Biogeography of living and fossil Nitellopsis (Charophyta) in relationship to new finds from Morocco

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Abstract

Aim To document the distribution of two closely related macrophyte species, the fossil Nitellopsis (Tectochara) merianii (A. Braun ex Unger) Grambast & Soulié-Märsche and Nitellopsis obtusa (Desvaux) J. Groves, the single living species of genus Nitellopsis and to draw the relationships between first finds of N. merianii in North Africa and previously known records.

Location South part of the High Atlas Range, Aït Kandoula basin, Morocco.

Methods New finds of fossil charophyte gyrogonites were determined and illustrated. Using a large bibliographic database of both fossil and extant charophytes, we depict the biogeographical distribution N. merianii and N. obtusa and summarize the ecological requirements of N. obtusa as a modern analogue.

Results The Aït Kandoula deposits, dated by magnetostratigraphy and vertebrate fossils to Upper Miocene, provided the first fossil populations of N. merianii in Africa. The distribution patterns of the Tertiary N. merianii and the living N. obtusa superimpose on a large area that extends from Spain to East Asia and characterize them as typically Eurasian taxa indicative for permanent, relatively cold and deep freshwater lakes. During the Quaternary, similar palaeolakes in the Sahara were colonized by N. obtusa.

Main conclusions The presence of the Eurasian species N. merianii in North Africa is the result of dispersal by migratory waterbirds and attests to N–S migration occurring during the Upper Miocene (10–5 Myr ago). Gyrogonites imported from Southern Europe could germinate and fulfil their life cycle so as to form a new seed bank of gyrogonites because they had been deposited in a suitable environment consisting of a freshwater mountain lake.

Keywords
Historical biogeography, palaeolimnology, Tertiary, Messinian, charophytes, Aït Kandoula basin, Africa, Eurasia.

INTRODUCTION

The charophytes are a particular group of rooted water plants forming large stands of submerged vegetation in all kinds of continental waters. They fossilize mainly by the means of gyrogonites that is the typically spiralled and calccified female fructifications (Tappan, 1980). Similar to seeds of land plants, the gyrogonites are generally produced in great number to ensure the dissemination and annual offspring. The fossil record of the Charophyta, based on the gyrogonites, goes back to the Upper Silurian, c. 420 Myr ago. Because of their specific morphology, the gyrogonites have long been used for stratigraphical purposes (Grambast, 1968; Riveline et al., 1996) and become more and more considered as a tool for palaeoecological reconstructions (Soulié-Märsche, 1991a, 2002; Garcia, 1994). To this

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regard, the living ecotype species *Nitellopsis obtusa* (Desv.) J. Groves represents a significant biomarker in palaeolimnology (Kroppelin and Soulé-Marsche, 1991).

*Nitellopsis obtusa*, whose stratigraphical account runs from the Early Quaternary to Recent, is the unique ‘survivor’ of an evolutionary lineage that started at the Cretaceous–Tertiary boundary (Soulé-Marsche, 1979). The fossil species *N. (Tectochara) merianii* (Al. Braun ex Unger, 1850) Grambast and Soulé-Marsche, originally described as *Chara merianii*, was a long-lived species whose stratigraphical record extends over more than 30 Myr, from the Lower Oligocene to the Lower Pliocene. Totalling records from more than 500 sites, it was the most frequent Charophyte species over the Neogene in Eurasia. Labelled as *Tectochara meriani*, the taxon was quoted in a short list of fossils collected in the same area as our study (Görler & Zucht, 1986).

The present paper reports on new populations of *N. merianii* from the Upper Miocene which were recovered during research for vertebrate remains in the Aït Kandoula basin, southern Morocco and gives a comparative synthesis of the distribution of *N. merianii* and *N. obtusa* in order to depict the biogeographical domain of these taxa.

**GEOLOGICAL SETTING AND AGE OF THE FLORA**

The Aït Kandoula basin is located north-east of Ouarzazate in the High Atlas Mountain Range, at an altitude of 1700–2000 m a.s.l. The NE–SW striking basin is 50 km long and c. 6 km wide (Fig. 1).

The geological structure of the basin was determined by tectonic movements which brought a thick series of Jurassic limestones and dolomite to overlay the much more larger Ouarzazate basin filled with Tertiary sediments (El Harfi et al., 1996). The Aït Kandoula basin was then mostly filled with coarse clastic sediments, but also displayed a series of palaeolakes which provided the fossiliferous localities. Charophyte gyrogonites, were found in four of seven sections studied for micromammal remains. Detailed description of the sections, lithology and location of the fossiliferous levels were provided by Benammi et al. (1995) and Benammi (2001).

The stratigraphical distribution of *N. merianii* encompassing a timespan of c. 30 Myr, from the Oligocene (Grambast & Paul, 1965) to the Pliocene (Papp, 1951), the biochronological significance of the species is rather low. The age of the new finds was determined by the geological arguments summarized below.

According to magnetostratigraphic and $^{40}$Ar/$^{39}$Ar dating, the lacustrine deposits in the Aït Kandoula basin span from 10.9 Myr at Oued Tabia in the western part to younger than 5.9 ± 0.5 Myr in the centre of the basin. This age was obtained from volcanic ash layers from the Afoud section (Benammi et al., 1996). The charophyte-bearing levels were sampled from outcrops located between 30 and 120 m below the volcanic ash layer. According to the Neogene mammal biochronozones, they range from MN 9, lower Tortonian to MN 13 Messinian (Benammi et al., 1996).

**RESULTS**

From the description presented in appendix 1, it appears that the gyrogonites of the fossil *N. merianii* (Fig. 2) are extremely similar to those produced by the living *N. obtusa* except for two points. The main distinctive feature makes use of the basal pole morphology (BPM) which is currently used to distinguish evolutionary stages of *Nitellopsis* (Soulé-Marsche, 1975). The BPM was quantified here for population Azaghar (Upper Miocene) and Altenheim (Extant) (Fig. 3).

The gyrogonites of *N. merianii* show a major proportion of specimens with a basal funnel; 74% in population Azaghar, which can be subdivided into specimens with a
star-like funnel (BPM 1) and those showing a simple but relatively deep and large funnel (BPM 2) illustrated in Fig. 2d. Only 16% of the specimens have no funnel at all, 8% show an intermediate type with a shallow depression. In contrast, the *N. obtusa* populations always show a clear majority of specimens without a basal funnel i.e. 77% in the sample from Altenheim. The star-like type of BPM reduced to 1%. The basal funnel being the cast of the nodal cell through which the gyrogonite was attached to the plant, the reduction of the funnel can be tentatively explained by a downward migration of the nodal cell outside the space surrounded by the spiral cells.

A second difference, concerning the values of the spiral index, can be detected only on a statistical basis. The spiral index (Cs) proved meaningful to sort fossil *Nitellopsis* populations according to their age. *Nitellopsis merianii* has a Cs of 7.5–8 (Soulié-Marsche et al., 1997) whereas low average values of 6 ± 0.5 were only found in *N. obtusa* (Soulié-Marsche, 1989; Kröpelin & Soulié-Marsche, 1991).

The close similarity of the gyrogonites of *N. merianii* and *N. obtusa* underlines the continuity of the evolutionary
lineage from the Tertiary representatives of the genus to the single modern ‘survivor’, *N. obtusa*.

From the palaeobiogeographical point of view, *N. merianii* appears as a strictly Eurasian taxon. The species was widely distributed from Spain and the west coast of France over the Paratethys realm to NE China and SE Asia where it spans from latitude 18° N to 50° N. It has never been found neither in the Americas nor the southern hemisphere (Figs. 4a and 5a).

The distribution dots represent a synthesis of the records from each region, based on the references listed in the synonymy of Soulée-Marsche *et al.* (1997) and the present paper. Many of the dots point to a great number of individual localities. For instance, according to Berger (1997), not less than 500 different localities with *Nitellopsis* gr. *merianii* were mentioned for Switzerland. Occurrences in France total up to one hundred local finds, mainly in the south of the country. The first find of the species in Africa is recorded here with four one hundred local finds, mainly in the south of the country, mentioned for Switzerland. Occurrences in France total up to 100 localities. For instance, according to Berger (1997), not less than 500 different localities with *Nitellopsis* gr. *merianii* were mentioned for Switzerland. Occurrences in France total up to one hundred local finds, mainly in the south of the country. The first find of the species in Africa is recorded here with four different sites in the Aït Kandoula basin.

The fossil populations of *N. obtusa* show a quite similar distribution over Eurasia but extend a little farther north in Europe and Central Asia. The species was identified from interglacial sediments in UK and North Germany. Fossil *N. obtusa* shows significant occurrences in the Sahara, below the tropic of Cancer (Fig. 4b), although it has never been found living in Africa (Soulée-Marsche, 1991b).

Extant *N. obtusa* is present from the west coast of Europe to Japan (Fig. 4c). The distribution map summarizes records up to today using a database of references as well as previously published syntheses (Corillion, 1957; Krause, 1997) or distribution maps for individual countries (Comperé, 1992 for Belgium; Stewart & Church, 1992 for Great Britain; Nat *et al.*, 1994 for the Netherlands; Ling *et al.*, 2000 for China). Compared with *N. merianii*, the distribution of *N. obtusa*, growing up to a latitude of 65° in southern Finland, appears to have shifted to the north for about 15° (Fig. 5b). A possible explanation is proposed in the discussion below.

Two occurrences have been recorded from the Great Lakes region, North America. They occur in male plants only. This ‘intriguing pattern’ (Mann *et al.*, 1999) raises the suspicion that they originate from recent accidental introduction by man (V.W. Proctor, pers. comm.).

**DISCUSSION**

The comparative analysis of the two principal species of genus *Nitellopsis* shows strong concordance of both the morphological traits and the biogeographical distribution of *N. merianii* and *N. obtusa* suggesting they form successive chronological terms of one evolutionary species. Until the morphological link from the former fossil and artificial organ-genus *Tectochara* to *Nitellopsis* had been demonstrated (Krassavina, 1971), the living *N. obtusa* was long considered the ‘survivor’ of an unknown Tertiary species.

*Nitellopsis obtusa* is widely distributed in Europe and Asia. Because of its preference for cold water, it was classified as a ‘boreal’ species (Corillion, 1957). The largest surface cover exist in northern Europe (Scandinavia, Poland and Russia) where *N. obtusa* forms dense stands in so-called Chara-lakes. However, these plants do not form calcified gyrogonites and thus leave no fossil record. Vegetative reproduction is dominant in these lakes and takes place by means of specific bulbils which have never been found as fossils.

and transparency of the water play a major role for sexual reproduction of the Characeae in general. The palaeogeographical context of the saharian fossil localities was indeed linked to deep natural dam lakes permanently filled with groundwater. Subsequently, *N. obtusa* has not been found in North Africa in deposits younger than 4500 yr BP.

In their quality of autochthonous fossils, the gyrogonites witness to the presence of former submerged vegetation and indicate the hydrological parameters at the very place where the plants grew. The palaeolimnological characteristics of the lakes where *N. merianii* thrived can be tentatively inferred through comparison with the ecological requirements of *N. obtusa*, the single living representative of the genus. Optimal growth of the modern *Nitellopsis* occurs in permanent cold oligotrophic freshwater lakes at a depth range of 4–11 m (Krause, 1985). A palaeoenvironment close to these optimal conditions is suggested for the fossil populations from the sections studied here.

At the time of deposition, the High Atlas being already formed, the palaeoaltitude of the Aıt Kandoula basin can be estimated to about 1500–1700 m. This context compares well to some mountain lake occurrences of the modern *N. obtusa* in the Himalayan Range (Pal et al., 1962) and in Japan (Kasaki, 1962) both located at more than 1500 m a.s.l. Fossil *Nitellopsis* of Late Pliocene age were also recorded from palaeolakes in the Kashmir valley (Bhatia et al., 1998).

Through comparison with the ecology of *N. obtusa* as a modern analogue, the palaeoenvironment of the fossil charophytes studied here corresponded to a mountain lake with permanent, cold, relatively deep alcaline water.

The findings of *N. merianii* reported in the present paper can be related to dispersal by migratory water birds. Indeed, many kinds of water birds feed on Charophytes and proved to release viable oospores and gyrogonites after digestion (Proctor, 1962). Analyses of the stomachs of waterfowl from Laguna de Gallocanta, a renowned stop over of migratory birds revealed up to 95% of charophyte material (Guiral & Pellegrin, 1981). Particular species like the red crested pochard, *Netta rufina*, was found to be a specific Characeae consumer in the Netherlands (Van den Berg & Coops, 1999).

The start-ups of the African populations are likely to have been gyrogonites originating from European habitats which were imported by migratory water birds and developed because they found suitable ecological conditions in the Aıt Kandoula palaeolakes. Similar to the conclusions from the micromammal studies, the Charophytes indicate trans-mediterranean exchange occurring already between 10 and 5 Myr ago, during the Late Miocene.

**REFERENCES**


**BIOSKETCHES**

**Ingeborg Soulie-Marsche** is a researcher at the French National Research Centre (CNRS) and is currently the President-elect of the International Research Group on Charophytes. Her research focuses on the interface botany/palaeobotany and ecology/palaeoecology. She has developed the use of Charophytes as lacustrine biomarkers and contributes to multidisciplinary studies of palaeolakes, mainly in the Mediterranean realm.

**Mouloud Benammi** has recently finished his PhD at the Institute for Evolutionary Sciences at University Montpellier II with focus on biogeography and phylogeny of fossil vertebrates in Morocco. He has started a post-doctoral position as a vertebrate palaeontologist and palaeomagnetist at the University of Mexico.

**Pierrette Gemayel** is interested in statistical analysis of the charophyte gyrogonites and is working on a database of the fossil species world-wide. She is also concerned with genetic aspects of charophyte populations.
Appendix 1 Systematic Palaeontology of the key taxa

Order Charales Lindley 1836
Family Characeae L. Cl. Richard 1815
Genus Nitellopsis Hy 1889

The gyrogonites of genus Nitellopsis differ from all other gyrogonites of the Characeae by their apical morphology. They display a characteristic peripheral apical groove and prominent apical nodes. Because of this apex, they had long been classified as genus ‘Tectochara’ L. & N. Grambast (1954). Krassavina (1971) has demonstrated that this precise type of apex is also present in the gyrogonites of the living Nitellopsis and thus all former Tectochara species were transferred into the genus Nitellopsis (Grambast & Soulié-Marsche, 1972).

The characteristics of the basal region of the gyrogonites shows a wide range of variation which gave rise to the distinction of subgenera. Populations with a marked basal funnel were distinguished as subgenus Tectochara with N. (T.) merianii as the type of the subgenus. Subgenus Nitellopsis, with N. (N.) obtusa as the type-species, was defined by the absence of a basal funnel or the presence of only a shallow basal depression (Grambast & Soulié-Marsche, 1972). Further analyses depicted progressive chronological changes from the Tectochara-type to the Nitellopsis-type with a major shift at the Tertiary–Quaternary boundary (Soulié-Marsche, 1975, 1982; Bhatia et al., 1998).

For comparison, the gyrogonites from the Tertiary Aït Kandoula population and the gyrogonites of N. obtusa, collected in a modern lake are described below.

Subgenus Tectochara Grambast & Soulié-Marsche (1972) Nitellopsis (Tectochara) merianii (Al. Braun ex Unger) Grambast & Soulié-Marsche (1972) (Fig. 2a–d).

The complete synonymy of N. merianii was listed in an earlier paper where the species was described from Thailand (Soulié-Marsche et al., 1997). Here we update the synonymy with complementary records to that list including citations of N. globula which has been transferred to N. merianii as forma globula.

<table>
<thead>
<tr>
<th>Year</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>Nitellopsis (Tectochara) meriani forma globula (Mädler) nov. comb., Soulié-Marsche et al. (1997), Figs 6 and 7.</td>
</tr>
<tr>
<td>1997</td>
<td>Nitellopsis (Tectochara) meriani (Braun ex Unger) Grambast and Soulié-Marsche, Schwarz (1997), p. 30, Pl. 6, Figs 7 and 8.</td>
</tr>
<tr>
<td>1997</td>
<td>Nitellopsis (Tectochara) globula (Mädler) Grambast and Soulié-Marsche, Schwarz (1997), p. 31, Pl. 6, Figs 10 and 11.</td>
</tr>
<tr>
<td>1999</td>
<td>Nitellopsis (Tectochara) meriani L. &amp; N. Grambast, Baciu &amp; Feist (1999), p. 28</td>
</tr>
<tr>
<td>1999</td>
<td>Nitellopsis (Tectochara) merianii forma globula (Mädler), Baciu &amp; Feist (1999), p. 28.</td>
</tr>
</tbody>
</table>

Present material: 150 gyrogonites from the Aït Kandoula basin distributed as follows: Seventy from the Azaghar, thirty from the Afoud, thirty from Oued Tabia and ten poorly preserved specimens from the Wanou section. The measurements of the Azaghar population are given as histograms (Fig. 6).

Table 1 Nitellopsis merianii, biometrical data of the fossil gyrogonites from the Azaghar section (Aït Kandoula basin, Morocco)

<table>
<thead>
<tr>
<th>Length (µm)</th>
<th>Width (µm)</th>
<th>ISI</th>
</tr>
</thead>
<tbody>
<tr>
<td>70</td>
<td>70</td>
<td>70</td>
</tr>
<tr>
<td>Mean</td>
<td>1075</td>
<td>929</td>
</tr>
<tr>
<td>Min.</td>
<td>930</td>
<td>776</td>
</tr>
<tr>
<td>Max.</td>
<td>1192</td>
<td>1062</td>
</tr>
<tr>
<td>Conf. int.</td>
<td>1060 &lt;= 1090</td>
<td>913 &lt;= 945</td>
</tr>
<tr>
<td>Variance</td>
<td>3751</td>
<td>4424</td>
</tr>
<tr>
<td>Var index</td>
<td>6%</td>
<td>7%</td>
</tr>
</tbody>
</table>

Description: Gyrogonites voluminous and large, varying from 900 to 1200 μm in length and from 750 to 1100 μm in width, length/width ratio (ISI) between 104 and 132 (mean 116) (Table 1). Shape ovoidal, inversely pear-shaped to subprolate, apex rounded or slightly flattened, basal pole rounded or truncate in lateral view. Lime spirals smooth, mostly flat to slightly convex, seven to ten convolutions visible in lateral view; spiral index (Cs), as calculated from the ratio of length of the gyrogonite vs. spiral width at the equator is 7.6. Tips of the lime spirals forming distinct prominent apical nodes or clustered to an apical rosette; basal morphology displaying typically a pentagonal basal funnel, c. 300 μm large, basal plug disk-shaped.

Subgenus Nitellopsis Grambast & Soulié-Marsche (1972) Nitellopsis (Nitellopsis) obtusa (Desvaux in Loiseleur) J. Groves (1919)

1966 Tectochara diluviana (Madler) Grambast, Maslov (1966), p. 51–57, text-figs 2, 3, 13, 14; Pl. VI, Figs 1–12.
1975 Tectochara diluviana (Madler) Horn af Rantzien, Notzold (1975), p. 51, Pl. 4, Figs 1–12; Pl. 5, Figs 1–6.

Non Tectochara diluviana (Madler) Grambast, Wang et al. (1982), p. 25, Pl. IX, Figs 9(a–c) and 10(a–c).
1991 Nitellopsis obtusa (Desvaux) Groves, Kröpelin & Soulié-Marsche (1991), p. 215, Fig. 5(a–f).
1996 Nitellopsis obtusa (Desvaux) Groves, Baciu et al. (1996), p. 90, Fig. 2.
1996 Nitellopsis obtusa (Desvaux) Groves, Zalat (1996), p. 509, Fig. 4 (1–9).

Present material: 130 gyrogonites from the gravel-pit lake Altenheim (South Germany) from where abundant vegetation of N. obtusa was described by Krause (1985).

Description: Gyrogonites voluminous and large, varying from 830 to 1350 μm in length and 625–1160 μm in width, length/width ratio (ISI) between 104 and 142 (mean 121) (Table 2). Shape mostly cylindrical or broadly cylindrical, apex flattened, basal pole rounded or truncate in lateral view. Lime spirals smooth, concave to slightly convex, six to nine convolutions visible in lateral view; spiral index (Cs), as calculated from the ratio of length of the gyrogonite vs. spiral width at the equator is 6.7. Tips of the lime spirals forming distinct prominent apical nodes, basal morphology mostly without any funnel, basal plug disk-shaped.

Table 2 Nitellopsis obtusa, biometrical data of the extant gyrogonites from lake Uhleloch Altenheim (South Germany)

<table>
<thead>
<tr>
<th></th>
<th>Length (μm)</th>
<th>Width (μm)</th>
<th>ISI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1082</td>
<td>896</td>
<td>121</td>
</tr>
<tr>
<td>Min.</td>
<td>830</td>
<td>625</td>
<td>104</td>
</tr>
<tr>
<td>Max.</td>
<td>1350</td>
<td>1156</td>
<td>142</td>
</tr>
<tr>
<td>Variance</td>
<td>11848</td>
<td>14789</td>
<td>61</td>
</tr>
<tr>
<td>Var index</td>
<td>10%</td>
<td>14%</td>
<td>6%</td>
</tr>
</tbody>
</table>

ISI, Isopolarity index = L/w × 100; n, number of measurements; Mean, mean value of the measured sample; Min., lowest value; Max., highest value; Conf. int = mean ± 2 SD = confidence interval at 95%; Var., variance σ²; Var, variation index as calculated from 100 × σ/mean.