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Charophyte Remains from Wadi Howar as Evidence for Deep Mid-Holocene Freshwater Lakes in the Eastern Sahara of Northwest Sudan

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Field research in the eastern Sahara (Northwest Sudan) revealed extensive early- to mid-Holocene lake marl deposits bearing gyrogonites of Charophytes (green algae, stoneworts) along the lower course of the Wadi Howar, an extinct tributary to the Nile. The Charophyte flora of a paleolake southwest of Jebel Rahib (17°31'N/26°52'E) dated prior to 4720 ± 110 yr B.P. is mainly composed of the ecologically sensitive species *Nitellopsis obtusa* which indicates permanent, relatively deep (4–12 m) and cool oligotrophic freshwater. The study of *Nitellopsis* sites provides a new and promising approach to the reconstruction of Quaternary paleoenvironments of deserts. © 1991 University of Washington.

Des recherches sur le terrain dans le Sahara oriental (Nord-Ouest Soudan) ont révélé, le long du cours inférieur du Wadi Howar, un ancien affluent du Nile, de grandes étendues de dépôts lacustres, d'âge Holocène ancien à moyen, contenant des gyrogonites de Charophytes (algues vertes). La flore de Charophytes d'un de ces paléolacs, situé au Sud-West du Jebel Rahib (17°31'N/26°52'E), datée comme antérieure à 4720 ± 110 a B.P., se compose essentiellement de *Nitellopsis obtusa,* une espèce qui indique un milieu oligotrophe d'eau douce permanente, relativement froide et profonde (4–12 m). L'utilisation des Charophytes comme biomarqueurs lacustres constitue une méthode nouvelle et prometteur pour la reconstitution des paléoenvironnements Quaternaires des régions désertiques. © 1991 University of Washington.

Quartärgeologische Geländearbeiten in der östlichen Sahara (Nordwest-Sudan) erbrachten ausgedehnte Vorkommen früh- bis mittelholozäner Armleuchteralgen-führender Seesedimente entlang des Unterlaufs des Wadi Howar, eines ehemaligen Zustroms des Nils. Die Charophytenflora eines südwestlich des Jebel Rahib (17°31'N/26°52'E) gelegenen und älter als 4720 ± 110 a B.P. datierten Paläosees besteht hauptsächlich aus der Art *Nitellopsis obtusa,* welche permanentes, relativ tiefes (4–12 m) und kühles oligotrophes Süßwasser anzeigt. Die Untersuchung von *Nitellopsis*-Fundstellen stellt einen neuen und vielversprechenden Ansatz zur palökologischen Rekonstruktion der quartären feuchtzeitlichen Umweltverhältnisse in Wüstengebieten dar. © 1991 University of Washington.

INTRODUCTION

Field research in the southeastern Sahara along the previously unknown lower course of the Wadi Howar, an extinct tributary of the Nile at around 17°30'N, revealed various fluvial sediments (Kröpelin, 1990) and numerous extensive outcrops of lacustrine carbonates. These still-water accumulations mainly consist of lake marl deposited between about 9500 and 4000 yr B.P. along the 500-km-long paleovalley (Fig. 1). They are evidence of groundwater- and run-off-supported lakes that were surrounded by a highly developed savanna scenery (Pachur and Kröpelin, 1987). Widespread fossil dunes stabilized by a thick cover of countless Neolithic artifacts indicate intense human occupation of the wadi banks (Gabriel and Kröpelin, 1986). Today, the virtually uninhabited region forms the southeastern part of the largest hyperarid area of the earth and receives less than 40 mm of average rainfall per annum (Henning and Flohn, 1977; Leroux, 1983).

Such calcareous lake sediments crop out

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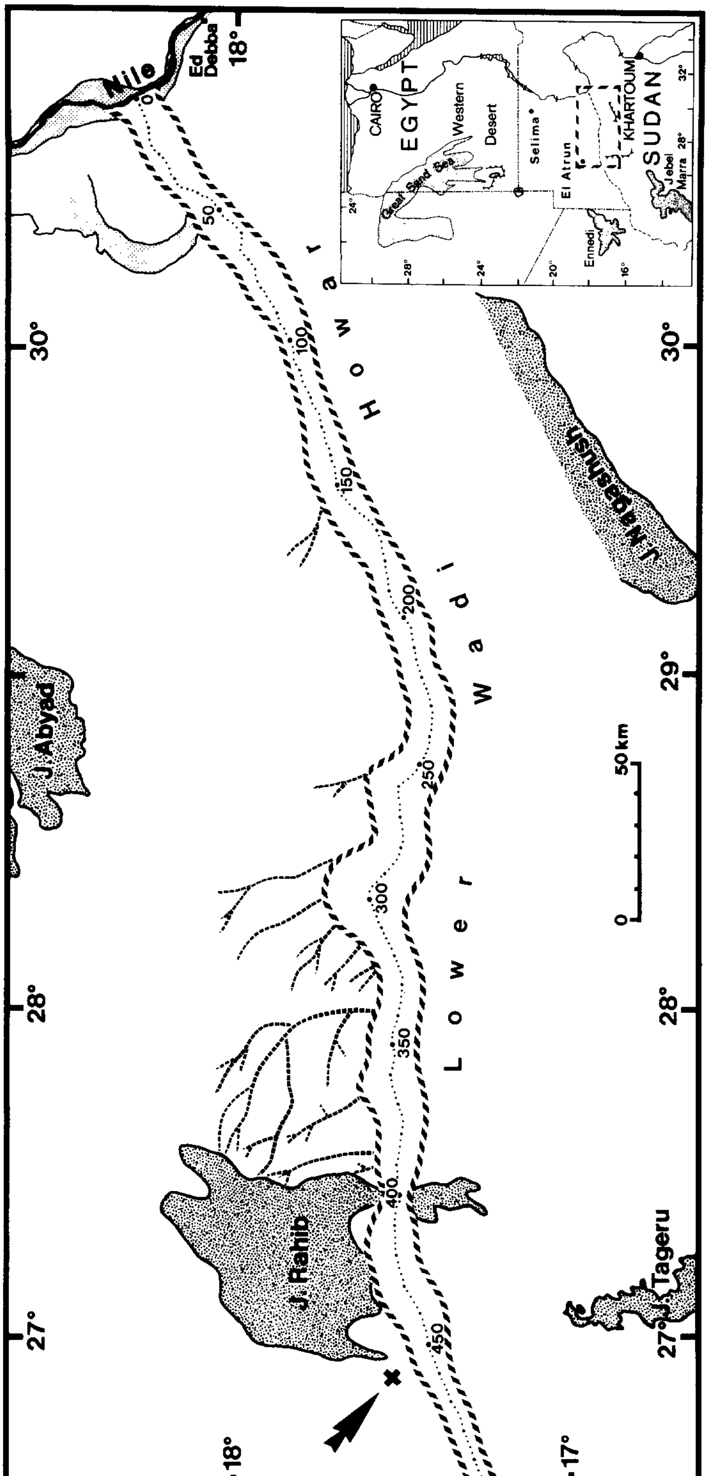
Nile
Ed Debba
18°
30°
29°
28°
27°
17°
Wadi Howar
Lower Wadi Howar
J. Abyad
J. Rahib
J. Tageru
J. Magashush
0
50
100
150
200
250
300
350
400
450
0
50 km
CAIRO
EGYPT
Western Desert
Great Sand Sea
Selima
El Atrun
Ennedi
KHARTOUM
SUDAN
Jebel Marra
24°
28°
32°
20°
16°

in the foreland of the southern spur of the westernmost ridges of Jebel Rahib. Because of their facies differentiation, size, and fossil content the sediments are representative of most of the early Holocene paleolakes along the lower Wadi Howar. These interconnected paleolakes (sites U 502 and U 578) are situated only a few kilometers away from the northern bank of Wadi Howar which is bordered by 10- to 20-m-high dunes at about 520 m altitude. Owing to their extremely abundant microfossil content, these localities yield unique information about the lacustrine paleoecology between latitudes 17° and 18°N. Considered in the context of the unusual wealth of prehistoric occupation remnants in this particular area (Kuper, 1981, 1986, and unpublished data), these data also help to elucidate the environmental context of Neolithic settlement.

GEOMORPHOLOGICAL AND SEDIMENTOLOGICAL SETTING

Figure 2 gives a schematic overview of the facies subdivisions of the sites described below. In the northern part of the sequence, coarse gravelly wadi sediments unconformably overlie the weathered granite bedrock (U 500) and, in thinner layers, the marginal lake deposits. At a low slope gradient and with increasing proximity to Wadi Howar there is a gradual transition to a dark-grey, silty to fine-sandy littoral facies with occasional carbonate enrichment (U 501).

Because of its sedimentological composition and fossil content, section U 502 is a significant one for the paleolacustrine stratigraphies along the Wadi Howar. It is situated in the middle of a wide shallow depression where the lake floor is exposed over at least 1 km^2, except for a thin cover of pale orange eolian sand and alluvial deposits that are interspersed with concretions of carbonate-cemented sands (Fig. 3a). Consisting of low ridges and small, only decimeter-high yardangs, the microrelief of the lake floor is chiefly a product of eolian activity. The extensive interior of the lake basin contains no coarse material, apart from diffuse artifact litter.

The lake sediments contain mollusks throughout and consist of at least 70 cm (depth of excavation) of relatively homogeneous lacustrine carbonates and marls. At the sampling site they were divided at about 50 cm below the surface by a distinct mollusk horizon. At the surface the highly calcareous deposits are consolidated, bleached pale white, and partly platy in structure, whereas the deeper parts are less consolidated and light- to dark-grey in color.

The bulk X-ray diffraction pattern of a typical sample taken at 45–55 cm depth shows both the major minerals calcite and quartz, minor quantities of feldspars, and aragonite which is probably due to mollusk shells. After HCl treatment, 43.8% by weight of the sample was noncarbonate residue. The quartz content belonged exclusively to the <63-μm fraction, suggesting that when the lake carbonate was deposited there was no input of eolian sand. This may have been due to the large size of the lake, with additional protection possibly offered by a dense reed belt or a close plant cover that may have fixed or at least partially stabilized the surrounding sandy material during formation of the lacustrine carbonates. Neither thin-section analysis nor direct light microscopy of the solution residue of sample U 502b indicated whether it was eolian dust or alluvial silt. Probably because of strong bioturbation, the microstructure showed no features such as rhythmic fine lamination of silty silicate clasts found in dust-storm deposits in the lake sediments at Selima, a paleolake basin nearly 500 km to the NNE (Pachur and Kröpelin, 1989; Fig. 1).

Iron crusts up to 60 cm thick that cover terrace-like ridges several meters high separate the different lake basins (U 509; Fig. 2). They overlie unconsolidated orange dune sands and consist of poorly sorted

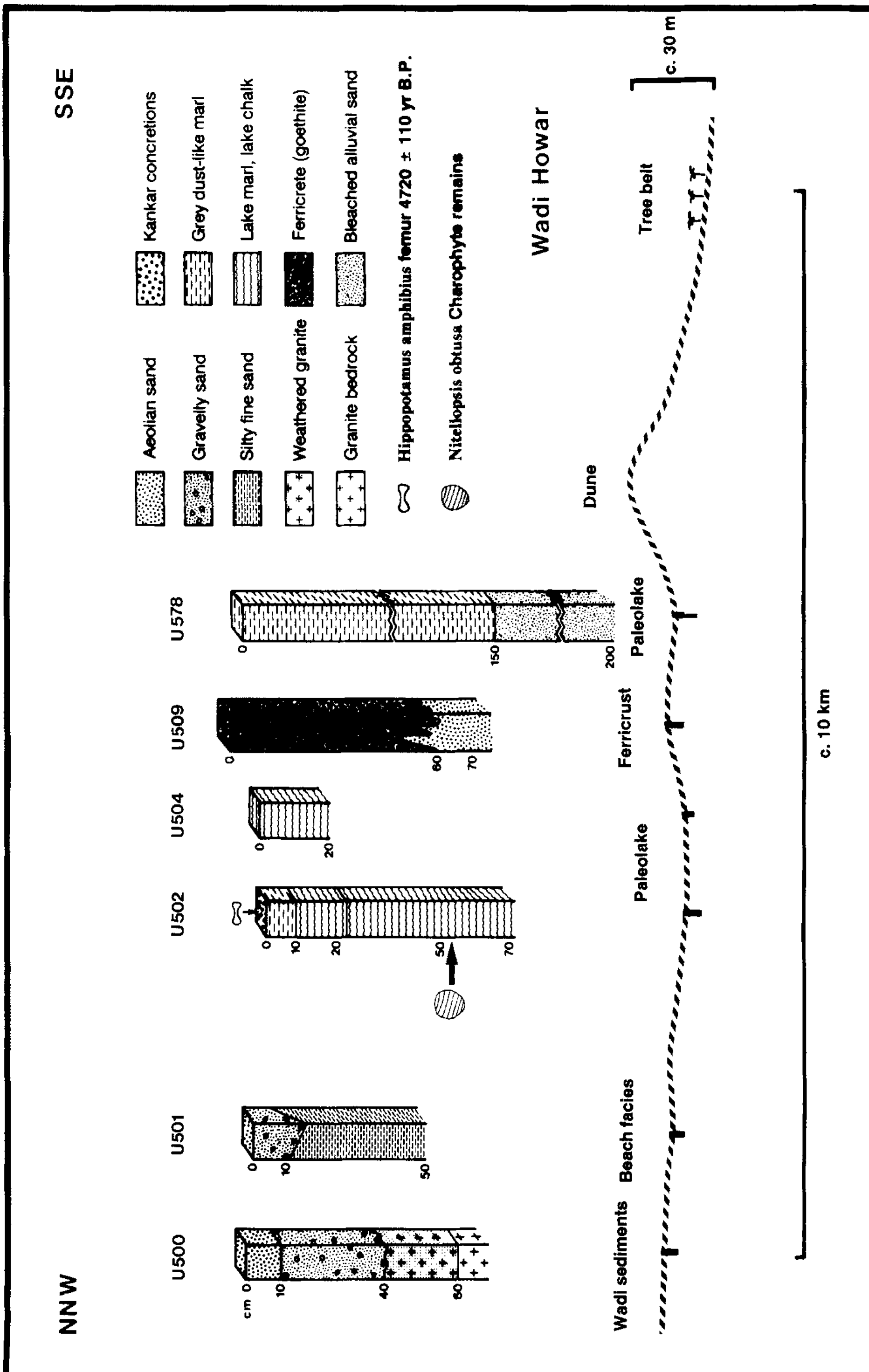

FIG. 2. Cross-section of paleolake complex U 502/U 578.

FIG. 3. (a) Paleolake U 502 with extensive lacustrine carbonates. (b) Lake bed of paleolake U 578 showing *Aspatharia arcuta* bivalve, Hymenopteran insect nests (arrow), and bioturbational features.

fine- to medium-grained quartz sands which are densely consolidated by a goethite matrix. Centimeter-thick cylindrical holes indicate a former dense reed vegetation (probably of *Phragmites communis*). Because they interlock with the adjacent lacustrine sediments, these crusts are considered contemporaneous littoral facies of the Holocene paleolakes (Pachur *et al.*, 1990). Their formation may be explained by lateral migration of ferrous soil solutions due to reducing conditions in the waterlogged sediment and the action of organic compounds, including both secretions from the roots and the products of plant decomposition in the reed belt.

Site U 578 is situated about 2 km SSE of paleolake U 502. It lies directly beneath the southwestern spur of Jebel Rahib (Fig. 2) and about 20 m above the present floor of Wadi Howar in a depression bounded on the south and west side by ancient dunes. The lake floor, about 400 m across, is covered by coarse alluvium, densely scattered artifacts, and windblown sand. The sediments consist of dark-grey marls with a dust-like consistency and are slightly consolidated in the top 10 cm only. The proportion of carbonate in the marls is 50.7% by weight; the carbonate-free residue chiefly consists of quartzitic silt. Probing has shown the highly calcareous silts in the mid-basin to be 1.5 m deep. At their base lie at least 50 cm of light-colored fluvial or colluvial sands.

The exposed lake floor of site U 578 displays numerous specimens of *Aspatharia arcuta* and *A. rubens* bivalves (det. Schütt, H., Düsseldorf), up to 13 cm long and mostly preserved in life position (Fig. 3b). While these large Nile bivalves normally prefer flowing water, the closed shells indicate a low-energy environment for this site. Deflation also revealed many Hymenopteran insect nests, which were built on the still-wet bottom and on the banks of the desiccating lake (Fig. 3b). The cellular cylindrical constructions point to solitary wasps (possibly Eumenidae) or mason bees (possibly Megachilidae; cf. Kelner-Pillault, 1983; Schlüter, 1984).

DESCRIPTION OF THE CHAROPHYTE FLORA

Of particular interest is the frequent occurrence of Charophyte remains in the form of gyrogonites in the sediments of paleolake U 502 (Fig. 4a). Gyrogonites, the calcified parts of the fructified oogonia, i.e., the female reproductive organs of the charophytes, generally show an ovoidal form with a typical sinistrally coiled structure and are 250 to 1250 μm in size depending on the species.

As a distinctive group of green algae, Charophytes include freshwater and brackish water species, up to a meter or more high. Growing as submerged Charophyte meadows in both shallow waterbodies and deep lakes, they inhabit mainly places with slight water movement. As one single plant is easily able to produce a hundred female reproductive organs, the heavily calcified parts of the oogonia (gyrogonites) are the most frequently preserved fossil parts of the voluminous biomass of the bushy plants. Fragments of calcified charophyte "stems" also are common, but they cannot be identified to species.

Order Charales
Family Characeae L. Cl. Richard
Genus *Nitellopsis* Hy
Species *Nitellopsis obtusa* (Desv. in Lois.) J. Groves
(Figs. 5a–f)

Description:

Gyrogonites subprolate, ovoïdal to broadly subprolate; apical pole broadly rounded, subtruncate, heavily calcified. Length (L) ranging from 925 to 1275 μm, width (W) from 750 to 1100 μm. Shape as indicated by isopolarity index (100 L/W) varying from 100 to 135 with clear frequency maxima between 110 and 120 (Fig. 6); biometrical values of gyrogonites listed in Table 1.

Lime spirals five, sinistrally coiled, smooth, showing seven to eight turns in lateral view (Figs. 5a–b). Mean of spiral index (CS) as calculated from gyrogonite length to width of the spiral cell (L/W_{sp}) corresponding to 6.2 (Table 1).

Apical junction with distinct narrowing of the spiral cells and well developed apical rosette (term used by Horn af Rantzien, 1959) in the center (Fig. 5c). Basal pole rounded or truncate in lateral view, basal opening either superficial (Fig. 5d) or cone-shaped (Fig. 5e). Basal plug very thin, plate-like, about five times wider than high (Fig. 5f).

The above characteristics, established from 120 entire and many broken specimens washed out from only 50 g of raw sediment, are typical of gyrogonites of the genus *Nitellopsis*. The genus *Nitellopsis* has only one living species *Nitellopsis obtusa*. An accurate specific comparison has been made with a sample collected at Altenheim (Western Germany) whose frequency distribution of gyrogonites has been established by Soulié-Märsche (1987). Although the modern population has a larger number of small-sized gyrogonites and appears to be slightly more elongated in shape (displacement from one class to the next

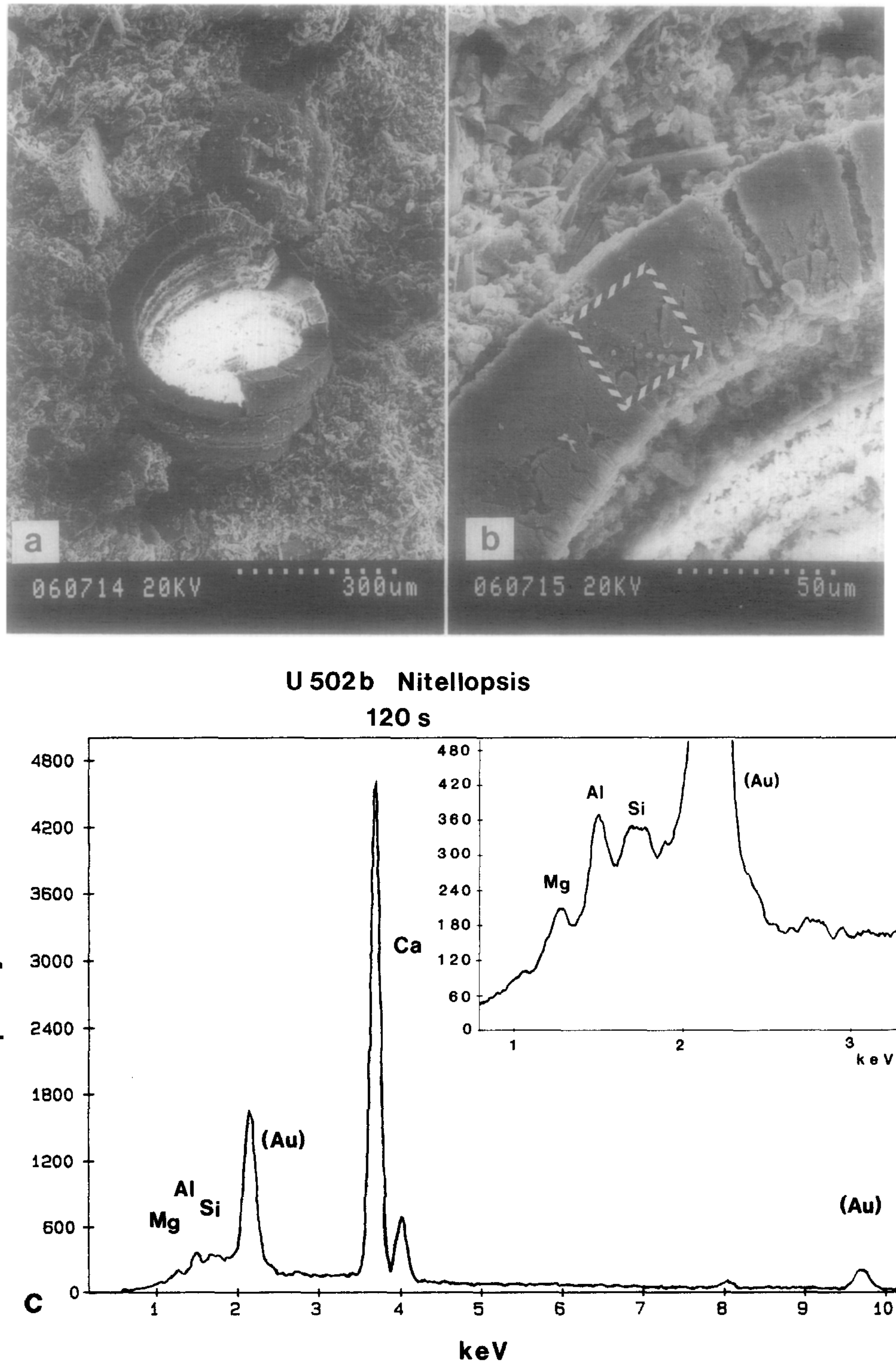

FIG. 4. (a) Scanning electron microscope micrograph of broken gyrogonite of *Nitellopsis obtusa* in lake marl. (b) Detail surface view of lime spiral. Striped line indicates scan area of EDAX spectrum in Figure 4c. (c) Energy dispersive X-ray spectrum showing elemental composition of gyrogonite (Au from sputtering). Enlargement in inset.

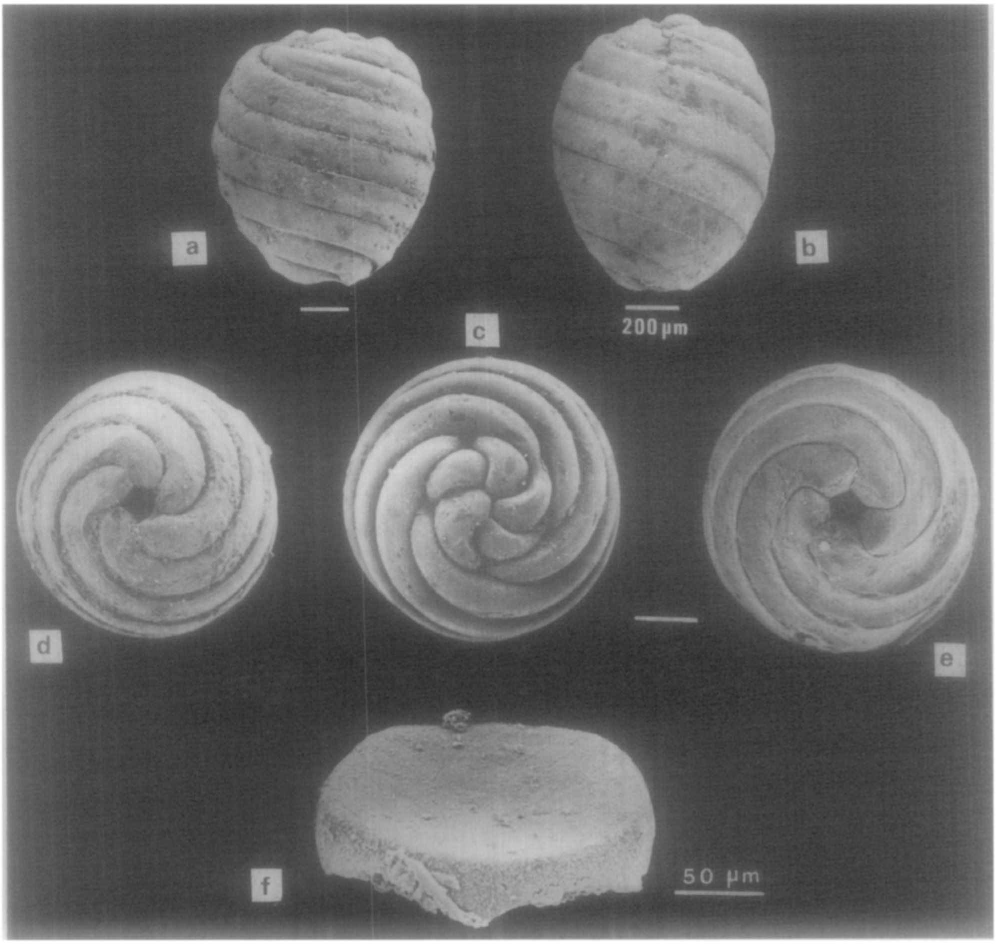

FIG. 5. *Nitellopsis obtusa* from site U 502/Wadi Howar. (a, b) Lateral view of gyrogonites (×32); (c) Apical view (×40); (d, e) Basal view (×40); (f) Isolated basal plug (×240). Scale bars are 200 μm for views a–e.

higher), a very good correspondence is seen if the histograms are superimposed (Fig. 6).

These differences could justify the distinction of a separate, new species, but the final decision depends on whether we apply the philosophy of the "splitters" or the "lumpers." As shown by studies on morphological variation among living populations of a given species belonging to the genus *Chara* (Soulié-Märsche, 1989), differences like these concerning the dimensions and shape of the gyrogonites of Wadi Howar and Altenheim would more probably reflect population variations than differences between species. On the basis of their morphological characteristics, the gyrogonites of Wadi Howar belong to *Nitellopsis obtusa*. Thus, the ecological requirements known for the extant representatives can be applied to paleoecological reconstruction.

Energy-dispersive microanalysis of X-rays (EDAX) shows that the gyrogonites of that species mainly consist of Ca with traces of Mg; Al and Si are thought to stem from superficial pollutants (Figs. 4b and c).

Associated with the dominant species *N.*

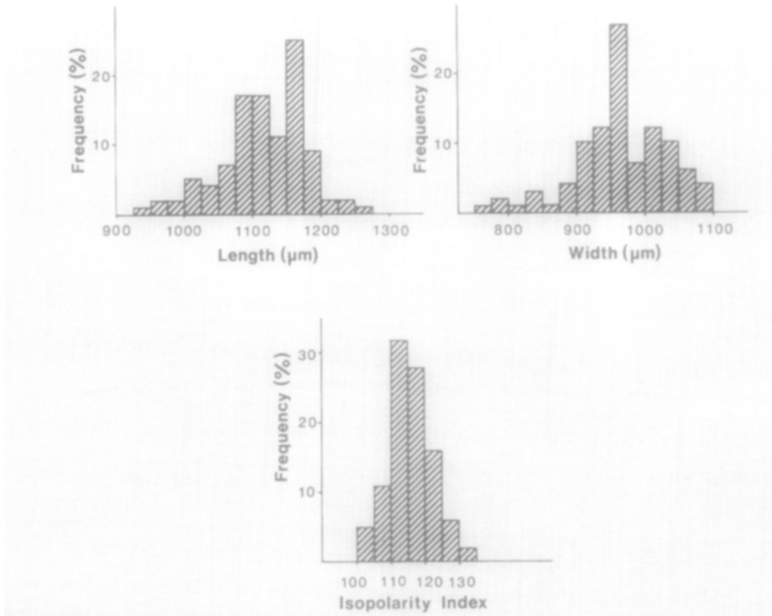

FIG. 6. *Nitellopsis obtusa* from site U 502/Wadi Howar. Frequency distribution of length (L), width (W), and length/width ratio (ISI = isopolarity index) measured on 100 gyrogonites.

obtusa are much smaller obovoidal gyrogonites belonging to the genus *Chara*.

Genus Chara Linné
Species *Chara pappii*
Soulié-Märsche 1979
(Figs. 7a–f)

Description:

Gyrogonites cylindrical, barrel-shaped in lateral view; apical pole and basal pole rounded (Figs. 7a–b). Protruding apical rosette, delimited by very distinct circular apical groove (Fig. 7c). Basal opening superficial (Figs. 7d–e) containing the pentagonal basal plug. Sides of the basal plug curved, external surface smaller than the internal one (Fig. 7f).

The material consists of a dozen well-preserved gyrogonites, probably drifted from shallow parts of the lake. This type of gyrogonite was first described from Pliocene strata of Greece as a new fossil species, dedicated to the late paleobotanist A. Papp of Vienna (Soulié-Märsche, 1979). The fact that *Chara pappii* has been found in young strata such as the Holocene of Mali (Soulié-Märsche, 1982) and here in Sudan indicates that this organ-species

TABLE 1. BIOMETRY OF *Nitellopsis obtusa* GYROGONITES FROM SITE U 502/WADI HOWAR

	Length (L) μm	Width (W) μm	Isopolarity index (ISI)	Spiral width (W_{sp}) μm	Spiral index (CS)
n	100	100	100	96	96
$\bar{x}$	1112	965	116	184	6.2
$\bar{x} \pm 2s_d$	988–1237	832–1097	103–129	151–217	5.2–7.2
σ^2	3884	4386	42	274	0.27
V	5.6%	6.9%	5.6%	9.0%	8.4%

Note. n, number of measurements; $\bar{x}$, mean value; $\bar{x} \pm 2s_d$, confidence interval at 95%; σ^2, variance; V, 100 $\sigma/\bar{x}$ is the variation index.

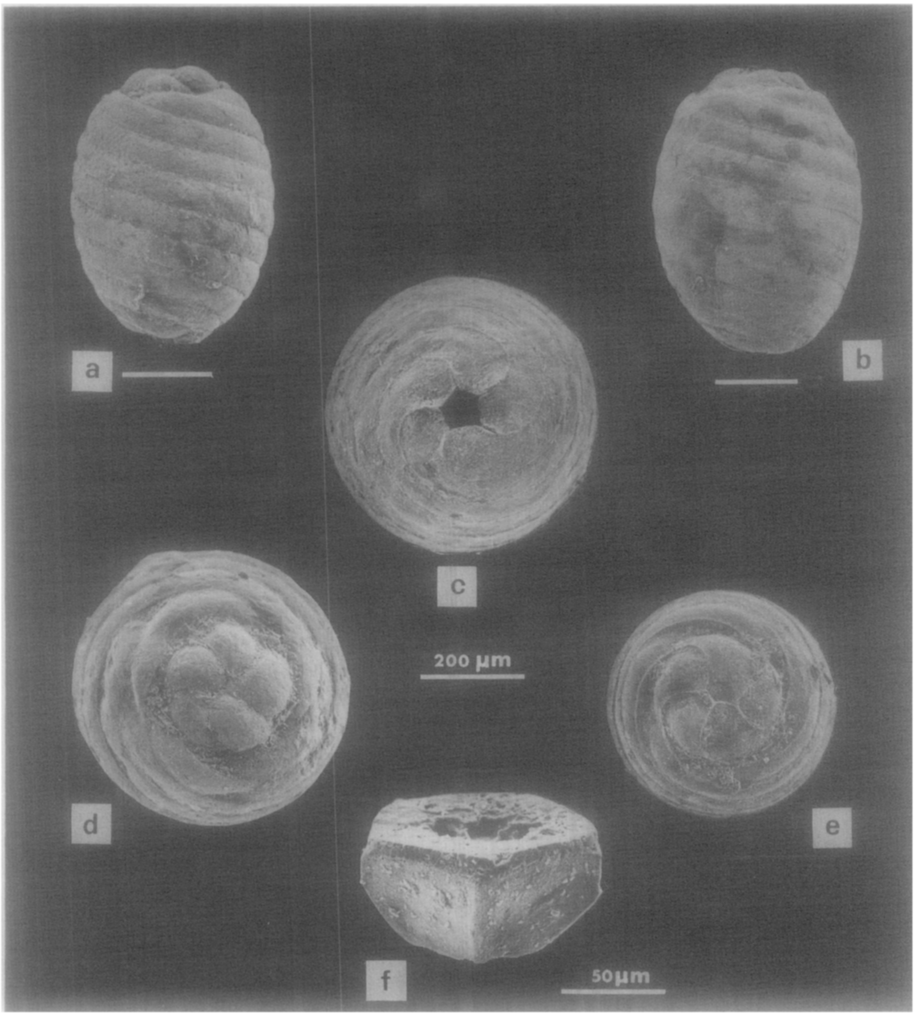

FIG. 7. *Chara pappii* from site U 502/Wadi Howar. (a, b) Lateral view of gyrogonites (×60); (c) Apical view (×80); (d, e) Basal view (×80); (f) Isolated basal plug (×290). Scale bars are 200 μm for views a–e.

could probably be referred to an extant botanical species whose gyrogonites are not yet known. Thus, we fully agree with Bhatia and Singh (1989) that *Chara pappii* may still be found alive somewhere on the Asian or African continent. Until modern representatives have been investigated, however, this species cannot provide any paleoecological indications.

PALEOECOLOGICAL DISCUSSION

The interest of the population study of *Nitellopsis obtusa* from site U 502 at the Wadi Howar lies in its paleoecological significance (Kröpelin and Soulié-Märsche, 1989). Indeed, *N. obtusa* can be considered as an ecologically sensitive species (Soulié-Märsche, 1986, 1987), attesting to lakes with permanent, relatively cold and deep freshwater. Culture experiments on the salt tolerance of *Nitellopsis obtusa* revealed the amount of 100 mmole NaCl (5.85‰) to be lethal for 80% of the cells after only 3 hr, and no survival at all is noticed after 24 hr (Katsuhara and Tazawa, 1986). Consequently, the species never occurs in deposits of inland sebkhas or playas (temporary rainpools) which contain water for weeks or months only (cf. Kröpelin, 1987, 1989).

Kasaki (1962) and also Krause (1980, 1985) indicate depths of water of 5–11 m as the range where the optimal development of *Nitellopsis obtusa* takes place in undisturbed oligotrophic environments. The temperature in the rooting zone of *N. obtusa* has to be constantly low as, for example, in the groundwater-fed gravel-pit lake at Altenheim (Krause, 1980) where the recorded temperature is lower than 10°C over the whole year (W. Krause, personal communication, 1987).

Independently, low water temperatures have also been inferred from oxygen isotope studies of individual aquatic snail shells from other sites along the Wadi Howar (analyses by Abell, P., Rhode Island; S. Kröpelin, unpublished data). At this latitude (17°30′N), such cold water can only be explained by groundwater influx. This underlines the hypothesis that all carbonate-forming paleolakes in the Sahara have been at least partially groundwater supported when the regional groundwater level was substantially higher than today due to recharge by local rainfall during wet phases.

While the Charophytes were the first indicators for a paleoenvironment of this type in paleolake U 502, the conclusions have since been corroborated by other fossil evidence. Permanent deep oligotrophic freshwater at Wadi Howar is also attested by findings of teeth and bone fragments of large predatory Nile fish species more than 60 cm long (det. Van Neer, W., Tervuren; S. Kröpelin, unpublished data) as well as ostracods (det. Günther, J., Schleswig) from the same site (Table 2).

This locality is remarkable for its abundance of gastropods, in both species and numbers of individuals (Table 2). The site contains almost the entire spectrum of aquatic gastropods found in the lower Wadi Howar. Most of the listed taxa are freshwater species. *Melanoides tuberculata* generally also tolerates slightly brackish (NaCl-dominated) water; however, the large, well-developed shells, up to 3 cm long, point to optimal living conditions for this species too.

TABLE 2. Aquatic Gastropods, Fish Remains, and Ostracods from Site U 502

Prosobranchia[a]
Lanistes carinatus
Valvata nilotica
Gabiella senaariensis
Melanoides tuberculata
Pulmonata[a]
Lymnaea natalensis
Gyraulus costulatus
Segmentorbis angustus
Biomphalaria pfeifferi
Bulinus truncatus
Osteichthyes[b]
Alestes sp. (Pebbly fish)
Tilapia sp. (Nile perch)
Tilapia zillii (Nile perch)
Synodontis sp. (Shield-head catfish)
Ostracoda[c]
Cyprideis sp.
Darwinula sp.
Sclerocypris sp.

[a] Det. Schütt, H., Düsseldorf.
[b] Det. Van Neer, W., Tervuren.
[c] Det. Günther, J., Schleswig.

The only direct age for lacustrine sediments containing *Nitellopsis obtusa* is an accelerator radiocarbon date of 4720 ± 110 yr B.P. (UZ 2168; Pachur and Kröpelin, 1987) for the collagen of a hippopotamus femur (*Hippopotamus amphibius*) found at the present surface. However, this should be regarded as a minimum age, since the above-mentioned microrelief indicates that the lake sediments have been lowered by deflation by an unknown amount, possibly causing a minor projection of the smoothly polished bone. Furthermore, the fossiliferous Charophyte-bearing horizon with its rich species diversity that possibly indicates the optimum lake phase, lies a further 50 cm below the present surface.

No detailed leveling has been conducted

at this site, but leveling has been done in other lake basins in northwestern Sudan, i.e., in Selima Oasis and El Atrun where *Nitellopsis obtusa* has also been found (Pachur *et al.*, 1987; Soulié-Märsche, in press). At these paleolakes, early Holocene water depths of 12 and 14 m, have been deduced from leveling of contemporary beach and lake-bottom deposits in the center of the paleolake basins where the gyrogonites of *Nitellopsis obtusa* were found (Pachur and Kröpelin, 1987, 1989).

BIOGEOGRAPHICAL DISTRIBUTION

The first fossil representative of *Nitellopsis* in Africa has been described from early Quaternary deposits from Louga, Senegal (Soulié-Märsche, 1982). There are no other Pleistocene records so far. In early Holocene deposits, however, in addition to the occurrences mentioned above, *Nitellopsis obtusa* has been observed in the western Sahara in the paleolakes of Mauritania (Monteillet, 1988), at Taoudenni, Mali (Soulié-Märsche, 1988) and at Tin Ouffadenne, Niger (Dubar, 1988; Soulié-Märsche, in press). Its modern biogeographical distribution, according to Corillion (1957a), is limited to Europe and some isolated localities in India, such as the Kashmir lakes at 1500 m altitude. Kasaki (1962) has supplemented stations in central Asia, Burma, China, and Japan.

The genus *Nitellopsis* as a whole is unknown within the modern flora of the African continent. Nevertheless, because abundant populations of *Nitellopsis obtusa* were developing in the Sahara earlier during the Holocene, it seems likely that this species still exists somewhere farther south, for example in the deep lakes of Kenya or Tanzania. The study of fossils can thus provide impetus for botanical research because the Charophyte flora of these regions has not been sufficiently explored and surviving *Nitellopsis obtusa* may not have been noticed.

The introduction of the species was most probably due to migratory water birds, whose role as a dispersal factor for oogonia is well known for the Charophytes in general (Proctor, 1962) and for *Nitellopsis obtusa* in particular, as evidenced by gyrogonites taken from the stomachs of ducks in the northern U.S.S.R. (Krassavina, 1971).

The presence of *Nitellopsis obtusa*, a species considered by certain authors as a circumboreal species (Corillion, 1957b), may be indirect proof of the former existence of the major migration routes of aquatic birds. The one axis connecting western Europe and western Africa with the Pliocene–Quaternary outcrops bearing *Nitellopsis megarensis* in Senegal may be a very old route, while the other axis between central Europe and eastern Africa via the respective outcrops in northwestern Sudan may have been functional during the early and middle Holocene.

CONCLUSION

Charophyte remains are frequent in most of the Holocene lacustrine sediments of the eastern Sahara (Gabriel, 1986; Kröpelin, unpublished data; Pachur *et al.*, 1990). While most of these Charophytes belong to cosmopolitan floras with a wide ecological range, ecologically sensitive species such as *Nitellopsis obtusa*, whose precise ecological requirements are known from living examples, are valuable environmental indicators. Their occurrence in the southeastern Sahara indirectly supports the existence of an early to mid-Holocene humid phase correlated to global climatic phenomena between about 9500 and 3500 yr B.P. (Gabriel and Kröpelin, 1984; Haynes *et al.*, 1989; Haynes and Mead, 1987; Neumann, 1989; Pachur *et al.*, 1990; Pachur and Kröpelin, 1987; Ritchie *et al.*, 1985).

In the case of Wadi Howar, the fossil *Nitellopsis* remains indicate an *in situ* vegetation in permanent cool oligotrophic freshwater with depths of about 4 to 11 m. Gyrogonite populations reflect characteristics of the aquatic environment at the very moment and place where the plants grew. As autochthonous indicators, they yield direct and precise information on freshwater conditions, water depth, and temperature.

Certain Charophyte remains have a distinct role as lacustrine biomarkers. Their analysis represents a new and promising approach to multidisciplinary paleoecological investigations and should aid in developing an increasingly complete reconstruction of Quaternary lake environments in present-day desert regions.

ACKNOWLEDGMENTS

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