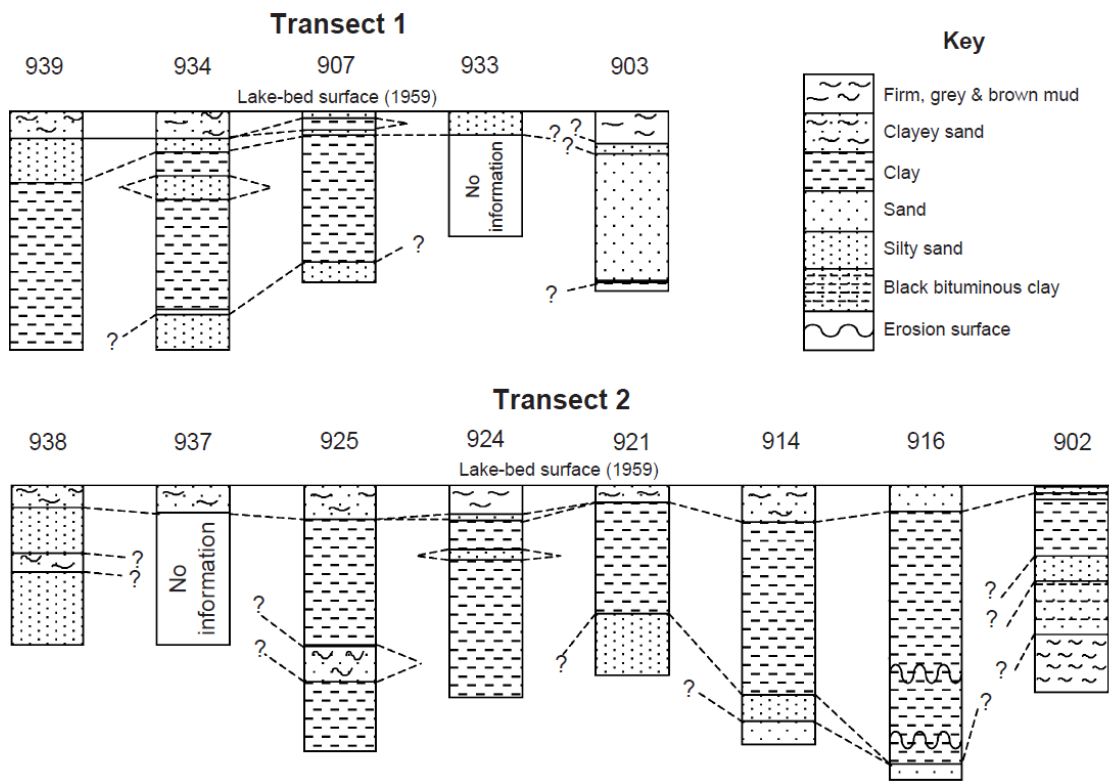


Fig. 3

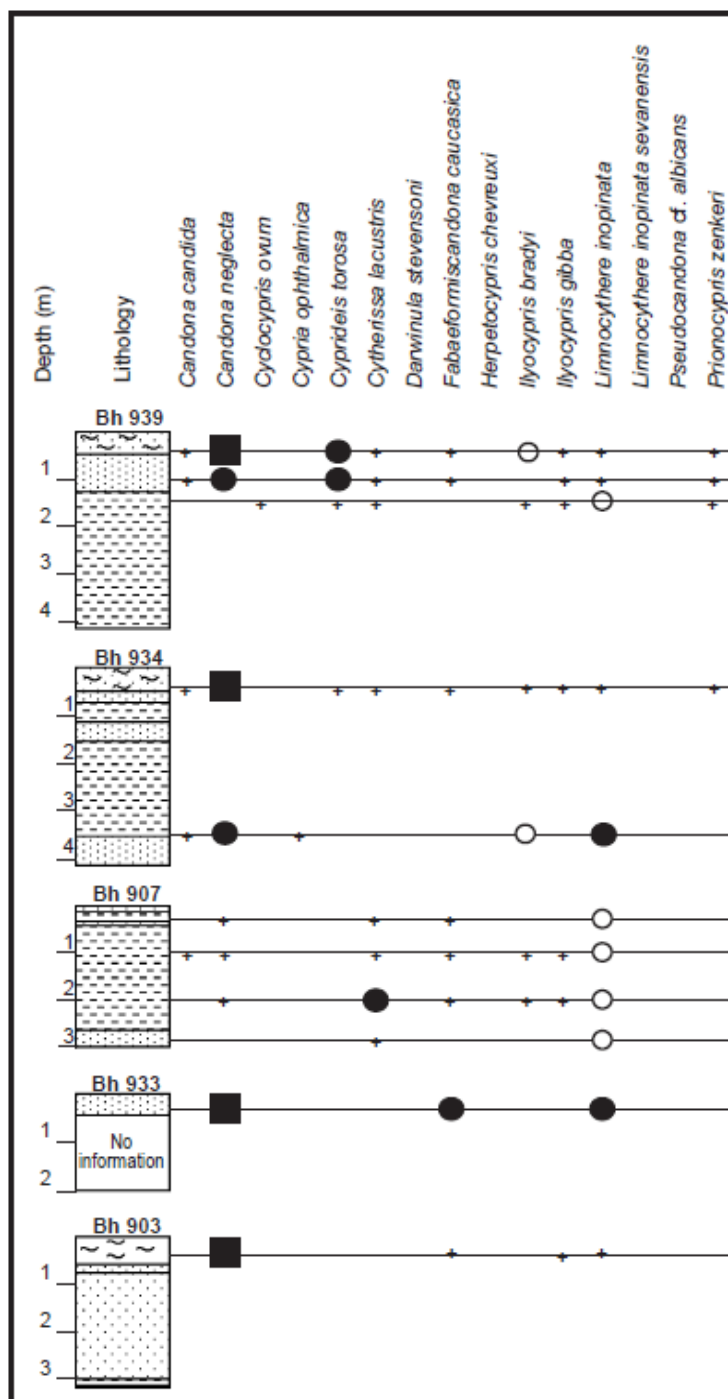


Fig. 4

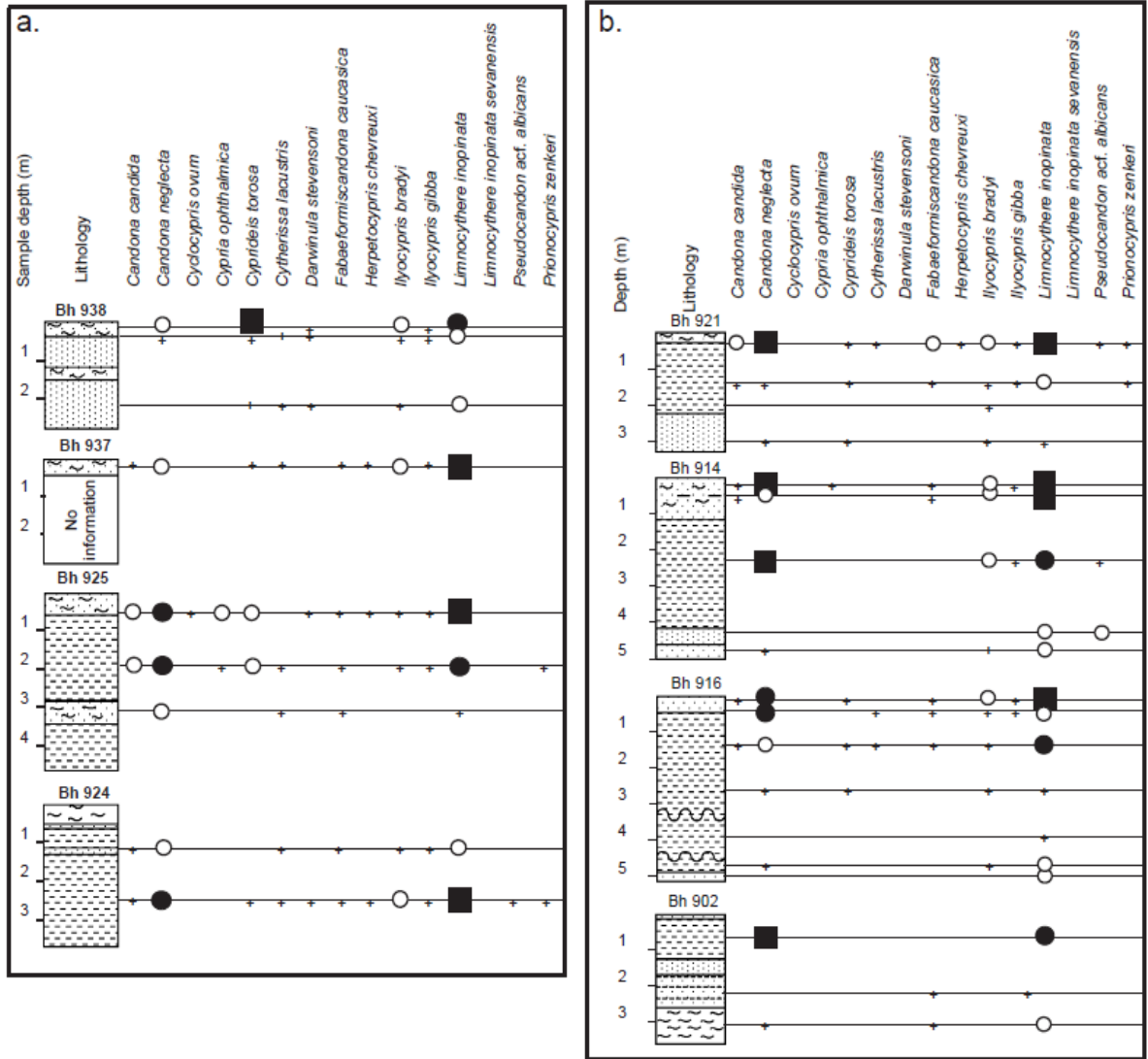


Fig. 5

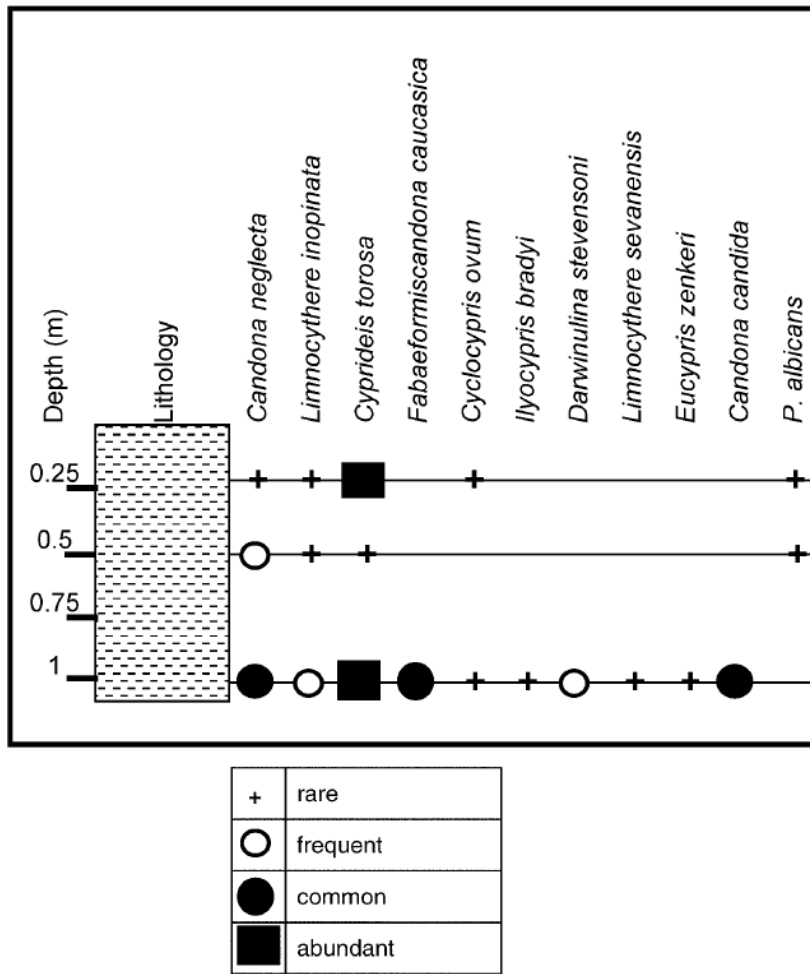


Fig. 6.

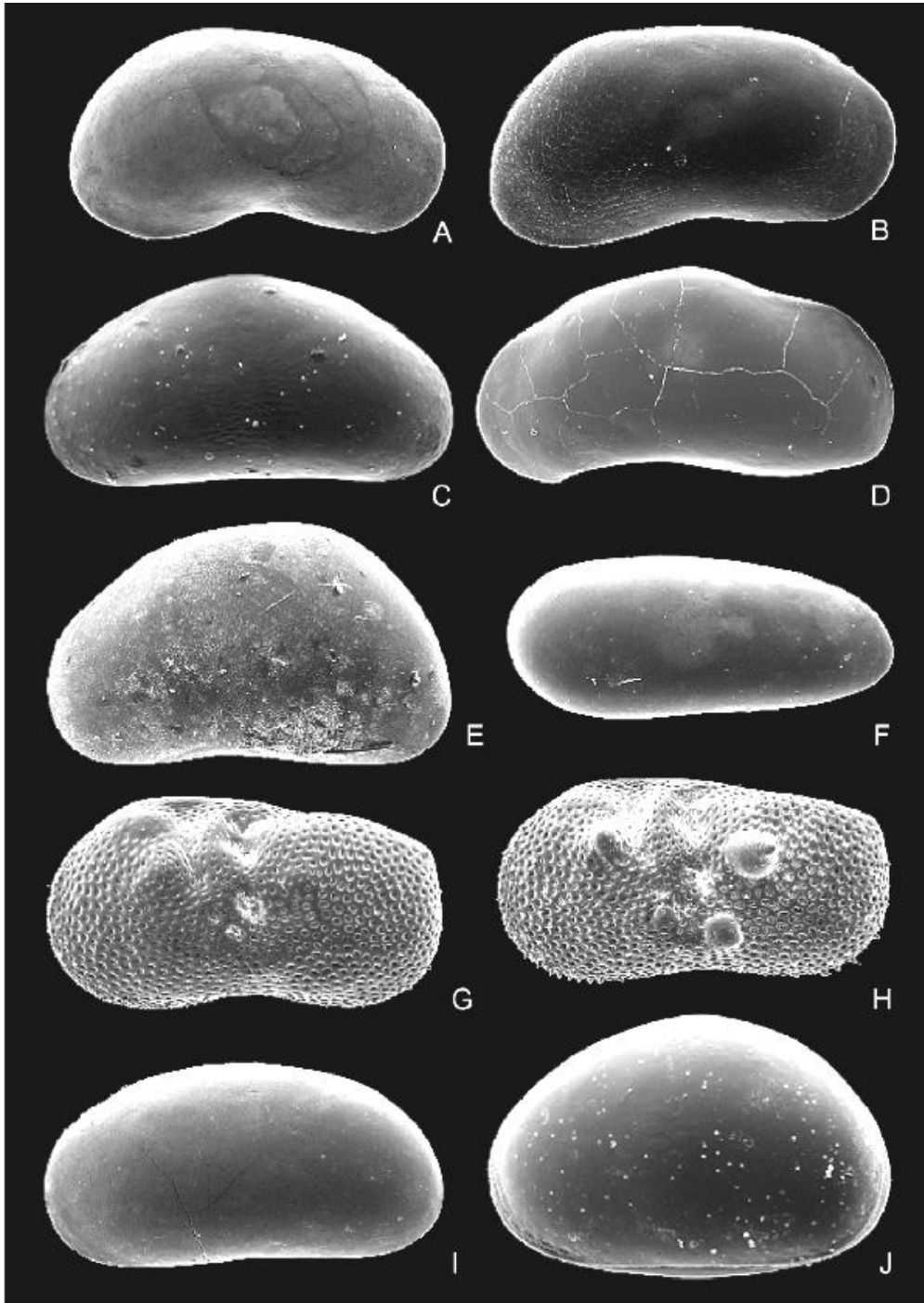


Fig. 7

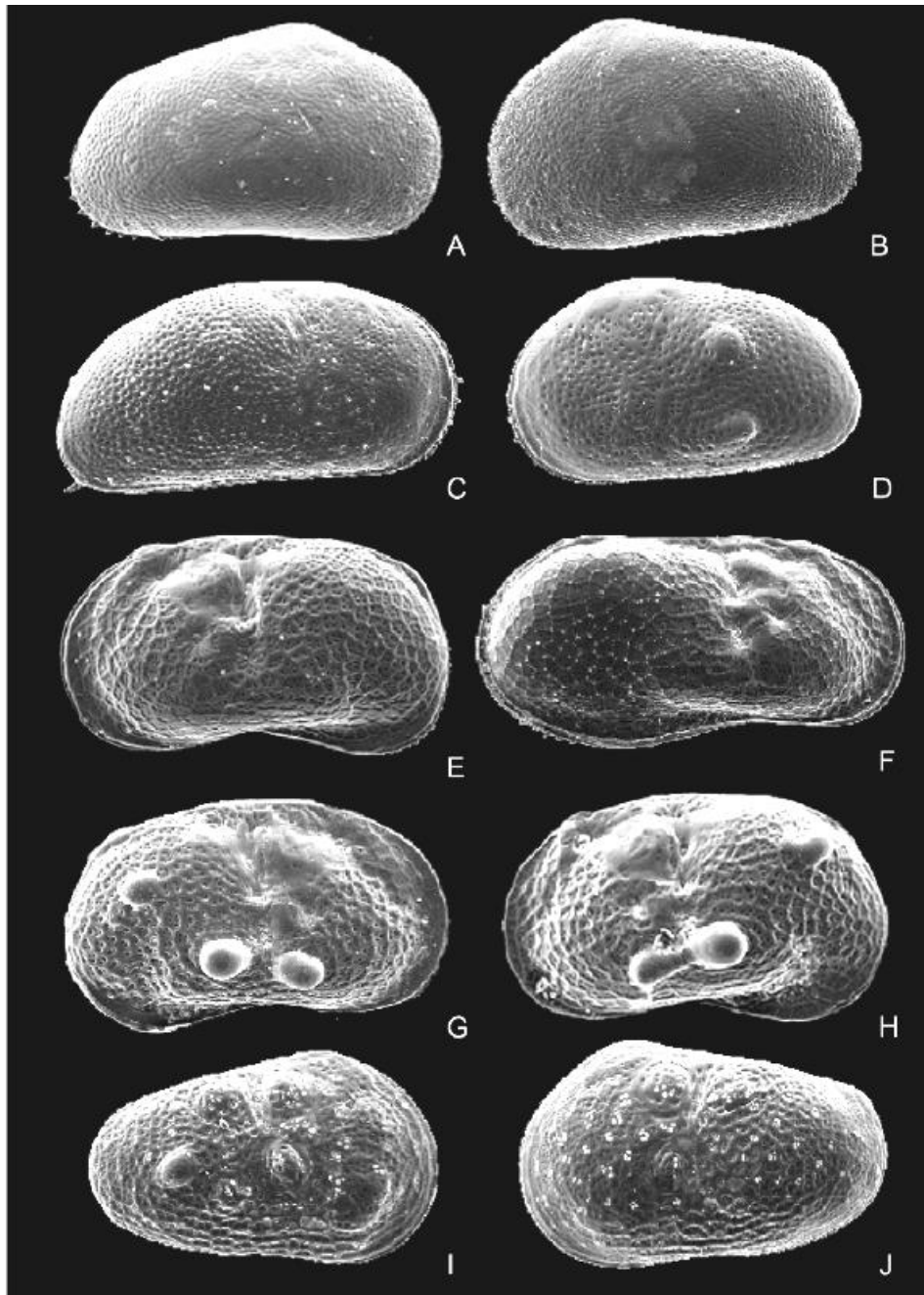


Fig. 8