

THECAMOEBIANS AS A TOOL FOR RECONSTRUCTION OF PALEOENVIRONMENTS IN SOME ITALIAN LAKES IN THE FOOTHILLS OF THE SOUTHERN ALPS (ORTA, VARESE AND CANDIA)

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ABSTRACT

A study of thecamoebians was carried out on three sediment cores collected in three Northern Italian lakes (Orta, Varese, Candia). The recognition of distinct morphotypical populations ("morphs") within three species of thecamoebians in varying paleolimnological settings resulted in a refined understanding of the environmental parameters controlling their distribution. For example, *D. proteiformis* morph "proteiformis" is well adapted to environments rich in organic matter and sulphides whereas *D. proteiformis* morph "rapa" tolerates polluted and acidified waters (presence of copper sulfates, ammonium sulfates, high content of ammonium and nitrite nitrogen, and water with pH values between 3.9 and 4.5).

Although most questions about the ecology of thecamoebians are still unresolved, this study strongly suggests that with further research these protozoans can be a valuable tool for paleoenvironmental reconstructions and detection of environmental deterioration.

INTRODUCTION

Studies on thecamoebians, from the last century to the present day, have usually concentrated on the taxonomic and biologic aspects of these organisms. The few earlier paleoecological studies that have appeared are referenced and reviewed in Medioli and others (1990). However, there has been a renewed interest in the paleoecologic aspects of this group, albeit largely limited to Canada. In these studies it has been recognized that thecamoebians are sensitive to environmental fluctuations, and consequently they have been used as bio-environmental indicators in late Quaternary paleoenvironmental reconstructions (Medioli and Scott, 1983, 1988; Scott and Medioli, 1983; Medioli and others, 1985, 1987, 1990; Patterson and others, 1985; Honig and Scott, 1987; Collins and others, 1990; McCarthy and others, 1995). Most recently, Patterson and others (1996) demonstrated a link between thecamoebian distribution and mercury and arsenic contamination in several small lakes polluted by mine tailings in northeastern Ontario.

A few lakes in the foothills of the southern Alps were also the subject of some extremely general studies on thecamoebian distribution performed at the turn of the century. Recent paleoenvironmental works in that area, however, are limited to Medioli and others (1985), Asioli and Medioli (1992), and Asioli (1993) on some short cores collected at the bottom of Lake Garda (Italy), Parenti (1992) on surface

samples from Lake Mantua (Italy), and Bénier (1993) on surface samples from Lake Geneva (Switzerland).

Here we present results from the study of three cores (Orta 1, Varese 1 and Candia 1) collected in the Orta, Varese and Candia lakes located in the foothills of the southern Alps (Northern Italy). This is the first study of thecamoebians from these lakes, but we have avoided limiting our results to the traditional descriptive listing of the species, instead focusing in detail on the high variability of the morphotypes. We believe that the various morphotypes of the same species, when abundant or dominant, represent the response of the species to the current environmental conditions. We selected populations of specific morphotypes ("morphs") to verify whether or not each one of them was related to specific detectable environmental characteristics.

NOMENCLATURE

In order to understand the paleoecological significance of the material under investigation, it is essential to keep the various morphotypical populations clearly separated from each other but within the appropriate species. The criteria used for this separation can vary and must be adapted to the realities of the observed populations. Such criteria are strictly opportunistic, thus differences in size, shape, presence/absence of spines, presence/absence and shape of the collar etc., when they reoccur consistently, are all legitimate features on which to base such separation.

The choice of the appropriate comprehensive terminology to indicate morphotypical populations is complex and requires some attention in order to avoid nomenclatural confusion.

The terms "*phenotype (phenom)*" and "*ecophenotype (ecophenom)*" indicate the product of influence of the environment on the genotype. This, in our opinion, implies the clear knowledge of the environmental factor(s) controlling the appearance of morphotypical populations, which can only be decided "*a posteriori*." Thus both terms appear inappropriate, at least at this early stage of the research.

The term "*forma*," according to the I.C.Z.N. [Art. 45g, ii], indicates infrasubspecific level, if published after 1960. Consequently, its use would be perfectly proper and legal. Art. 45g, ii, however, specifies that if "*forma*" was published prior to 1960 it can have subspecific value. This term could, conceivably, be misinterpreted by some as equivalent to a "*subspecies*."

As it is not our intention to create subspecies, deliberately or accidentally, we have adopted an informal trinomial nomenclature to keep the infrasubspecific morphotypical populations separated. For this purpose, we identify them as "*morphotypes (morphs)*" by means of a non-italicized descriptive Latin name in quotation marks. This nomenclature is non-committal and has no legal value under the International Code of Zoological Nomenclature.

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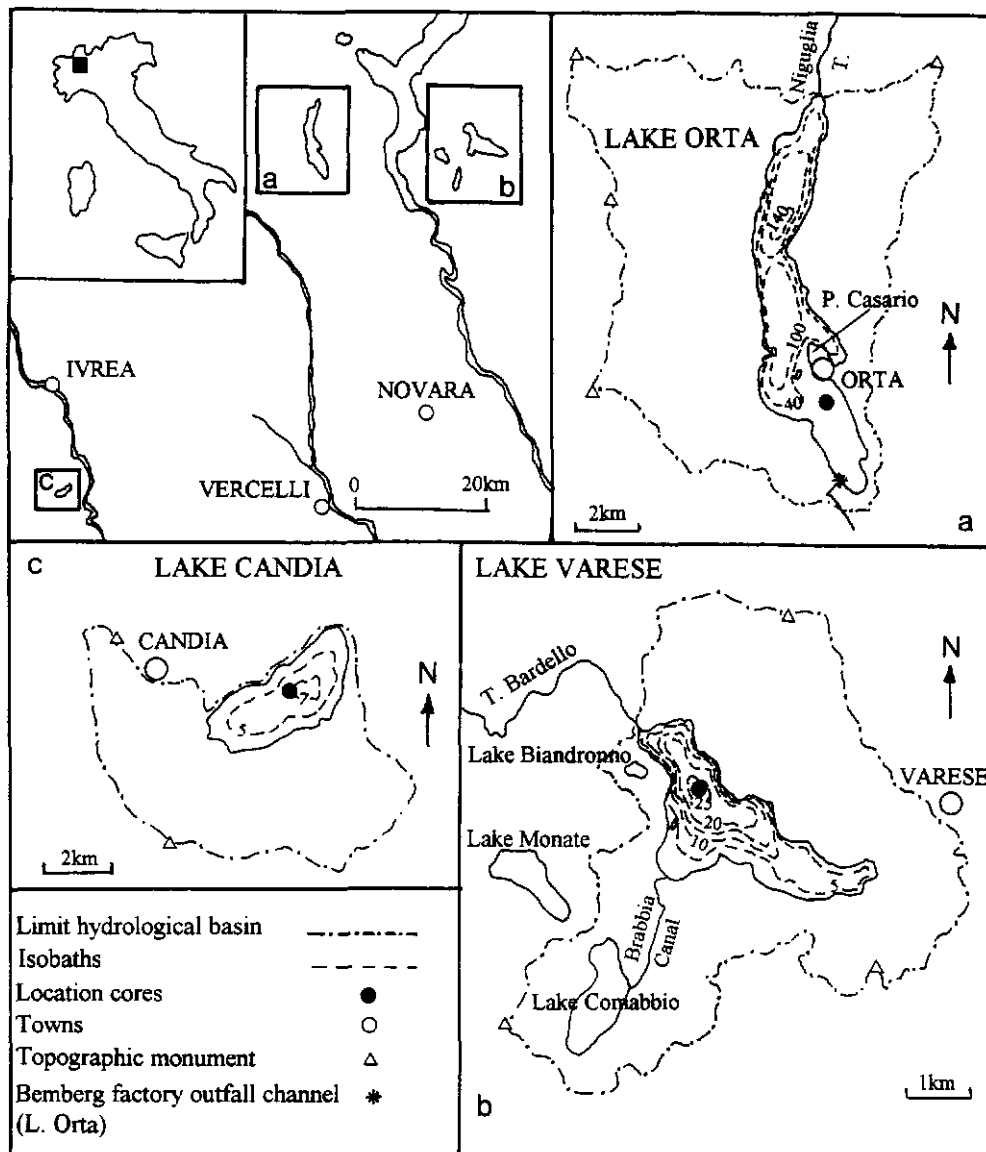


FIGURE 1. Index map of lakes Orta, Varese and Candia, with isobaths and location of the sites where the cores Orta 1, Varese 1 and Candia 1 were collected.

PURPOSE

The purposes of this paper are to: 1) utilize knowledge from other sources to establish some thecamoebian morphological responses to environmental variables; 2) determine basic information on the relationships between morphs and environmental variables in hopes that this will lead, in due course, to the firm definitions of some ecophenotypes; and 3) reconstruct paleoenvironmental successions in the three lakes based on the distribution of different morphs.

STUDY AREA

LAKE ORTA

Lake Orta (Fig. 1a) is included in the hydrographic basin of Lake Maggiore; it is elongated in a roughly N-S direction and is located at an elevation of 290 m above mean sea level (a.m.s.l.). To the south, the lake is blocked by a moraine so that its outlet, the Niguglia torrent, is at the northern

end. The lake is composed of three basins: 1) the southern, slightly over 30 m deep, roughly delimited to the north by the line connecting the Orta peninsula with Punta Casario; 2) the central, delimited to the north by a sill slightly over 100 m deep; and 3) the northern, where the maximum depth of 143 m is reached.

Industrial pollution of Lake Orta started around 1927 when copper sulfates and ammonium sulfates were dumped into the Lake by the Bemberg Co. (Monti, 1930). Recently, the problem has been re-studied and documented in detail by Calderoni and Mosello (1990). The dumping of copper was substantially reduced in 1958, but effluent from several electrogalvanic factories that were subsequently built around the Lake resulted in further deterioration of water quality due to nitrification (strong increase in average content of ammonium nitrogen and nitrite nitrogen, and persistent acidification of the water with pH values declining to between 3.9 and 4.5).

The Lake Orta zooplankton, which before 1926 were typical of an oligotrophic lake, disappeared completely when industrial pollution began. During subsequent years, small and unbalanced zooplankton communities occasionally reappeared, a situation that, although the quality of the water has substantially improved, still persists (Bonacina, 1990). In contrast to prepollution conditions in Lake Orta, the recorded values of primary production between 1958 and 1986 were more typical of a mesotrophic lake.

LAKE VARESE

Also included in the hydrographic basin of Lake Maggiore is Lake Varese (Fig. 1b). Its outlet, the Bardello torrent, drains into Lake Maggiore. Lake Varese, which reaches a maximum depth of 26 m, is in communication with Lake Comabbio through the artificial Brabbia Canal. The waters of Lake Varese are usually stratified from May to November; during this period the hypolimnion becomes strongly de-oxygenated. In the 1950's, the hydrographic basin of Lake Varese was the site of a dramatic demographic and industrial expansion. The consequent continuous dumping of untreated industrial and domestic sewage directly into the Lake increased the phosphorous and nitrogen salt content, which produced an abnormally large development of algae. Zooplanktic and zoobenthic populations were drastically affected and all but disappeared. Zoobenthic species became restricted to shallow waters as deoxygenation of the hypolimnion made conditions there lethal. The Lake, already eutrophic before the beginning of the pollution process, had become ipertrophic (Ruggiu and others, 1981).

LAKE CANDIA

This lake, located at an altitude of 226 m a.m.s.l., is included in the hydrographic basin of the Dora Baltea River and has a maximum depth of about 7 m (Fig. 1c). Lake Candia is a small eutrophic lake, rich in littoral vegetation and densely populated by phyto- and zoo-planktic organisms (Guilizzoni and others, 1989; Giussani and Galanti, 1992). It is frozen in January and February and has a very low concentration of oxygen in the hypolimnion (0.5–3.0 µg/L).

MATERIALS AND METHODS

The cores were collected in July 1990 with a Mackereth corer. They were subsequently frozen at –23°C to allow proper slicing and the observation of the sedimentary structures. In Orta 1 and Candia 1 sub-samples 1.5 cm thick were collected where the sediment appeared homogeneous. In Varese 1 sub-samples were collected where laminations could be observed and, in some cases, the size of the sample had to be adapted to the thickness of the laminae. The sediment of the sub-samples was temporarily stored in ethylic alcohol (95%) and subsequently was wet-sieved through a 45-µm mesh (instead of the standard 63 µm) in order to retrieve most of the small specimens. As some thecamoebians are smaller than foraminifera, the use of a 63-µm mesh could have caused the loss of significant information (Medioli and others 1994, p. 334). The residues were examined in stereoscopy and at least 300 individuals were counted in each.

The tests appeared mostly clean and well preserved. Those filled with clay were presumed to be reworked and consequently ignored.

Forty-four of the 53 samples examined contained thecamoebians. Of these, 40 thecamoebian-bearing samples contained populations large enough for statistical analysis (Patterson and Fishbein, 1989; Appendix I). Twenty-seven species and morphotypes of thecamoebians were identified. The percent error associated with each species tally was calculated using the standard error equation (S_{x_i}):

$$S_{x_i} = 1.96 \sqrt{\frac{X_i[1 - X_i]}{N}}$$

where N is the total number of counts, and X is the fractional abundance of a species (Patterson and Fishbein, 1989). The percents error calculated for all twenty-seven species and morphotypes are included in Appendix I.

Q-mode cluster analysis was carried out on the data using a technique that has been demonstrated to closely emulate the results of a statistically significant "error-weighted maximum likelihood" clustering method (Fishbein and Patterson, 1993). Q-mode cluster analysis determines similarity between samples. This method requires that only species present in statistically significant populations be analyzed. Eight species and morphs were not present in statistically significant numbers in any sample and were thus excluded from subsequent cluster analysis. These included *Arcella* spp., *Diffugia* cf. *D. oblonga*, *Diffugia proteiformis* morph "curvicaulis," *Diffugia* sp., *Diffugia urceolata*, *Diffugia urceolata* morph "elongata," *Lagenodiffugia vas*, and *Nebela militaris*. Q-mode cluster analyses were carried out on the 16 statistically significant species using SYSTAT (v. 5.2; Wilkinson, 1989). Euclidean distance correlation coefficients were used to measure similarity between pairs of species, and the Ward's linkage method was utilized to arrange sample pairs and sample groups into a hierarchic dendrogram (Fig. 2).

RESULTS

Before discussing our results in detail, we will clarify our concept of the infrasubspecific morphs utilized in this study. In *Diffugia oblonga*, two clearly distinct size-classes have prompted the recognition of two morphs: *D. oblonga* morph "magna" and *D. oblonga* morph "parva" (see Pl. 1). The same procedure was applied to *Cucurbitella tricuspis*, also subdivided into *C. tricuspis* morph "magna" and *C. tricuspis* morph "parva." *Diffugia proteiformis* proved to be morphologically extremely variable. Consequently, the following subdivision was necessary: *D. proteiformis* morph "proteiformis" (with cylindrical test, narrow and elongated), *D. proteiformis* morph "crassa" (test shorter and somewhat globose), *D. proteiformis* morph "rapa" (test very small and globose; see Pl. 2), and *D. proteiformis* morph "bicornis" (similar to morph "rapa" but with two spines at the fundus).

Cluster analysis, performed throughout the three cores, strongly suggests the existence of six clusters (= assemblages; Fig. 2). We name each assemblage after the most characteristic species or morph.

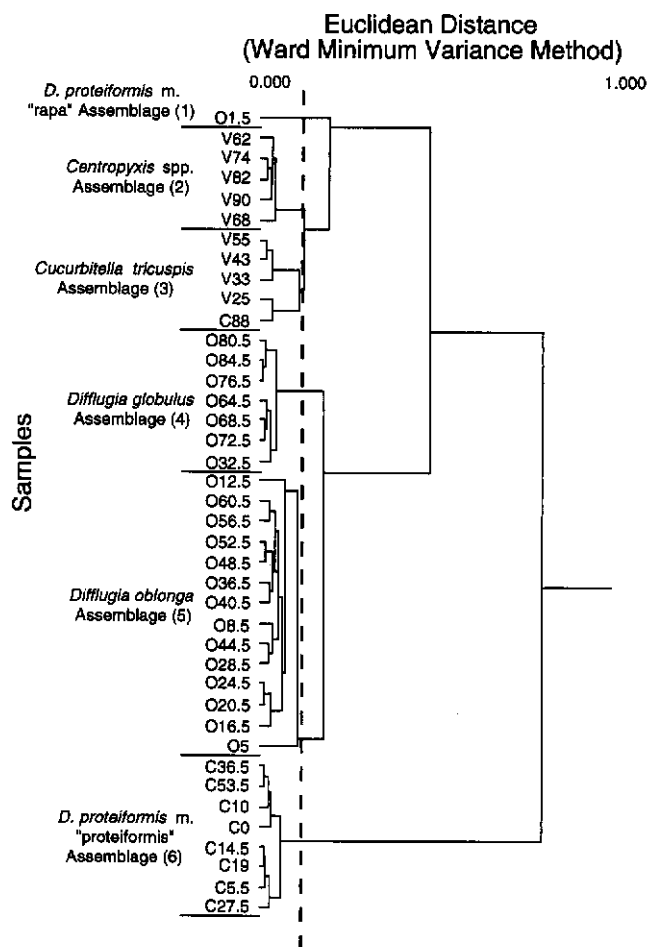


FIGURE 2. Q-mode cluster analysis dendrogram showing the 40 most populous samples (listed vertically by sample number) from Lake Orta (O-prefix), Varese (V-prefix) and Candia (C-prefix), divided into distinct assemblages. Distinct clusters of samples with correlation coefficients greater than a selected level (dashed line) were considered assemblages.

LAKE ORTA

The cores contain two lithologies (Fig. 3): 1) a lower (89–11 cm) light brown silty clay, changing sharply into 2) an upper (11–0 cm) black silty clay. The graphs of Fig. 2 show the variation of the thecamoebian populations as a function of time. Three assemblages present in core Orta 1 are described below.

Diffugia globulus-Assemblage (84.5–64.5 cm)

The most abundant species are *Diffugia globulus*, *D. oblonga* (the *D. oblonga* morph "magna" is relatively more abundant), and *Pontigulasia compressa* (Figs. 2, 3; Appendix 1). *Cucurbitella tricuspid* and *D. proteiformis* are less abundant (the former is dominated by the morph "magna," while the latter comprises only the morph "crassa"). *Lesquereusia spiralis* has abundances similar to those of *C. tricuspid*, whereas the occurrence of *Nebela militaris*, *D. viscidula* and genus *Centropyxis* is sporadic (see also Appendix 1). Cluster analysis indicates that the sample at 32.5 cm also belongs in this assemblage.

Diffugia oblonga-Assemblage (62.5–5 cm)

In this zone, the relative abundance of *D. oblonga* morph "parva," *D. proteiformis* morph "crassa," and *D. viscidula* increases (Figs. 2 and 3; Appendix 1), the abundance of *D. globulus* drops dramatically, and *L. spiralis* shows extremely low abundances. *D. oblonga* morph "magna" decreases in the lower part but increases again between 20.5 cm and 32.5 cm, along with a very small increase of *D. globulus*. *Pontigulasia compressa* abundance shows no significant variation through this interval, but *D. proteiformis* (morph "proteiformis") abundance increases suddenly at 12.5 cm. Planktic, and extremely rare benthic foraminifera, have been found at 12.5 cm and 16.5 cm.

The boundary between the *D. oblonga*-Assemblage and the overlying *D. proteiformis* morph "rapa"-Assemblage is not sharp. In fact, by 5 cm there has already been a progressive and drastic reduction in the number of species (Fig. 2, Appendix 1). At 8.5 cm, 70% of the assemblage consists of *D. oblonga* morph "parva." *Diffugia proteiformis* morph "crassa" and *D. viscidula* are also important, as well as lower percentages of *D. oblonga* morph "capreolata," *D. globulus* and *P. compressa*. At 5 cm, 90% of the assemblage is composed of *D. proteiformis* morph "crassa" and *D. viscidula*.

Diffugia proteiformis morph "rapa"-Assemblage (1.5 cm)

This assemblage is present only in the sample at 1.5 cm. It contains only *D. proteiformis*-morph "rapa" (80%) and *D. viscidula* (20%; Figures 2, 3; Appendix 1).

LAKE VARESE

This core (Fig. 4) can be subdivided visually into three lithologies: a lower (97–33 cm) brown silty clay, a middle black silty clay (33–23 cm), and an upper (23–0 cm) unit characterized by alternating laminae of black silty clay and lighter colored calcite. The lower part of the core shows some chromatic variations. For example, three light brown silty clay zones (97–84 cm, 78–60 cm and 44–33 cm) grade into dark brown silty clay (84–78 cm, 60–44 cm and 33–23 cm). The transitions between the chromatic units are gradual. Two assemblages are present (Figs. 2, 4; Appendix 1):

Centropyxis spp.-Assemblage (96–62 cm)

This assemblage is dominated by a combination of the genera *Centropyxis* and *Cyclopyxis* (about 50% of the entire association), *C. tricuspid*, and *D. proteiformis* followed by *D. oblonga*. The combination of *Centropyxis* and *Cyclopyxis* was necessary because we have reservations about the validity of the genus *Cyclopyxis* (for detail see Medioli and Scott, 1983). Within the genus *Centropyxis*, the species (see also Appendix 1) *C. aculeata*, *C. eornis* (see Pl. 3 and *C. constricta* are present, in decreasing order of frequency. Although Medioli and Scott (1983) put *C. eornis* in synonymy with *C. aculeata* (Ehrenberg), we considered it useful to distinguish them in view of the special purpose of this paper. *Cucurbitella tricuspid* is represented almost exclusively by the morph "parva," while *D. oblonga* is represented mainly by the morph "magna." *Diffugia proteiformis*

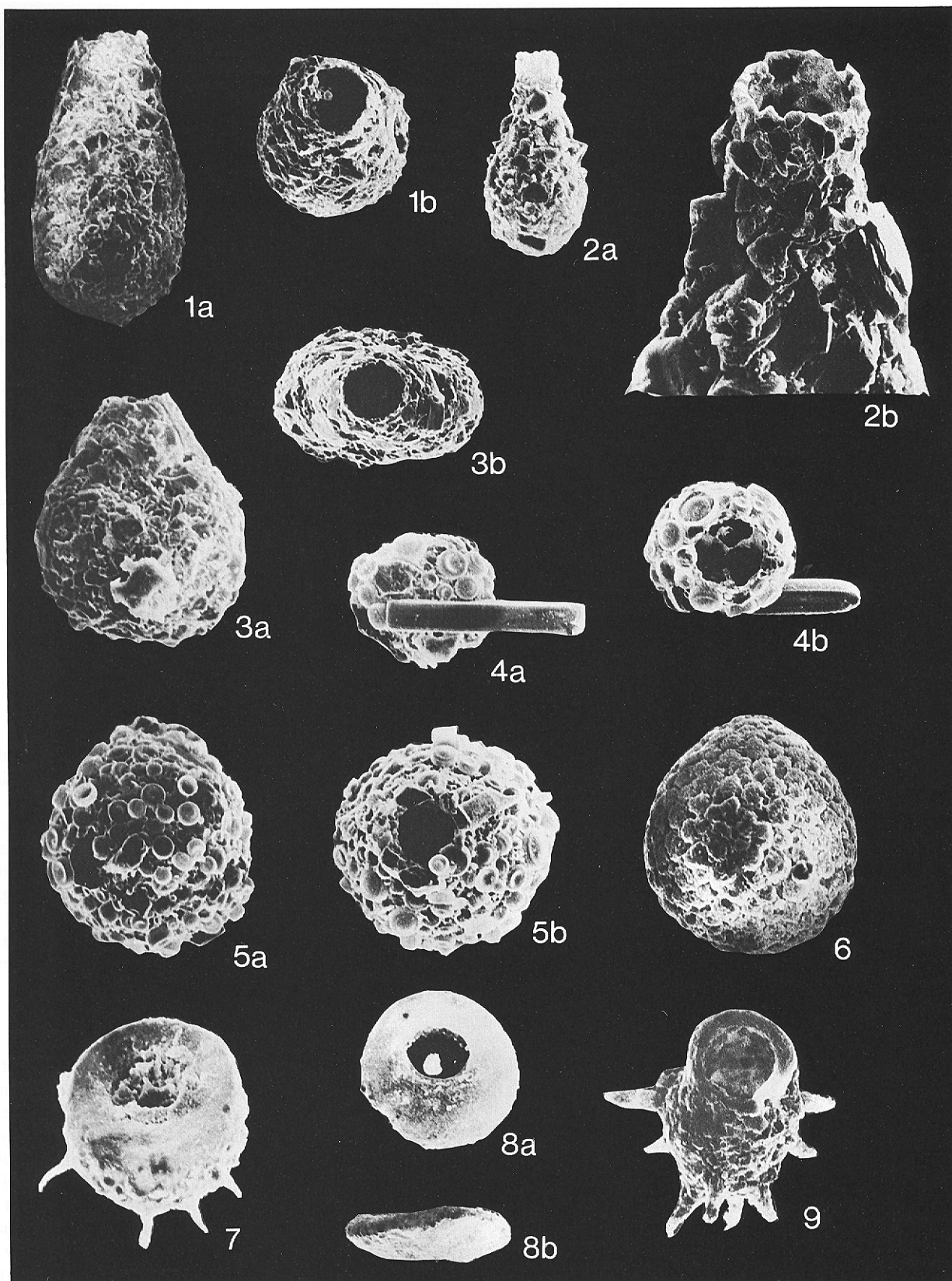


PLATE 1

1 *Diffflugia oblonga* (Ehrenberg) morph "magna". a lateral view. b apertural view, $\times 200$ (core Orta 1, cm 84.5–86.5). 2 *Diffflugia oblonga* (Ehrenberg) morph "parva". a lateral view, $\times 300$. b apertural view, $\times 1000$ (core Orta 1, cm 84.5–86.5). 3 *Pontigulasia compressa* (Carter). a lateral view. b apertural view, $\times 200$ (core Orta 1, cm 84.5–86.5). 4 *Diffflugia globulus* (Ehrenberg). a "fundus". b apertural view, $\times 200$ (core Orta 1, cm 84.5–86.5). 5 *Cucurbitella tricuspis* Carter morph "magna" with xenogenous test. a lateral view. b apertural view, $\times 200$ (core Orta 1, cm 84.5–86.5). 6, 7, 8, 9: other specimens as indicated in the figure labels.

mis is split between the morph "proteiformis" and the morph "rapa."

Cucurbitella tricuspis-Assemblage (55–25 cm)

This interval is characterized by a relative increase in abundance of the *C. tricuspis* morph "parva," the disappearance of *C. ecornis*, and a slight increase in the proportion of *C. aculeata*. The abundances of the other species present do not seem to change significantly through the interval of the core. The sample located at 25 cm is characterized by a strong increase of *D. proteiformis* morph "proteiformis," the disappearance of *C. constricta* and *Cyclopyxis* spp, and a decrease of *D. oblonga* morph "magna." Virtually 90% of the population is represented by three species: *D. proteiformis*, *C. aculeata*, and *C. tricuspis*. Thecamoebians are absent from the 22-cm level up to the top of the core.

LAKE CANDIA

This core (Fig. 5) is made up of dark brown silty clay (100–65 cm, 44–30 cm), light brown silty clay (65–44 cm), and black silty clay (30–0 cm). As in Lake Varese, the transitions between the chromatic variations are gradual.

Thecamoebians are extremely scarce in this core (the number of individuals/sample varies from 15 to 115; see Appendix I). Thecamoebian distribution is quite homogeneous, the assemblage being dominated by *D. proteiformis* morph "proteiformis," characterized by extreme fragility of the test. The *D. proteiformis* morph "proteiformis"-Assemblage occupies almost the entire core except for the lower sample (88–90 cm), which clustered with the *C. tricuspis*-Assemblage. This result suggests a possible link between the lower part of the Candia 1 core and the 25-cm interval of the Varese 1 core, although we have been unable to explain convincingly the reasons for such a link.

Worth noticing is the presence, albeit very rare, of *Cucurbitella corona* (see Pl. 3, which was absent in Lakes Varese and Orta. Other species (*D. oblonga*, *C. tricuspis*, *P. compressa*, and the genus *Centropyxis*) are also present at very low frequencies.

DISCUSSION

LAKE ORTA

Presumably, the three distinct assemblages of core Orta 1 correspond to distinct chronological events. As we have no ecological information on the thecamoebians of these lakes, our own paleoecological interpretation had to be based on the most common forms and on those for which we have some ecological information derived from the study of North American lakes.

Collins and others (1990) suggested that *D. globulus* is probably a species indicative of cold climate. Due to the scarcity of ecological information, the trends shown by *D.*

oblonga morph "parva" and *D. oblonga* morph "magna" are difficult to interpret. The only data supported by field observation come from a paper by Collins and others (1990) in which study of a transect from Baffin Island to Florida suggests that for some species there is a close correspondence between size and latitude. These authors suggest that under conditions of high latitude and relatively short summers, reproduction would slow down and result in the formation of individuals of large dimensions (for detail see Collins and others, 1990). However, the latitude/size relationship is not simple and direct. Numerous other factors, such as insulation and consequent relative abundance or shortage of food, may influence the size of the individuals. A vaguely similar phenomenon, although through a somewhat different mechanism, has been suggested repeatedly for benthic foraminifera (e.g. Bradshaw, 1961; DeLaca and others, 1980; Brasier, 1984; Hallock and others, 1991). As a working hypothesis, we have extended the interpretation of Collins and others (1990) to other thecamoebians. Thus, we interpret the decrease in size of *D. oblonga* and the lower abundances of *D. globulus* above the boundary between the *D. globulus*-Assemblage and the *D. oblonga*-Assemblage (Fig. 3) as the consequence of a relative improvement in climatic conditions.

²¹⁰Pb dates (Alvisi and others, in press) indicate that the top 13 cm of the core cover about the last 70 years and, based on the ²⁴¹Am peak, that sediment deposited during 1963 is located 5 cm below the core surface. Sediment deposited during 1926 is located at approximately 13 cm below the core surface and is marked by the disappearance of phytoplankton and benthos, and the accumulation of organic matter at the bottom (Guilizzoni and Lami, 1988). A change in the color of sediment from brown to black at this horizon also confirms the change in conditions. The sudden increase of *D. proteiformis* morph "proteiformis" suggests that this morph is particularly well suited for environments accumulating high levels of organic matter.

The top 5 cm of the core, corresponding to the period from 1963 to today, is characterized by high numbers of *D. proteiformis* morph "rapa" and *D. viscidula* (Figs. 2 and 3). We know that at the beginning of the 1960's the Lake experienced a substantial increase in ammonia and nitric nitrogen, a lowering of pH, oxygen depletion, and increased concentrations of copper at the bottom (Calderoni and Mossello, 1990). Hence, it appears reasonable to hypothesize that *D. proteiformis* morph "rapa" and *D. viscidula* are particularly resistant to a level of pollution (at least of the type that took place in Lake Orta) that was fatal to all other morphs of *D. proteiformis*, as well as all other thecamoebians.

Scott and Medioli (1983), Medioli and others (1987), and Collins and others (1990) considered high percentages of *Cucurbitella tricuspis* to be good indicators of eutrophic conditions. In this core, *C. tricuspis* is never particularly

84.5–86.5). 6 *Cucurbitella tricuspis* Carter morph "parva" with autogenous test, lateral view, ×300 (core Orta 1, cm 84.5–86.5). 7 *Centropyxis aculeata* (Ehrenberg) with spines, ventral view, ×300 (core Orta 1, cm 44.5–46.5). 8 *Centropyxis aculeata* (Ehrenberg). a lateral view. b side view, ×200 (core Orta 1, cm 60.5–62.5). 9 *Centropyxis constricta* (Ehrenberg) with spines, apertural view, ×300 (core Orta 1, cm 56.5–58.5).

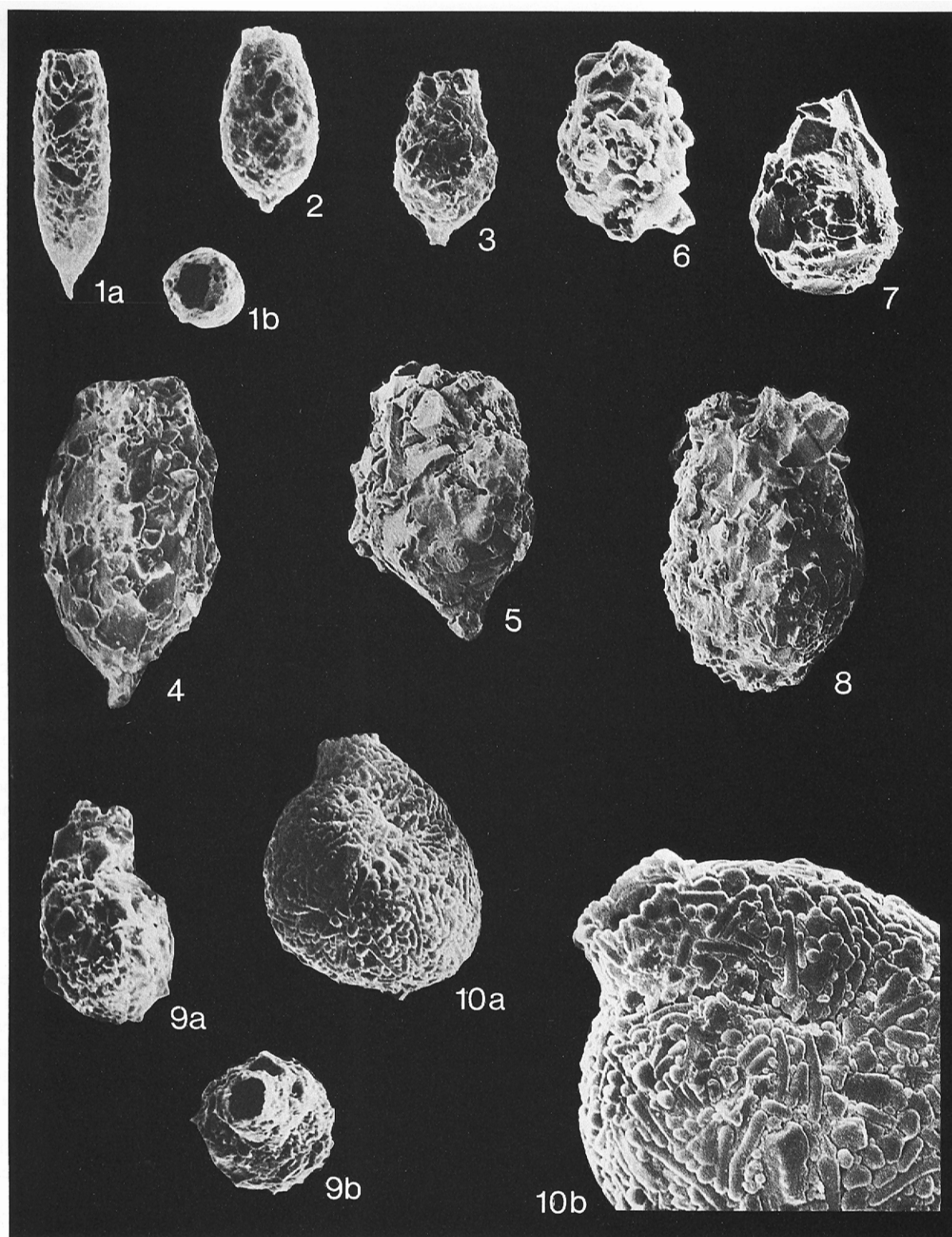


PLATE 2

1 *Diffugia proteiformis* Lamarck morph "proteiformis". a lateral view. b side view, $\times 200$ (core Orta 1, cm 12.5–14.5). 2 *Diffugia proteiformis* Lamarck morph "crassa", lateral view, $\times 300$ (core Orta 1, cm 20.5–22.5). 3 *Diffugia proteiformis* Lamarck morph "rapa", lateral view, $\times 300$ (core Orta 1, cm 1.5–3.5). 4 *Diffugia proteiformis* Lamarck morph "rapa", lateral view, $\times 750$ (core Orta 1, cm 1.5–3.5). 5 *Diffugia proteiformis* Lamarck morph "rapa", lateral view, $\times 750$ (core Orta 1, cm 1.5–3.5). 6 *Diffugia viscidula* Penard, lateral view, $\times 750$ (core Orta 1, cm 80.5–82.5). 7 *Diffugia viscidula* Penard, lateral view, $\times 750$ (core Orta 1, cm 1.5–3.5). 8 *Diffugia viscidula* Penard, lateral view, $\times 750$ (core Orta 1, cm 1.5–3.5). 9 *Lagenodiffugia vas* (Leidy). a lateral view. b apertural view, $\times 300$ (core Orta 1, cm 72.5–74.5). 10 *Lesquereusia spiralis* (Schlumberger). a lateral view, $\times 300$. b particular of the autogenous test with siliceous rods, $\times 600$ (core Orta 1, cm 84.5–86.5).

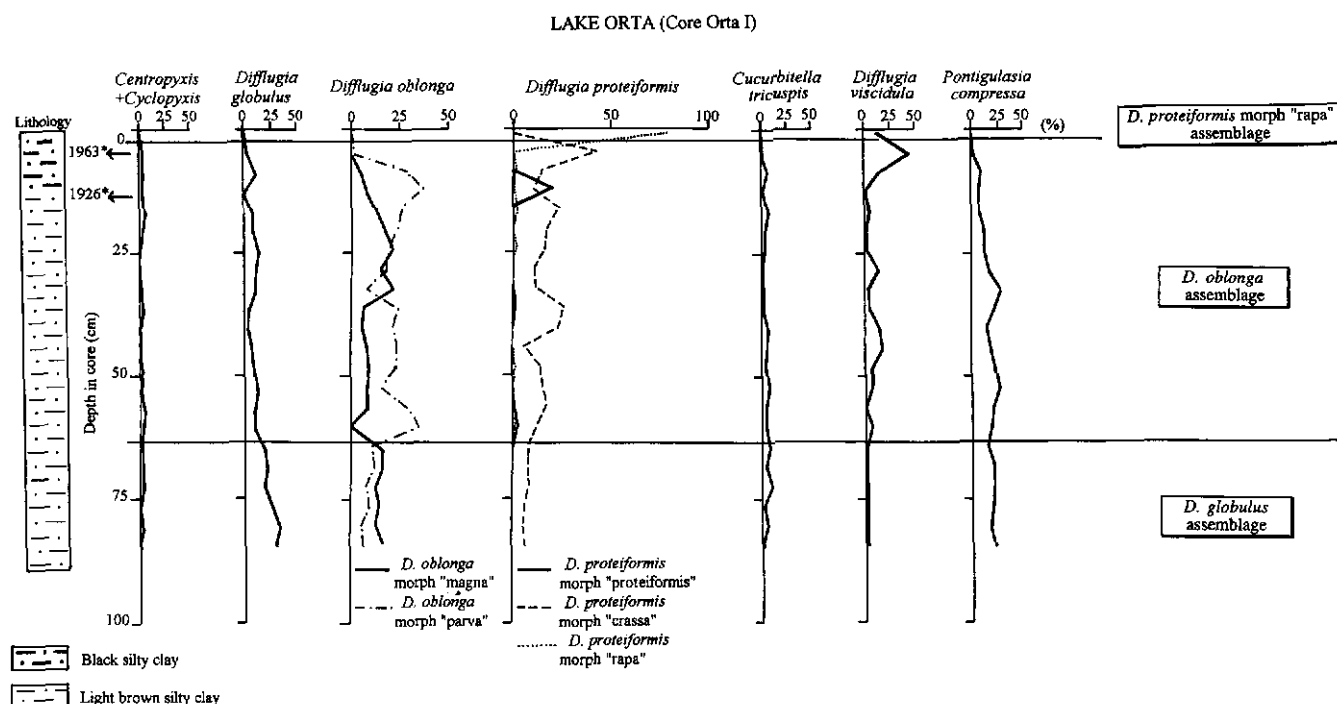


FIGURE 3. Lithologic column, thecamoebian assemblage distribution, and distribution curves of the main species and morphs in core Orta 1. ^{210}Pb date from Alvisi and others, in press.

abundant, probably due to the oligotrophic nature of Lake Orta before becoming polluted.

The presence of planktic foraminifera in the interval 20.5–12.5 cm coincides with an increase in the rate of sedimentation from 0.4 to 0.8 gr/cm²/year (Alvisi and others, in press). This horizon was deposited just prior to 1926 (the date that construction of the Bemberg plant began). We conclude that both the increased sedimentation rate and the presence of planktic foraminifera are the result of construction site activity (possibly the dumping of marine sand).

The result of palynological studies (Alvisi, 1993) on the lake indicate that the sediments between 77 and 43 cm are characterized by an increase in taxa suggestive of increased anthropogenic activity in the area. More specifically, these results indicate increased agricultural output, primarily of cereal grains, that peaked at about the 50 cm level. This period was immediately preceded by increased detrital input to the lake (mainly quartz) which has been interpreted to indicate either deforestation to increase farm land and/or increased precipitation. Analysis of sediments between 43 and 19 cm indicate a moderate expansion of forests (walnut) as a consequence of the decrease in farm land. The interval between 19–0 cm provides evidence of a prolonged anthropogenic disturbance that caused a vegetational diversification in the area. Deforestation and/or increased precipitation must have favored erosion of the surrounding areas with consequent increased input of nutrients in the lake.

From the above information, the assemblages characterizing the core can be interpreted as follows. 1) The early *D. globulus*-Assemblage may indicate relatively colder water conditions during deposition of the basal core unit (as suggested by the abundance of *D. globulus* and the scarcity of *D. oblonga* morph "parva"). 2) The overlying *D. oblonga*-

Assemblage indicates an improvement of climatic conditions, possibly accompanied by greater availability of food. The sample at 32.5 cm, included with the *D. globulus*-Assemblage by cluster analysis, may indicate a temporary return to colder conditions. 3) The makeup of the *D. proteiformis* morph "rapa"-Assemblage is profoundly different from the previous assemblage and is a proxy for drastic limnological change due to severe pollution that affected the lake starting in 1927. The early consequences of this pollution, an increase of *D. proteiformis*-morph "proteiformis," are detectable at the top of the core.

LAKE VARESE

The thecamoebian assemblage found in core Varese 1 is quite different from that of core Orta 1. In Lake Varese, *Cucurbitella tricuspidis* and the genus *Centropyxis* predominate while both taxa, particularly the genus *Centropyxis*, are rather scarce in Lake Orta. However, a very similar assemblage to the one found in Lake Varese has been reported from the eutrophic Lake Superior of Mantua (Parenti, 1992).

The boundary between the *Centropyxis* spp.-Assemblage and *C. tricuspidis*-Assemblage is marked by a transition from light brown silty clay to dark brown silty clay (Fig. 4). This boundary also coincides with the disappearance of *C. ecoris* and a relative increase in the proportion of *C. tricuspidis*. The increased abundance of *C. tricuspidis*, prima facie, provides evidence of a shift of the lacustrine waters towards eutrophic conditions. This eutrophication appears to be confirmed by the overall decrease of thecamoebians by 55 cm (only 126 specimens in the entire sample; see Appendix II). The number of specimens of *C. tricuspidis* morph "parva," however, remains rather constant, thus suggesting that this

LAKE VARESE (Core Varese I)

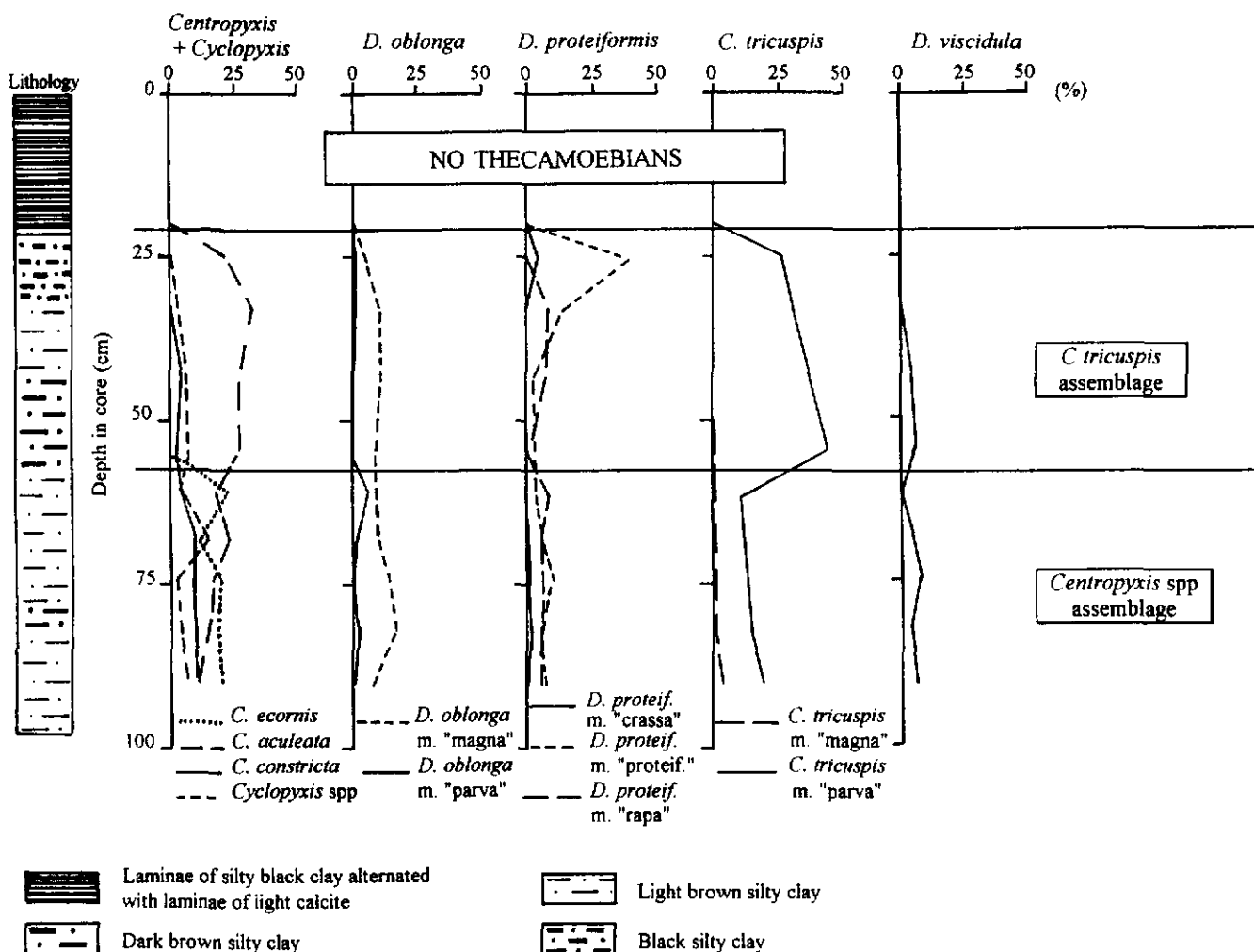


FIGURE 4. Lithologic column, thecamoebian assemblage distribution, and distribution curves of the main species and morphs in core Varese I.

morph is unaffected by the development of eutrophic conditions.

From analysis of an earlier 90-cm core, core FC collected in the deepest part of Lake Varese, Lami (1986) described three lithologic intervals (Fig. 6) that can be correlated well with the stratigraphy found in the Varese 1 core. This comparison is useful as no dates were obtained in the Varese 1 core. The lower 60-cm interval of core FC is composed of gray clay and corresponds to the interval dominated by the *Centropyxis* spp.-Assemblage of core Varese 1. This interval was deposited prior to 1945 when the lake was naturally eutrophic, as indicated by the presence of strictly anaerobic photosynthetic sulfur bacteria (Guilizzoni and others, 1986). The 33 cm-level of core Varese 1 was deposited around 1945, and thus the deeper parts of this core must be attributed to the same period. The thecamoebian fauna of this interval, therefore, is directly comparable with that studied by Parenti (1992) in the Lake Superior of Mantua.

An intermediate interval (20–30 cm) in core FC of non-laminated dark clay rich in organic matter and iron sulfates was deposited during the period 1945–60 when the region became more industrialized. The corresponding interval in

Core Varese 1 is non-laminated black silty clay in the 33–25-cm interval that is dominated by the *C. tricuspis* Assemblage. The relative increase of *D. proteiformis* morph "proteiformis" in core Varese 1 between 33 and 23 cm, compared to the lower interval (Fig. 5), suggests that this morph is particularly well adapted to environments rich in organic matter and/or to reducing conditions.

The uppermost 20 cm of core FC and 22 cm of core Varese 1 are composed of laminated clay corresponding to post-1960 deposition, when benthic organisms completely disappeared from the deepest part of the lake (Bonomi, 1962) in conjunction with the development of meromithic conditions (Bonomi, 1964). The lack of bioturbators is the primary factor that permitted preservation of the laminae. The absence of thecamoebians in the upper laminated clay interval is probably due to the development of adverse hydrochemical conditions in the hypolimnion. However, even by the 25-cm horizon there was a significant decrease in the number of thecamoebians (96 specimens at 33 cm and 116 at 25 cm), suggesting that the hypolimnion was already in critical condition during the deposition of the black non-

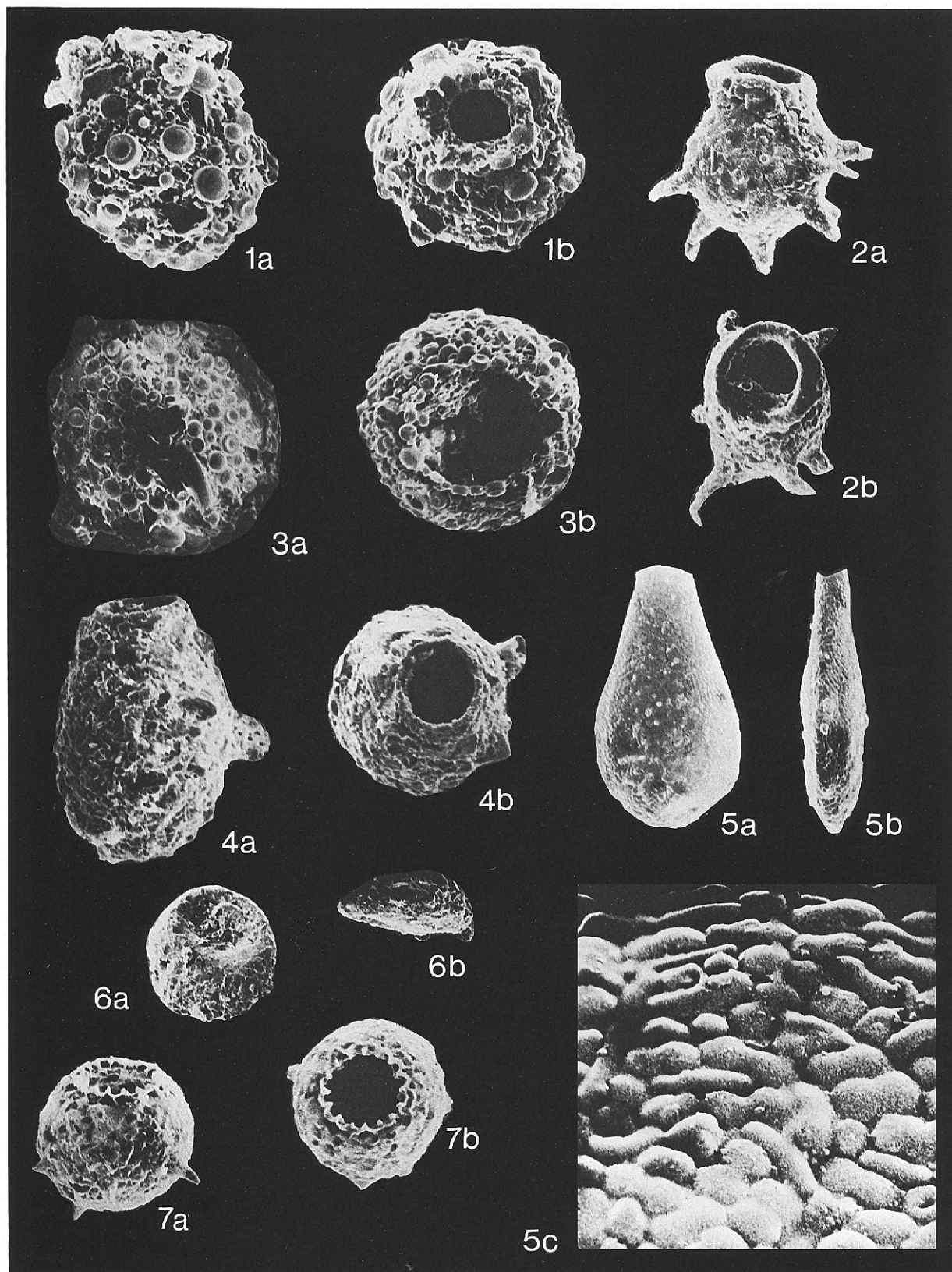


PLATE 3

1 *Diffflugia urceolata* Carter. a lateral view. b apertural view, $\times 200$ (core Orta 1, cm 76.5–74.5). 2 *Diffflugia urceolata* Carter with spines. a lateral view. b apertural view, $\times 300$ (core Orta 1, cm 64.5–66.5). 3 *Diffflugia urceolata* Carter morph "elongata" Patterson and others, 1985. a lateral view. b apertural view, $\times 150$ (core Orta 1, cm 84.5–86.5). 4 *Diffflugia oblonga* (Ehrenberg) morph "capreolata". a lateral view. b apertural view, $\times 200$ (core Orta 1, cm 84.5–86.5). 5 *Nebela militaris* Penard. a lateral view. b apertural view, $\times 300$. c particular of the autogenous test, $\times 3000$ (core Orta 1, cm 76.5–78.5). 6 *Centropyxis ecoronis* (Ehrenberg). a side view. b ventral view, $\times 500$ (core Varese 1, cm 62–64). 7 *Cucurbitella corona* (Wallich). a lateral view. b apertural view, $\times 200$ (core Candia 1, cm 0–3).

LAKE CANDIA (Core Candia I)

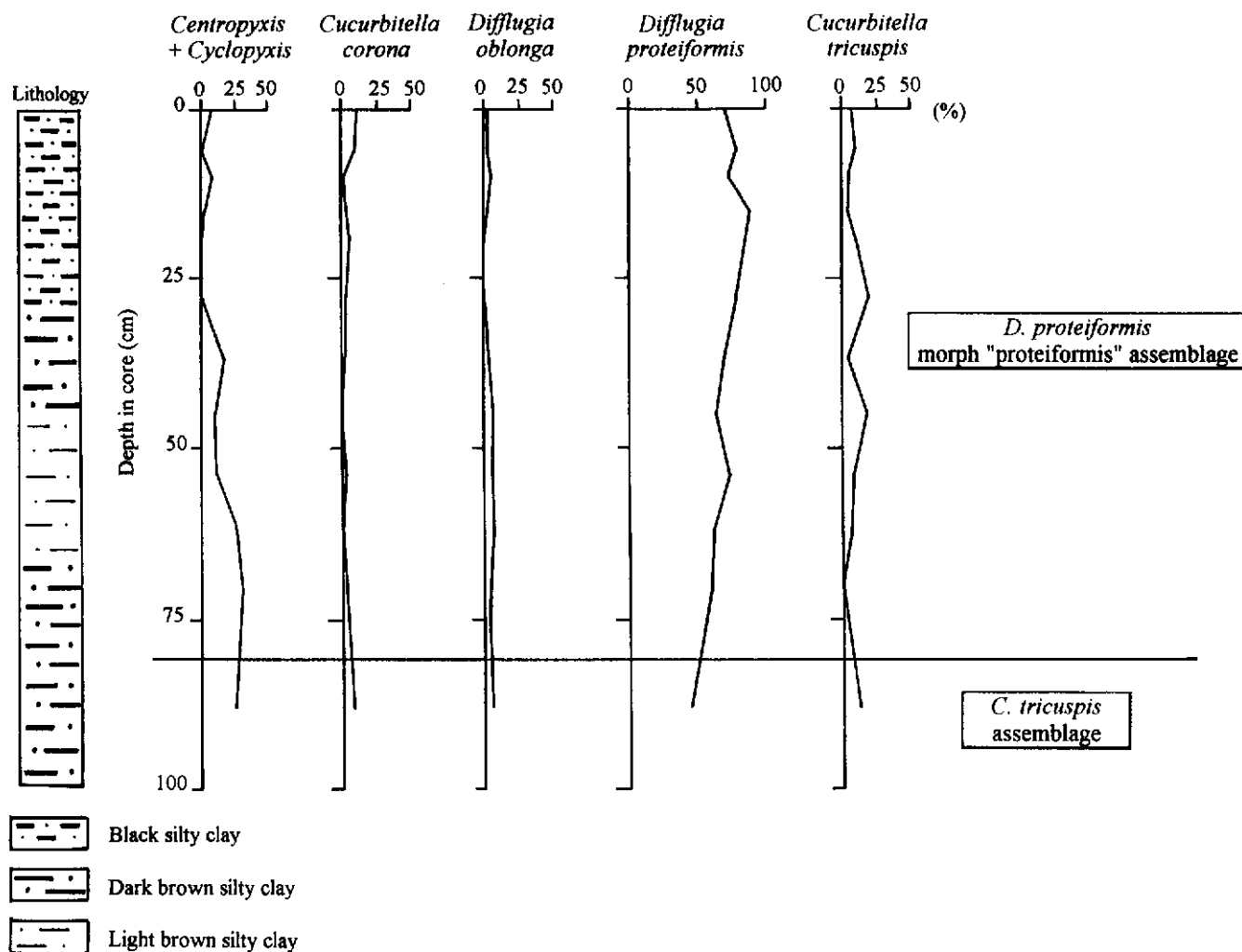


FIGURE 5. Lithologic column, thecamoebian assemblage distribution, and distribution curves of the main species and morphs in core Candia 1.

laminated silty-clay. These conditions were probably marginal although not yet fatal, for the thecamoebians.

Alvisi (1993) carried out a mineralogical analysis of core Varese 1. He interpreted the darker zones to denote periods when climate was relatively colder and more humid, based on the higher organic content, larger detrital content, lower Ca/Mg ratio relative to the lighter zones, and higher quantities of Fe_{tot} and P_{tot} . According to Alvisi, these data indicate enhanced preservation of organic matter due to prolonged periods of water stagnation, a situation likely to occur during winter when the lake freezes over. Thus, such intervals represent periods with colder and longer winters. It is also likely that the humidity was higher, as suggested by a larger detrital component derived from a larger load of tributary rivers during wet periods. This interpretation is partially supported by the patterns of thecamoebian distribution. Although in the 84–78 cm interval no significant variations of the assemblage are recorded, *C. eornis* disappears in the 60–44 cm interval. Simultaneously, *C. tricuspis* morph "parva" increases and by 55 cm the overall number of thecamoebians decreases as well. These faunal changes suggest that significant changes in the lake's phys-

iography must have occurred. Unfortunately, the lack of information on the ecology of most species of thecamoebians makes it impossible to confirm, on the basis of thecamoebians alone, that climatic variations occurred during this interval.

LAKE CANDIA

The thecamoebian assemblages of core Candia 1 are substantially different from those of the other two lakes. In a core collected in the deepest part of the lake and presently under study, Guilizzoni and Lami (personal communication, 1992) found that in the top 30 cm there is an increase in organic matter (about 20% to 40% of the dry weight). Also, there is an increase in the products of degradation of chlorophyll and of $CaCO_3$, both indicating an increase in primary productivity. In addition, Guilizzoni and others (1989) reported the presence, in recent sediments as well as in the lake's water, of okenone, a pigment characteristic of a photosynthetic sulfur bacteria, which indicates the presence of H_2S and anaerobic conditions. These observations suggest that during the last 200 years (Appleby, personal commu-

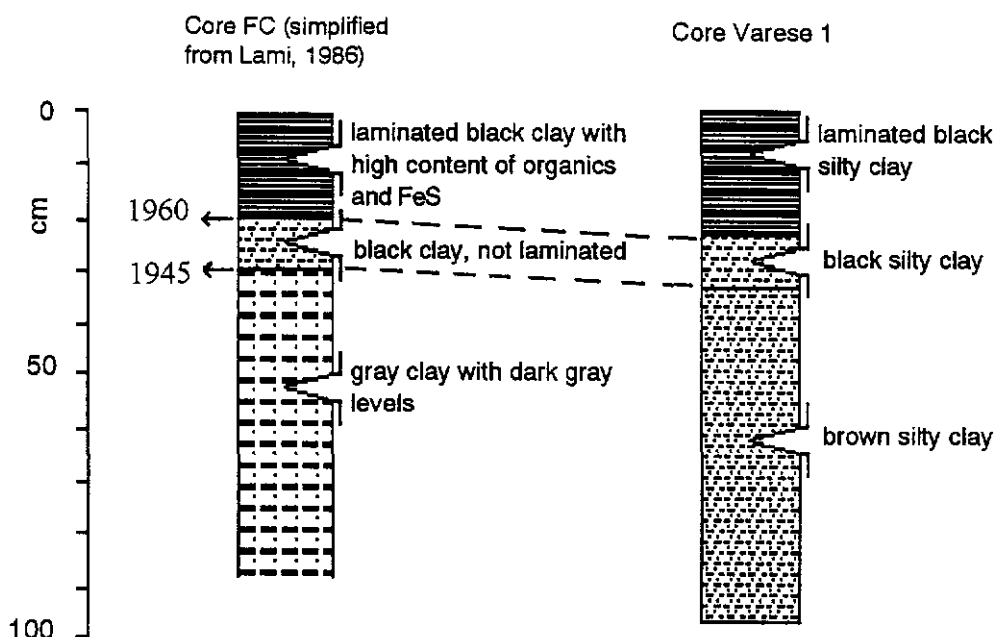


FIGURE 6. Lithologic correlation between cores FC and Varese 1.

nication, 1994), corresponding to the 30–0 cm interval, this eutrophic lake had an autochthonous production ($C/N < 10$) with high organic content in the sediment and frequent anaerobic episodes (Guilizzoni and Lami, personal communication, 1992). The fact that the *D. proteiformis* morph “proteiformis”-Assemblage clearly dominates the low abundance association confirms that this morph is particularly adapted to these conditions.

We have no explanation for the extreme fragility of tests observed in the lake. This phenomenon, not observed in Lake Orta or Lake Varese, was reported by Medioli and others (1985) in thecamoebian samples collected from Lake Garda. These authors, at the time, hypothesized a relationship between the fragility of the tests and the alkalinity of the lake. This hypothesis could not be confirmed here since only *D. proteiformis* morph “proteiformis” seems to have particularly fragile tests and because the thecamoebians of Lake Varese, where the environment is also alkaline, do not show any tendency to fragility.

Lake Candia is eutrophic, and yet *C. tricuspis* is present in unexpectedly low amounts (<10). While this does not necessarily conflict with results of previous studies indicating that this species peaks under eutrophic conditions, it suggests that eutrophism alone might not be sufficient to guarantee that the species will be abundant. A similar problem is posed by *D. oblonga* and *P. compressa*. Collins and others (1990) described these species as “ubiquitarian,” with *D. oblonga* being less frequent in oligotrophic lakes. Our data conflict with this interpretation as the greatest abundances of *D. oblonga* were found in oligotrophic portions of the core from Lake Orta, and *P. compressa* was rare or absent in eutrophic lake sediments.

Hence, we suggest that because of the variation in response, all distributions of species and morphs, regardless of how contradictory, with previous findings be recorded as a matter of routine. Causes of the contradictions may be

identified eventually, and the problems will become easier to solve.

CONCLUSIONS

The thecamoebian associations studied in lakes Candia, Varese and Orta differ from each other and further confirm the profound differences (morphometric, physiographic, trophic, chemical and productivity) between the three lakes. Lake Orta, except for the topmost sample which represents an anomalous situation, contains an association composed of *D. oblonga*, *D. globulus*, *D. proteiformis*, and *P. compressa*. In Lake Varese, the genus *Centropyxis* and *C. tricuspis*, both rare in Lake Orta, form a significant (50–80%) fraction of the association. In Lake Candia the association is dominated by *D. proteiformis*. This diversification appears to confirm that thecamoebians are sensitive to environmental differences.

Problems concerning the ecological significance of some species (e.g., *C. tricuspis*, *D. oblonga* and *P. compressa*) have emerged. Clearly, we are still in the stage of collecting information on this subject and some contradictory data are unavoidable. However, such contradictions underline the importance for future studies to record all available information in a systematic and thorough manner, because only in this way will the study of thecamoebian associations become an essential tool for interpreting the evolution of lacustrine paleoenvironments.

This study has shown separating the various morphs of each species as if they were independent taxa increases the paleoecological value of these organisms. The distinction, within the species *D. proteiformis*, of the infrasubspecific units *D. proteiformis* morph “proteiformis,” *D. proteiformis* morph “crassa,” *D. proteiformis* morph “rapa” and *D. proteiformis* morph “bicornis” has allowed the recognition of morph *D. proteiformis* morph “proteiformis” as an ex-

cellent indicator of environments low in oxygen and rich in organics and sulfites, and of morph *D. proteiformis* morph "rapa" as an indicator of environments strongly polluted for a long period of time, as is the case of Lake Orta.

This study has confirmed that although the number of genuine thecamoebian species is small, the ecophenotypic variability within each species is high, and that this variability can be used as a paleoecological indicator.

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APPENDIX I. Thecamoebian occurrences in samples from lakes Orta (O prefix), Varcse (V prefix) and Candia (C prefix). Samples were quantitatively analyzed and are recorded as fractional abundances. Total counts, depth in core (measured in cm and part of sample name), and biofacies designation of each sample are also indicated. Species and morphs not present in statistically significant numbers, and thus not included in the Q-Mode cluster analysis, are indicated by an (*). Samples not containing statistically significant populations, and thus not included in the Q-Mode cluster analysis, are indicated by a (†).

Species/Sample Assemblage	Q1.5	OS	Q8.5	Q12.5	Q16.5	Q20.5	Q24.5	Q28.5	Q32.5	Q36.5	Q40.5	Q44.5	Q48.5	Q52.5	Q56.5	Q60.5	Q64.5	Q68.5	Q72.5	Q76.5	Q80.5	Q84.5	(f)V0.0	(f)V3.3	(f)V5.0	(f)V8	(f)V12
Total Counts	289	340	313	339	365	309	307	304	331	326	319	394	308	303	273	283	309	305	294	336	319	308	—	—	—	—	—
*Aretia spp	0.003	0.000	0.003	0.003	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.007	0.000	0.006	0.006	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Centropomus aculeata	0.000	0.024	0.022	0.021	0.030	0.023	0.010	0.007	0.012	0.037	0.006	0.008	0.019	0.010	0.037	0.025	0.003	0.010	0.020	0.009	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.016	0.016	0.015	0.018	0.017	0.011	0.009	0.012	0.020	0.009	0.009	0.015	0.011	0.022	0.018	0.006	0.011	0.016	0.010	0.006	0.000	0.000	0.000	0.000	0.000	0.000
Centropomus constricta	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Centropomus ecoris	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cucurbitella tricuspid m. "magna"	0.000	0.000	0.042	0.003	0.019	0.013	0.029	0.003	0.027	0.015	0.034	0.033	0.026	0.066	0.029	0.018	0.071	0.036	0.082	0.024	0.034	0.013	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.022	0.006	0.014	0.013	0.019	0.006	0.018	0.006	0.020	0.018	0.028	0.020	0.020	0.013	0.025	0.013	0.003	0.010	0.000	0.013	0.000	0.000	0.000	0.000	0.000
Cucurbitella tricuspid m. "parva"	0.000	0.006	0.022	0.027	0.044	0.026	0.003	0.000	0.003	0.003	0.003	0.025	0.006	0.020	0.004	0.025	0.013	0.003	0.010	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.008	0.016	0.017	0.021	0.018	0.006	0.000	0.006	0.006	0.006	0.019	0.016	0.009	0.016	0.007	0.018	0.013	0.006	0.011	0.000	0.012	0.000	0.000	0.000	0.000	0.000
Cyclolophys spp	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cucurbitella corona	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Diffugia oblonga m. "caprolana"	0.000	0.024	0.099	0.000	0.068	0.078	0.127	0.109	0.094	0.337	0.019	0.058	0.078	0.106	0.081	0.071	0.168	0.197	0.173	0.230	0.326	0.269	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.016	0.033	0.000	0.026	0.030	0.037	0.035	0.031	0.025	0.015	0.023	0.030	0.035	0.032	0.030	0.042	0.045	0.040	0.043	0.040	0.050	0.000	0.000	0.000	0.000	0.000
Diffugia oblonga m. "magna"	0.000	0.012	0.054	0.006	0.008	0.058	0.042	0.076	0.039	0.020	0.015	0.023	0.026	0.003	0.015	0.018	0.039	0.039	0.031	0.024	0.041	0.039	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.011	0.025	0.008	0.009	0.026	0.023	0.030	0.021	0.017	0.019	0.015	0.018	0.006	0.014	0.015	0.022	0.022	0.020	0.016	0.022	0.022	0.000	0.000	0.000	0.000	0.000
Diffugia oblonga m. "parva"	0.000	0.000	0.051	0.083	0.134	0.178	0.221	0.161	0.227	0.101	0.066	0.094	0.107	0.092	0.095	0.007	0.168	0.174	0.139	0.152	0.141	0.172	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.024	0.029	0.035	0.043	0.046	0.041	0.045	0.028	0.027	0.029	0.035	0.033	0.035	0.010	0.042	0.043	0.040	0.038	0.038	0.042	0.000	0.000	0.000	0.000	0.000
Diffugia oblonga m. "parva"	0.010	0.021	0.284	0.386	0.266	0.243	0.202	0.191	0.100	0.248	0.223	0.244	0.244	0.168	0.308	0.353	0.120	0.131	0.092	0.107	0.069	0.078	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.012	0.015	0.050	0.052	0.045	0.048	0.045	0.044	0.032	0.047	0.046	0.042	0.048	0.042	0.055	0.056	0.036	0.038	0.033	0.033	0.028	0.030	0.000	0.000	0.000	0.000	0.000
*Diffugia cf. oblonga	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Diffugia proteiformis m. "bicornis"	0.014	0.032	0.006	0.003	0.016	0.026	0.020	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.003	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.013	0.019	0.009	0.006	0.013	0.018	0.015	0.010	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.013	0.006	0.000	0.000	0.000	0.000	0.000	0.000
Diffugia proteiformis m. "crassa"	0.000	0.421	0.103	0.233	0.172	0.169	0.115	0.118	0.264	0.235	0.061	0.146	0.152	0.176	0.127	0.084	0.075	0.085	0.056	0.062	0.060	0.060	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.052	0.040	0.032	0.043	0.042	0.036	0.035	0.045	0.047	0.024	0.039	0.040	0.045	0.039	0.031	0.030	0.032	0.025	0.025	0.027	0.000	0.000	0.000	0.000	0.000	0.000
*Diffugia proteiformis m. "curvicaulis"	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Diffugia proteiformis m. "proteiformis"	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Diffugia proteiformis m. "rapa"	0.785	0.000	0.000	0.009	0.022	0.000	0.013	0.000	0.000	0.000	0.003	0.009	0.000	0.006	0.003	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.047	0.000	0.000	0.010	0.015	0.000	0.013	0.000	0.000	0.000	0.006	0.011	0.000	0.006	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Diffugia spp.	0.000	0.000	0.000	0.013	0.006	0.003	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.043	0.005	0.000	0.000	0.006	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Diffugia ureclata	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*Diffugia urvclata m. "elongata"	0.000	0.000	0.003	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Standard Error (±)	0.000	0.000	0.006	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000</									

Species/Sample Assemblage	(T)V16	(T)V17	(T)V17.5	(T)V20	(T)V22	V23	V43	V55	V62	V68	V74	V82	V90	C0	C5.5	C10	C14.5	C19	C27.5	C36.5	(PK)4.5	C53.5	(TK)62.0	(TK)70.5	C88
Total Counts	0	—	0	0	—	3	3	126	306	300	200	298	301	2	6	6	6	6	6	6	6	6	6	6	3
<i>*Arcella spp</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.020	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
<i>Centropages aculeatus</i>	0.000	0.000	0.000	0.167	0.216	0.316	0.268	0.262	0.190	0.230	0.170	0.144	0.106	0.013	0.000	0.071	0.000	0.014	0.000	0.014	0.000	0.069	0.267	0.171	
Standard Error (±)	0.000	0.000	0.000	0.298	0.075	0.092	0.050	0.077	0.044	0.048	0.052	0.040	0.035	0.025	0.000	0.055	0.000	0.028	0.000	0.000	0.066	0.087	0.065	0.115	
<i>Centropages constrictus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.024	0.062	0.110	0.085	0.104	0.106	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.027	0.027	0.035	0.039	0.035	0.035	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
<i>Centropages eornis</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.178	0.203	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.003	0.000	0.000	0.000	0.013	0.065	0.000	0.036	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	
<i>Cucurbitella tricuspid m. "magna"</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.006	0.000	0.000	0.000	0.000	0.013	0.055	0.040	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.003	0.000	0.000	0.000	0.013	0.065	0.000	0.036	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	
<i>Cucurbitella tricuspid m. "parva"</i>	0.000	0.000	0.000	0.000	0.000	0.267	0.306	0.371	0.444	0.121	0.120	0.130	0.148	0.193	0.000	0.087	0.000	0.043	0.072	0.196	0.043	0.182	0.086	0.067	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.081	0.091	0.054	0.087	0.037	0.047	0.040	0.045	0.040	0.000	0.081	0.000	0.061	0.061	0.115	0.037	0.161	0.072	0.126	
<i>Cyclopoida spp</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.063	0.071	0.046	0.147	0.025	0.044	0.070	0.065	0.000	0.012	0.029	0.000	0.000	0.000	0.045	0.034	0.000	
Standard Error (±)	0.000	0.000	0.000	0.000	0.000	0.034	0.027	0.045	0.023	0.040	0.022	0.023	0.029	0.055	0.000	0.023	0.039	0.000	0.000	0.000	0.000	0.087	0.047	0.000	
<i>Cucurbitella corona</i>	0.000	0.000	0.000	0.000	0.009	0.010	0.000	0.000	0.003	0															