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Ecological parameters and dispersal routes of *Lychnothamnus barbatus* (Characeae) in the Early-Middle Holocene from the Ganga plain, India

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Abstract — This paper focuses on the ecology of fossil and extant *Lychnothamnus barbatus* (Characeae), considering the previously described subspecies *megalicarpus* Soulié-Märsche *et* Martín-Closas to be only an ecological variant of the species, as indicated by the analyses of proxy evidence from Early-Middle Holocene records from the Ganga plain, India. It is argued that the large-sized gyrogonites, commonly considered as *L. barbatus* subsp. *megalicarpus*, are the result of several factors such as oligotrophic status of the water body, shelly clayey silty type of substratum, and deep water, of 6.0m or more. In shallow water, 2.0-3.0 m, mesotrophic basins, only the smaller gyrogonites (comparable to those of the type species from Europe), are developed. The fossil and extant records suggest that the species dispersed progressively towards east and southeast since its earliest Late Miocene record from Western Europe. The Pleistocene records from the Ganga plain, India, and the Gulf of Carpentaria, Australia support the contention of an Asian route of colonization for the Australian population.

***Lychnothamnus barbatus* / ecology / dispersal / Holocene / Ganga plain**

Résumé — Paramètres écologiques et routes de dispersion de *Lychnothamnus barbartus* de l'Holocène inférieur à moyen de la plaine de Ganga (Inde). Il est suggéré, d'après l'écologie de *Lychnothamnus barbatus* (Characeae), connue dans la nature actuelle et à l'état fossile, que la sous-espèce *megalicarpus* Soulié-Märsche *et* Martín-Closas en est un variant écologique, comme l'indiquent les représentants provenant de l'Holocène inférieur à moyen de la plaine de Ganga (Inde). La grande taille des gyrogonites caractérisant la sous-espèce *megalicarpus*, résulte de plusieurs facteurs, comme l'oligotrophie des eaux, le type argilo-limoneux et à coquilles du substrat et une grande profondeur d'eau, de 6m ou plus. Dans les eaux peu profondes, de 2 à 3 m, des bassins mésotrophiques, seules des gyrogonites de taille inférieure (comparables à celles de l'espèce-type, en Europe) se développent. Les registres fossile et actuel de *L. barbatus* suggèrent que l'espèce s'est dispersée progressivement vers l'Est et le Sud-Est à partir de sa plus ancienne localité en Europe occidentale. Les registres du Pléistocène de la plaine de Ganga, en Inde, et le Golfe de Carpentaria, en Australie, suggèrent que les populations de *L. barbatus* sont parvenus en Australie par une voie asiatique de colonisation.

***Lychnothamnus barbatus* / écologie / dispersion / Holocène / plaine de Ganga**

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INTRODUCTION

The rediscovery of *Lychnothamnus barbatus* (Meyen) Leonhardi in Australia in 1996 (Casanova *et al.*, 2003a) has led to a renewed interest in the study and conservation of this endangered taxon not only in Australia (Casanova *et al.*, 2003a, b; García *et al.*, 2000; García, 2003; García & Chivas, this volume) but also in other countries. Almost identical *rbc*L sequences have been identified in isolates from disjunct populations from Germany, Croatia and Australia by McCourt *et al.* (1999) and more recently in Taiwan (Wang & Chou, this volume).

Analyses of modern gyrogonites by Soulié-Märsche (1989) and García (2003) showed more prolate and usually weakly calcified gyrogonites, called herein *Lychnothamnus barbatus* type. Robust gyrogonites, have been recorded mainly in the fossil record, and considered as ecological variants (this paper) or subspecies by different authors. Such gyrogonites are known from the Late Miocene of Switzerland (Berger in Kalin *et al.*, 2001), Spain (Soulié-Märsche & Martin-Closas, 2003), Late Pliocene-Early Pleistocene of Jammu and Kashmir, India (Bhatia *et al.*, 1998, 2001), Holocene deposits of Mali, Central Africa (Soulié-Märsche in Petit-Maire & Reiser, 1981) and the present work. A comprehensive review of the world-wide distribution of fossil *Lychnothamnus* and ecological parameters of extant plants is given by Casanova *et al.* (2003a).

The present paper attempts to complete the work of Bhatia & Singh (1989) who recorded fossil gyrogonites of *L. barbatus* and *Lychnothamnus* sp., later assigned to the ecological variant *L. barbatus megalicarpus* Soulié-Märsche *et* Martin-Closas (2003) from the Holocene sediments of the Indo-Gangetic plain. The proxy evidence provided by the Holocene assemblage of *L. barbatus* from the Ganga plain, being the unusual geomorphic setting, the depositional domain (basin bathymetry and configuration), the nature of substrate, and chemistry of the water are discussed. It is argued that the ecological parameters present during the Holocene in the Ganga plain were essential to facilitate the optimal growth of *L. barbatus* (producing well calcified gyrogonites), and therefore, should be taken into consideration when devising conservation strategies to protect *L. barbatus*.

L. barbatus and its ecological variant *megalicarpus* occur together at one of the studied localities, albeit in varying abundance. This locality lies about 60 km SW of Gonda, from where Allen (1925) recorded extant *L. barbatus* for the first time in India. Later, extant populations from the Ganga plain were studied by Pal *et al.* (1962).

The occurrence of extant and 5 ka old fossil gyrogonites in close proximity in the Ganga plain provides a unique opportunity to verify the proxy evidence of palaeoecological parameters with those of the living representatives. Furthermore, the new Holocene localities in conjunction with the Pliocene-Late Pleistocene records from the Himalaya (Bhatia *et al.*, 1998, 2001) provide interesting clues to the possible dispersal routes of this taxon. We thus see that the Indian subcontinent provides a unique record of *L. barbatus* and its variant *megalicarpus* from Pliocene through Recent. This helps in filling the lacuna referred to by McCourt *et al.* (1999) between Asiatic and Australian localities.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Indo-Gangetic plain is an active Quaternary foreland basin, which separates the Himalaya in the north from Peninsular India in the south. The foreland basin comprises a thick pile of sediments brought by the three major rivers (and their tributaries), namely the Indus, the Ganga, and the Brahmputra. The Ganga plain (Fig. 1) shows a wide range of regional geomorphic surfaces in the central part (Singh & Ghosh, 1992; Singh, 1992, 1996). The geomorphic surfaces, the three terraces, are attributed to climatic changes during Late Pleistocene-Holocene, especially associated to hydrological budget (monsoon activity) and base-level changes due to rise in sea level and neotectonic activity. The oldest of these terraces, the T2 surfaces (Fig. 2), which form the upland interfluve region between the major river valleys were formed between 128-74 ka. The broad river valleys (T1) (formed between 35 ka and 20 ka) and the present-day valley terraces (T0) of Holocene age are all entrenched into the T2 surfaces. Singh (1992, 1996) provided a comprehensive account of the geological evolution of the Ganga plain.

A significant geomorphic feature of the upland T2 surfaces is the presence of a large number of linear lakes and ponds (locally called Tal). These water-bodies are of various dimensions and formed by the filling of abandoned or relict cut-off meanders of highly sinuous and incised inactive river systems (Fig. 2) between 8 ka and 5 ka, coinciding with the global humid phase. According to Singh *et al.* (1999) sedimentation in different depositional domains of the upland interfluve regions is not related to overbank deposits, but to local movement of sediment during monsoon rains. Further redistribution of sediment in various domains through time produced a characteristic mud-dominant stratigraphy. The sediments of the ponds are sandy clayey silts with sporadic molluscan shells, while the sediments of the larger lakes are 2 to 5 m thick clayey silts with high clay content (up to 3%) and a rich aggregate of gastropod shells (carbonates up to 80%), designated therefore as marls. According to Agarwal *et al.* (1992) some of these lakes were more extensive and up to 6 m deep in the Early-Middle

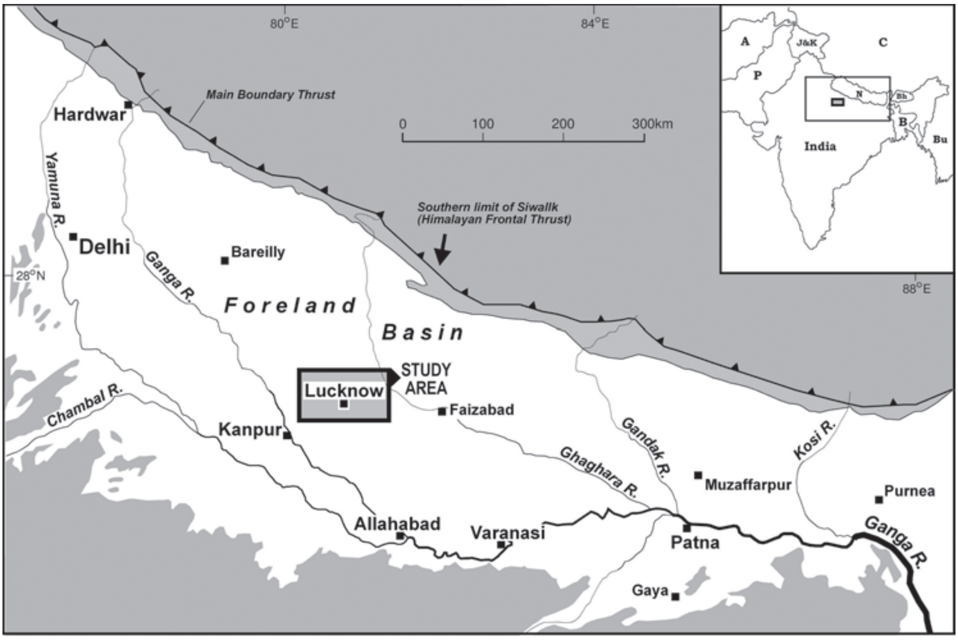


Fig. 1. Map showing the Ganga plain and the study area.

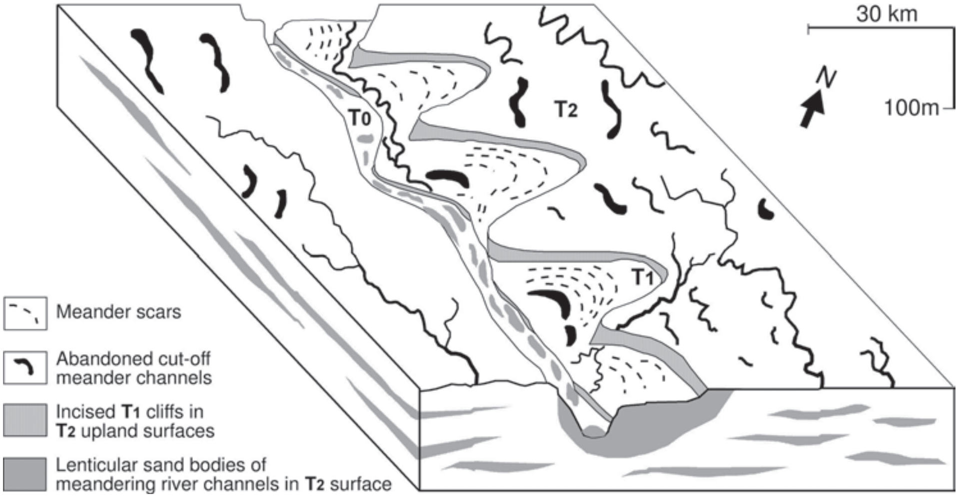


Fig. 2. Schematic diagram showing the geomorphic surfaces (terraces) T0, T1 and T2 with cut-off meanders, lacustrine basins and lenticular sand bodies in T2 surfaces.

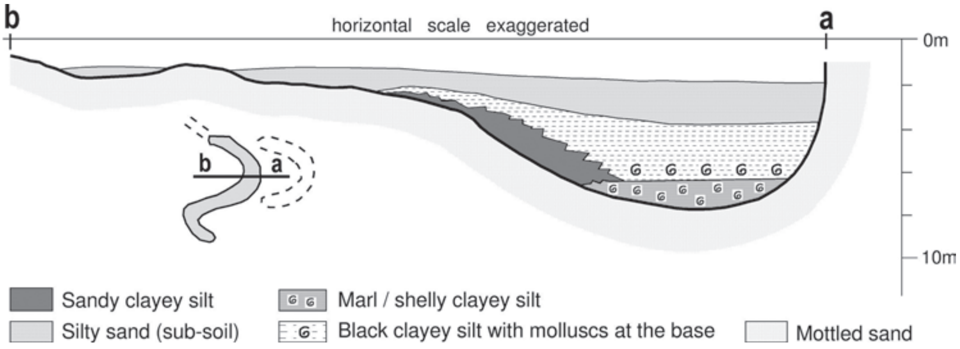


Fig. 3. Diagrammatic cross-section across a cut-off meander showing generalized stratigraphy.

Holocene. The shell-rich marls were deposited in the deeper concave side of the cut-off meanders. Besides gastropods, the marls are also rich in ostracods, charophyte gyrogonites, fish remains and palynomorphs.

Fig. 3 shows the general subsurface stratigraphy of the lacustrine sediments in the vicinity of Lucknow based on the works of Agarwal *et al.* (1992), Singh *et al.* (1999), Srivastava *et al.* (2003a), Sharma *et al.* (2004) and the present work. The charophytes studied in this paper were recovered from lacustrine sediments from 3 localities (Fig. 4), and the detailed lithological logs (Fig. 5), and the terminology used to describe the facies follows Singh *et al.* (1999) and Sharma *et al.* (2004). Radiocarbon dating of molluscan shells from the marl beds shows that the lacustrine Holocene sediments in several sections in the vicinity of Lucknow were deposited between 8 and 3 ka (Agarwal *et al.*, 1992; Singh, 1996). However, a Late Pleistocene age is indicated by luminescence dating of upland interfluve sediments between the Ganga and the Yamuna and marginal upland surfaces south of Yamuna (Singh *et al.*, 1999; Mathur, 2001; Srivastava *et al.*, 2003a, b).

MATERIALS AND METHODS

The charophyte gyrogonite-bearing marls are available from four localities in the vicinity of Lucknow in Uttar Pradesh (A-D, Fig. 4). Since fossiliferous marls occur in the subsurface at depths of 2 to 2.5 m, the samples were collected from natural gullies and pits excavated during peak summer season when the lake level was low. Composite lithological profiles were prepared only at localities A and B where detailed sampling was undertaken (Fig. 5), because from localities C and D only grab samples were collected from gully sections. Locality D has been studied by Sharma *et al.* (2004), and is used as a reference in this study (Fig. 5).

Representative samples, weighing approximately 1-2 kg were collected at 15-20 cm intervals from the lacustrine beds. Standard maceration techniques were used for separating charophyte gyrogonites and ostracods from the clayey matrix, and also for preparing samples for Scanning Electron Microscope (SEM) photography.

RESULTS

Charophyte flora

The gyrogonites of three taxa occur in the material studied from localities A-D: *Lychnothamnus barbatus* (Meyen) Leonhardi (Figs 8, 9), *L. barbatus* (= subsp. *megalicarpus* Soulié-Märsche and Martin-Closas) (Figs 10-13), *Chara rantzieni* (Tewari and Sharma) (Bhatia) (= *C. pappii* Soulié-Märsche *et auctorum*) (Fig. 14) and *C. aspera* Deth. ex Wildenow (Fig. 15). The biometric details and relative abundance of these taxa are given in Table 1 and the gyrogonites are illustrated in Figs 8-15.

Molluscs and ostracods

The samples have also yielded the following species of gastropods, identified only at genus level: *Viviparus* sp., *Gyraulus* sp., *Indoplanorbis* sp., *Succinea* sp., *Lymnea* sp., and *Melanoides* sp. The ostracod fauna includes *Strandesia weberi* (Moniez) Keyser *et* Bhatia (1989) (= *S. spinifera* Hartmann *et auctorum*), *S. indica* (Hartmann), *Candona* (*Fabaeformiscandona*) *fabaeformis* (Fischer), *Parastenocypris? subterranea* Hartmann, *Cypris subglobosa* Sowerby, *Cypridopsis vidua* (Müller), *Candonopsis kingsleii* (Brady *et* Robertson), *Darwinula stevensoni* (Brady *et* Robertson) and *Oncocypris* sp. This assemblage is similar to that recorded earlier from nearby Misa Tal (lake) by Bhatia (1983) (Fig. 4).

PALEOECOLOGY OF *LYCHNOTHAMNUS BARBATUS*

The lacustrine sediments comprising the shelly clayey silts (marls) at the base and the overlying black clayey silts (present work, Figs 3, 5; Sharma *et al.* (2004), Fig. 4: zones IIIb, IV) represent two distinct phases in the ontogeny of the Holocene lakes in the Ganga plain. Figure 3 shows the initial features of the

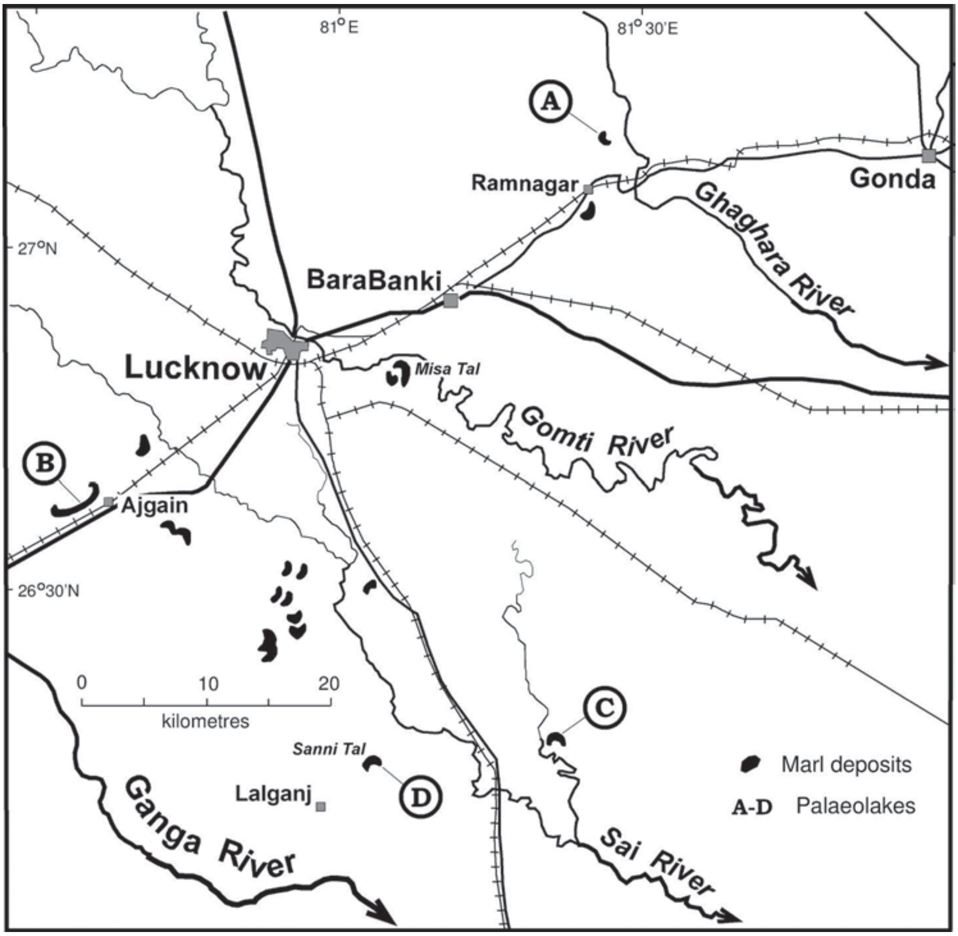


Fig. 4. Map of the vicinity of Lucknow showing the four fossil localities and other marl deposits. The locality of Gonda, vis-à-vis Lucknow, wherefrom Allen (1925) first recorded extant *Lychnothamnus barbatus* from the Ganga plain, is also included.

lacustrine basins with the deposition of mud dominated calcareous sediments in the deeper concave side of the cut-off meanders, which change to sandy silt sediments on the shallower convex side. The type of sediment had an important bearing on the initial invasion and colonization of the lakes by the aquatic macrophytes, gastropods and ostracods. The richness of these sediments in carbonates provided an ideal substrate for the colonization and eventual dominance of charophytes, which generally are the dominant submersed aquatic macrophyte in alkaline oligotrophic lakes with low nutrient concentration (Wetzel, 1973, 2001; Blindow, 1992). Gyrogonites belonging to the charophyte taxa *Lychnothamnus barbatus* and its ecological variant *megalicarpus, Chara aspera* and *C. rantzieni (= C. pappii*) occur in great abundance in the marl beds in all the four localities, particularly at Locality A (Table 1). Whilst *C. aspera* and *C. rantzieni* colonized the shallow littoral zones on sandy substrates, *L barbatus*, which is known to thrive best in muddy calcareous substrates (Blazencic &

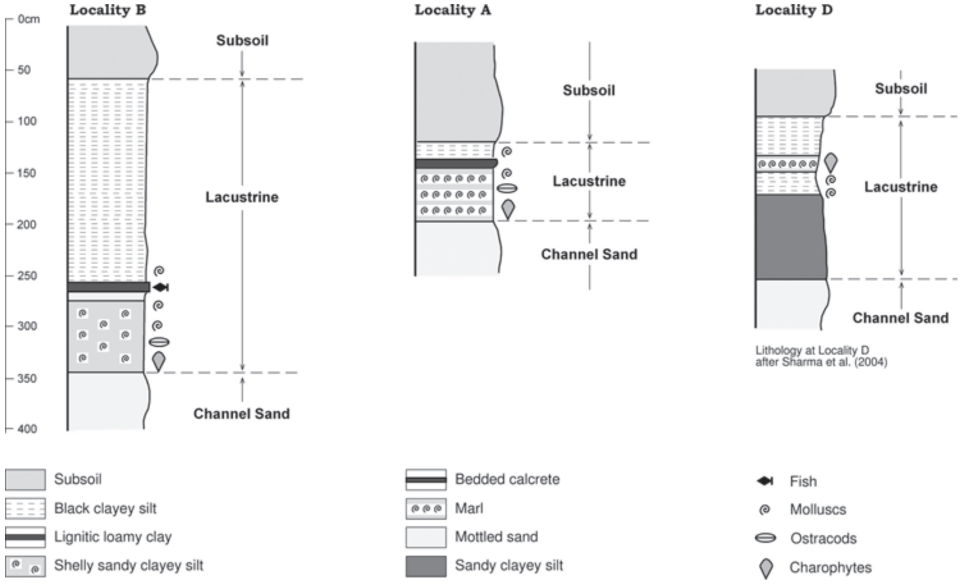


Fig. 5. Lithological profiles at localities A, B and D.

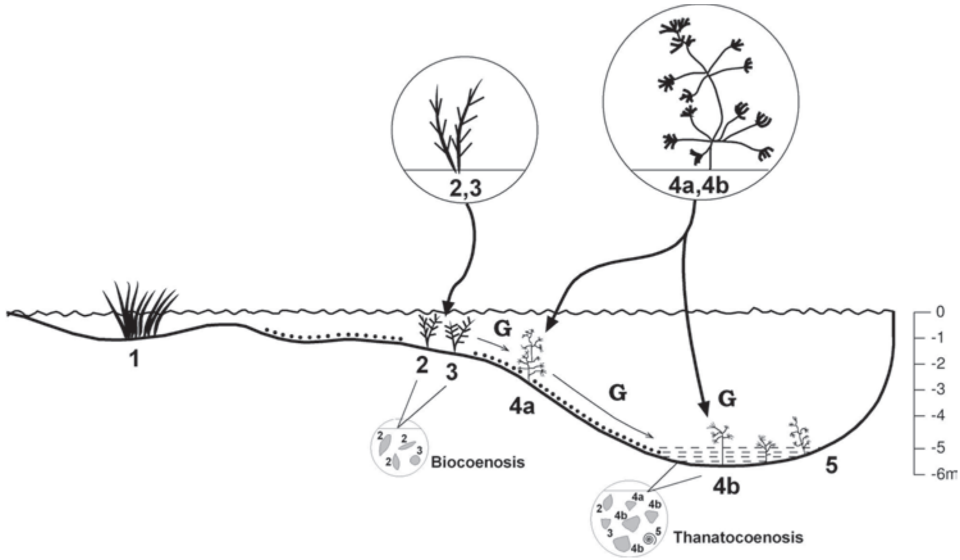


Fig. 6. Generalised cross-section of the meander (lacustrine basin) at locality A, showing the initial colonization of charophytes and emergent macrophytes, and fossilisation of gyrogonites of the various charophyte taxa as biocoenose and thanatocoenose in different parts of the basin.
1. *Typha* ; 2. *Chara aspera* ; 3. *C. rantzieni* ; 4a. *Lychnothamnus barbatus* (*s.s.*) ; 4b. *L. barbatus* (*megalicarpus* type) ; 5. Mollusc ; G. Gyronite.

Blazencic, 1983), became the dominant taxon in the deeper parts of the lakes on muddy substrates (Fig. 6). Besides charophytes, this initial phase is also characterized by the dominance of allochthonous terrestrial flora and

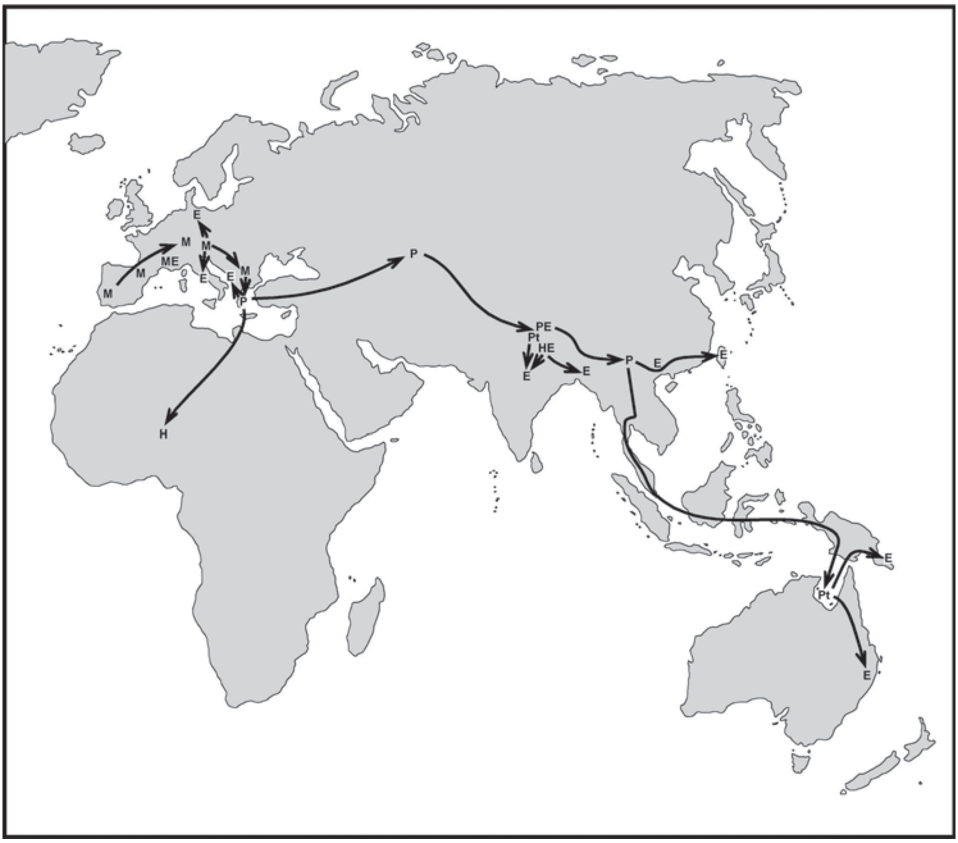
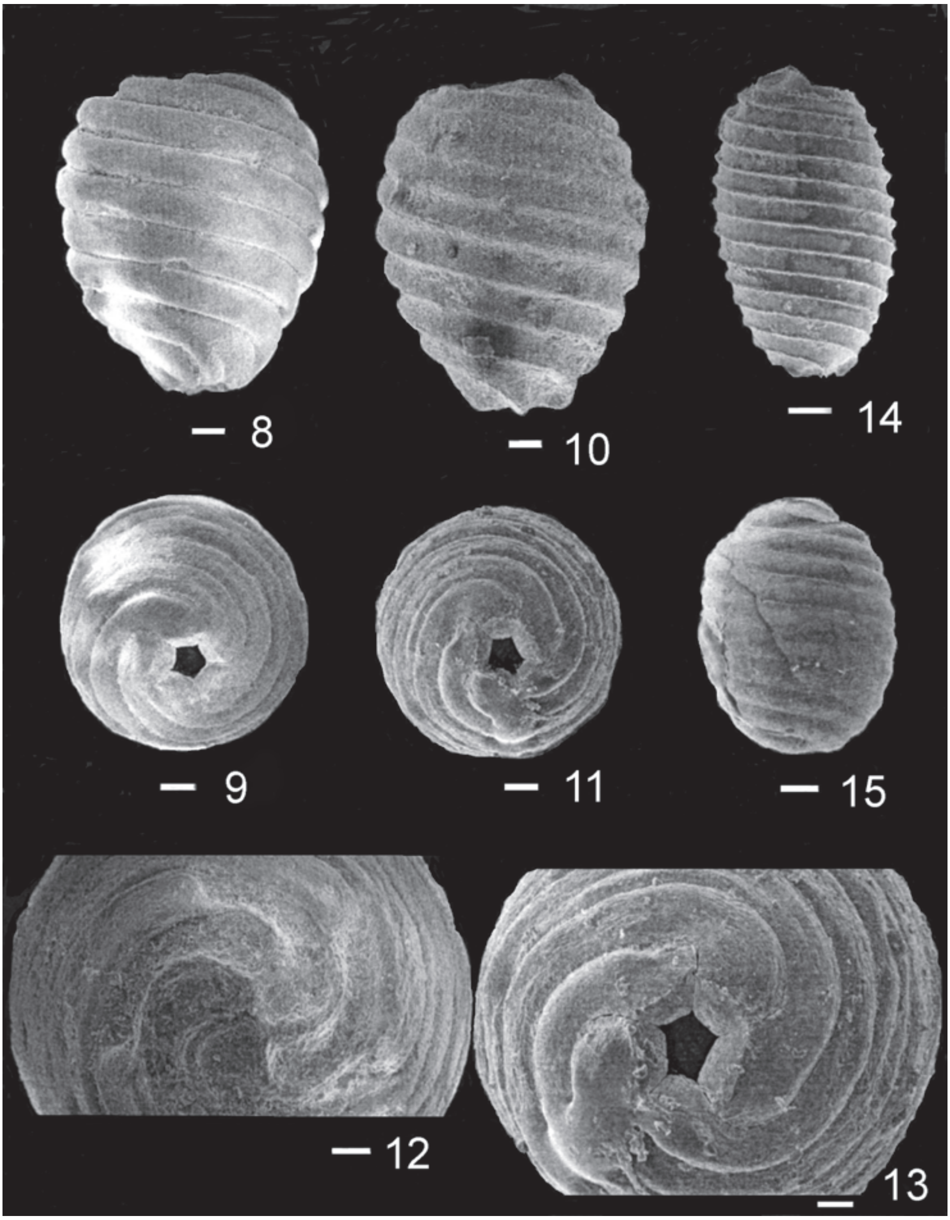


Fig. 7. World map showing the possible dispersal routes of *Lychnothamnus barbatus* from its earliest record in the Late Miocene from western Europe through the Himalaya, Ganga plain to Queensland, Australia: M = Miocene occurrences; P = Pliocene occurrences; Pt = Pleistocene occurrences; H = Holocene occurrences; E = Extant occurrences.

autochthonous emergent and floating-leaved aquatic macrophytes like *Typha, Potamogeton* and *Myriophyllum* as evident from the pollen diagram from Locality D (Sharma *et al.*, 2004). According to these authors, this particular phase in the ontogeny of Holocene lakes coincided with the global climatic optima (~10-5.8 ka ^{14}C) and the sensitive response of the lake ecosystem to increased rainfall and expansion of lakes.

The second phase of the ontogeny of shallow lakes is the progressive decrease in their depth, resulting in the deposition of black clayey silts and the complete absence or rarity of charophytes. This particular phase is dated between 5-2 ka ^{14}C from molluscan shells. The decrease in water during this drier phase is attributed to the negative balance between water loss/precipitation of monsoonal rains during summer months. Hot summer seasons, with median temperature of 32.5°C and evapo-transpiration about 2000 mm/yr, while monsoon rains are about 900 mm/yr, led to a negative water balance and the complete desiccation of the lakes during extreme summer seasons (Sharma *et al.*, 2004). Lower water level in the lakes encouraged productivity of emergent macrophytes and their advance towards the centre of the lakes decreasing the mean pH value and increasing



Figs 8-13. *Lychnothamnus barbatus.* **8.** Lateral view. **9.** Basal view. **10-13.** *L. barbatus (megalicarpus)*. **10.** Lateral view. **11.** Basal view. **12.** Apical view. **13.** Basal view. **14.** *Chara aspera*. Lateral view. **15.** *Chara rantzieni*. Lateral view. (Scale bars: 8-11, 14 & 15 = 100 µm; 12, 13 = 60 µm).

dominance of acidophilic flora, especially sedges and grasses (Wetzel, 2001), with the eventual formation of swamps and marshes. That the swamps had already started forming on the edges of the oligotrophic lakes is evident from the occurrence of lignitic loamy clay (Fig. 5, locality B). This view is corroborated by

Table 1. Biometric data and relative abundance of gyrogonites of the charophyte taxa from localities A-D. The lower part of the table shows the dimensions of the two ecological variants for comparison. n = number of gyrogonites; L = length; W = width; ISI = isopolarity index (mean); nc = number of convolutions; bpo = Basal pore opening.

Charophyte Taxa	*n/locality*				*L*	*W*	*ISI*	*nc*	*bpo*
	A	*B*	*C*	*D*	*µm*	*µm*	*(mean)*		*µm*
Lychnothamnus barbatus	20	10	5	10	700-833	550-600	130	10	70
L. barbatus megalicarpus	80	×	×	×	960-1030	760-830	125	10-11	80
Chara aspera	×	10	30	50	730-930	330-500	200	13-15	66
Chara rantzieni *(= C. pappii)*	15	5	×	×	630-700	460-560	130	8-11	60
Ecological variants of ***L. barbatus***									
L. barbatus antiquus					825-1080	730-960			
L. barbatus megalicarpus					875-1075	725-900	120		

the pollen diagram of zone locality D (Sharma *et al.*, 2004, pollen zone IV), which shows a shift in the aquatic vegetation, as indicated by the occurrence of palynomorphs belonging to floating-leaved macrophytes like *Potamogeton*, and of phytoplankton *Botryococcus* and diatoms. This ephemeral change in the ecosystem also resulted in the return of shallow, short statured charophytes like *Tolypella prolifera* (Zizermann ex A. Braun) Soulié-Märsche, now assigned to the genus *Sphaerochara* by Bhatia, 1999, p. 470). A few badly preserved gyrogonites of this taxon from this zone were identified by the author in slides sent to him by Prof. I.B. Singh.

ECOLOGICAL PARAMETERS OF *LYCHNOTHAMNUS BARBATUS*

The main objective of this work is to focus attention on the ecological parameters that are considered essential for the optimal growth and propagation of the endangered *Lychnothamnus barbatus*. An excellent summary of the ecological information pertaining to the extant records of *L. barbatus* from different parts of the world is given by Casanova *et al.* (2003a, Table 2). Of the various parameters listed by these authors, the following appear to be significant, and the presence of one or a combination of more than one may be critical for the growth and survival of the taxon:
1. Freshwater oligotrophic permanent lakes with fluctuations in lake level; 2. Temperate or tropical conditions, high altitude lakes like Dal Lake (1500 m a.s.l.) in Kashmir, India. Moraine or karstic lakes as in Europe; 3. Bathymetry from 0.5m to 12 m-optimum depth range being 2 m to 6 m; 4. Alkaline lakes--pH 6.5-8.6; 5. Common in calcareous muddy substrate; rare in coarse and sandy substrate; 6. Ephemeral streams and creeks as in Australia (after flooding small ponds remain with water for a long period), subject to water level fluctuation and as specific germination requirement from seed banks of at least two periods of drought and flooding; 7. Conductivity of water, as in Warrill Creek (410 $\mu S.cm^{-1}$) and in Wallace Creek (1430 $\mu S.cm^{-1}$) (data from Casanova *et al.*, 2003a); 8. Influence of co-occurring emergent macrophytes and their relative abundance vis-à-vis charophytes.

Specific ecological requirements for optimal growth

Charophytes, in general, prefer to grow in muddy substrates as noted by several workers in the case of many extant occurrences from Croatia and other parts of Europe (Blazencic & Blazencic, 1983). The record from the Dal Lake in Srinagar, Kashmir with a maximum depth of 6m is also from substrate of dark brownish coloured mud with abundant decaying vegetation.

It is interesting to note that ecological variants of fossil *Lychnothamnus barbatus* which have been given the taxonomic status of variety or subspecies, e.g. *L. barbatus* var. *antiquus* from France (Soulié-Märsche, 1989) and Portugal (Antunes *et al.*, 1992) and of *L. barbatus* subsp. *megalicarpus* from the Late Miocene of La Cerdanya, Spain and Holocene of Mali, Central Africa (Soulié-Märsche & Martín-Closas, 2003) are all based on the large size of gyrogonites (compared to the size of modern ones). The morphological differences are attributed to ecological factors. In the case of *L. megalicarpus*, it was suggested (p. 162) that "The subspecies may be related to longer periods of reproduction as compared to extant populations." Insofar as the substrate of these large-sized fossil gyrogonites are concerned, those of *L. antiquus* from Portugal came from lignitic clays with abundant gastropods, ostracods and microvertebrates, while those of *L. megalicarpus* came from grey clays and silts with abundant gastropods.

Similarly, the Plio-Pleistocene records of *L. barbatus* from the Karewa Group, Hirpur Formation, Methawoin Member (Samples F14, K12 and K13) from Kashmir (Bhatia *et al.*, 1998) which also comes within the size-range of gyrogonites of *L. antiquus* and *L. megalicarpus* came from compact bluish gray mudstones. The depth-range of the Karewa palaeolake was postulated to be from 5-10 m. The records from the Pliocene Nagrota Formation, Siwalik Group from Jammu (Bhatia *et al.*, 2001) also came from grey mudstones with a postulated depth-range of the palaeolake from 2 to 6 m. The Middle Holocene records of *L. barbatus* from Mali in Central Sahara (now considered as a synonym of *megalicarpus* (Soulié-Märsche & Martín-Closas, 2003) also came from greyish black silty or clayey sand with abundant molluscs. We thus see that while the large size of fossil gyrogonites from Late Miocene through Holocene has been attributed to "ecological factors", none has been specifically mentioned. The occurrence of such gyrogonites in bluish-grey to greyish-black shales and mudstones as mentioned above clearly implies that one of the ecological factors that possibly induces plants to produce robust gyrogonites is muddy substratum. Co-occurrence of abundant molluscan shells and ostracod carapaces in muddy substrate may also be another factor as they certainly enrich the substrate with high percentage of carbonates, which promotes the healthy growth of plants and production of well calcified and robust gyrogonites. This is in accordance with the view of Langangen (1974) that charophytes growing in oligotrophic lakes on lime-rich substrate form extensive subaqueous meadows. Another ecological factor that probably influences the production of large-size gyrogonites may be the bathymetry, as in the case of gyrogonites from the Plio-Pleistocene of Kashmir (Bhatia *et al.*, 1998) cited above. The deeper bathymetry (5-10m), as postulated by these authors, must have enabled plants to remain submerged for long duration and thus to have longer periods of reproduction as suggested by Soulié-Märsche & Martin-Closas (2003).

Against the obvious preference of *L. barbatus* plants for a muddy substrate in lacustrine environments, are those growing in ephemeral streams or creeks in Queensland, Australia (Wallace Creek), were the substrate is sandier. The plants from Wallace Creek are healthy though diminutive in height, and produce gyrogonites more prolate (ISI (130-) 140-170 (-190) and weakly calicified

(Garcia, 2003). However, it is thus obvious from the ecological conditions prevailing in Wallace Creek, viz. ephemeral streams, depth 0.5-1.5 m, black coarse to fine sandy substrate, low availability of ions in the water due to washout by monsoon floods, that the optimal ecological parameters for the growth and proliferation of the taxon do not exist in this location.

PROXY EVIDENCE FROM THE HOLOCENE SEDIMENTS

The previous discussion on the geological setting of the Holocene sediments of the Ganga plain and the ecological requirements of *Lychnothamnus barbatus* and its robust variant, showed that the basin configuration, depth of the abandoned cut-off meanders (Fig. 3), and the mud-dominated sediments of the Holocene palaeolakes (Singh *et al.*, 1999) played a significant role in the distribution, abundance and morphology of the charophytes (Tab. 1). The following inferences can be made based on evidence from palaeolakes A-D studied (Fig. 4; Fig. 5: C not represented, D from Sharma *et al.*, 2004).

1. The co-occurrence in locality A of gyrogonites of *L. barbatus* (*barbatus* type), with morphological characters and size-range similar to those of extant gyrogonites from Europe, and of its ecological variant, *megalicarpus* type, indicates that these gyrogonites were produced by two distinct populations of *L. barbatus*. They were growing in different parts of the palaeolake, at different depths and in different substrates as generalized in Fig. 6. The occurrence of well-preserved and abundant (> 80 specimens) of *megalicarpus* type gyrogonites compared to the less abundant (20 specimens, also well-preserved) of *barbatus* type, shows that the former population represents an in situ assemblage. The latter can be considered as thanatocenose, probably drifted from the shallower parts of the basin (2.0-3.0 m) in to the deeper parts (6.0m), corroborating the facies model developed by Singh *et al.* (1999).

2. In samples from localities B, C and D, the dominant charophyte taxon is *Chara aspera* with subordinate numbers of gyrogonites of *L. barbatus* (Tab. 1). The complete absence of *megalicarpus* type gyrogonites is significant. This may be attributed to the possibility that none of the three ecological parameters listed above, which are considered essential for the production of *megalicarpus* type gyrogonites, were present in the palaeolakes in these three localities. It is argued here that the palaeolakes in these three localities were much shallower (depth up to 3.0m) as compared to locality A and as a consequence they received a higher percentage of sandy silt sediments than clay-rich sediments. It is interesting to note from the pollen diagram of locality D (Sharma *et al.*, 2004, Fig. 4) that zone IIIb, which has yielded abundant *C. aspera* and *L. barbatus*, has a higher percentage of palynomorphs of *Botryococcus, Typha* and Cyperaceae. It is, therefore, likely that the trophic status of the palaeolake at locality D, as also at neighbouring localities B and C, bordered towards mesotrophic.

Similar conclusions have recently been drawn by Martín-Closas *et al.* (this volume) who discussed in greater detail the role of charophytes as indicators of trophic status of La Cerdanya Lake (Late Miocene of Spain). These authors distinguished two facies in the lutites — a disseminated facies with abundant *megalicarpus* type gyrogonites indicating oligotrophic conditions, alternating with a massive facies containing lime-encrusted *Potamogeton* and *Najas* seeds with freshwater molluscs indicating more mesotrophic conditions. These findings are comparable with the views expressed by the author above.

3. The co-occurrence of *Chara rantzieni* (= *C. pappii*) and *L. barbatus* at localities A and B (Tab. 1) seems to be ecologically significant, but since the extant representatives of *C. rantzieni* are still not known, precise comments about its ecological parameters are not possible. Nevertheless, the occurrence together of these two charophyte taxa in widely separated areas in the Pliocene of Greece (Soulié-Märsche, 1979), Holocene of Mali (Central Africa) (Soulié-Märsche in Petit-Maire & Riser, 1981) and also in the Holocene of the Ganga plain (this work) needs to be investigated in detail. The answer may well depend on finding the extant representatives of *C. rantzieni,* more likely in the Ganga plain where numerous freshwater lakes and ponds offer opportunities for dedicated charophyte workers to find out why and how these two species occur together. For details about the synonymy of *C. rantzieni* and its palaeobiogeographic implications, reference may be made to works of Bhatia (1999, 2003).

POSSIBLE DISPERSAL ROUTES OF *LYCHNOTHAMNUS BARBATUS*

The rediscovery of *Lychnothamnus barbatus* in Australia in 1996, thirty-four years after Wood (1962) first recorded the species in Queensland, raised pertinent questions about the possible mechanism, route and time of colonisation of this monoecious species in Australia. The broader questions — whether the species is native to Australia or an exotic one — have been discussed by McCourt *et al.* (1999), García *et al.*, (2000), García (2003), and Casanova *et al.* (2003a,b). While McCourt *et al.* (1999) ruled out the possibility of human source as an agent of dispersal and also the possibility of the Australian population being a representative of a residual population following the breakup of Gondwana some 150 million years ago, they admitted that the dispersal of *L. barbatus* by aquatic birds could account for its disjunct distribution. The role played by migratory aquatic birds in dispersing resistant eggs of cyprid ostracods is well known and has been emphasized for charophyte oospore/gyrogonites in general by Proctor (1962) and Proctor *et al.* (1967) and in the specific context of dispersal of *Nitellopsis obtusa* by Krassavina (1971) and Kropelin & Soulié-Märsche (1991). In the context of possibilities of dispersal of *L. barbatus* by aquatic birds from western Europe (where the oldest definite records are known from the Late Miocene) eastwards to other parts of Europe, Central Asia, Himalaya, southeast Asia and Australia, the discovery by García & Chivas (this volume) of fossil gyrogonites from freshwater sediments (dated 72 ka) of the palaeolake — Lake Carpentaria, in the Gulf of Carpentaria (Australia) is not only interesting but also very significant. This Late Pleistocene record, together with the earlier record of extant plants from Lake Wanum, near Lae in Papua New Guinea, not far from the Gulf of Carpentaria, by Leach & Osborne (1985) led García (2003) to support the palaeogeographic validation for the hypothesis of an Asian route of colonization, reaffirmed by the new findings of *L. barbatus* in rivers around the Gulf of Carpentaria (García & Chivas, this volume). A perusal of the comprehensive list of the hitherto known fossil and extant records of *L. barbatus* and its ecological variants as given by Casanova *et al.* (2003a) shows that the oldest records of this species are from the Upper Miocene (23.8-5.3 Ma) of Portugal, Spain, France, Austria, Switzerland, and Rumania (Fig. 7). Subsequent younger records are from the Pliocene (5.3- 1.7 Ma) of Europe in Tatar, and Greece and from Quinghai, China. The Late Pliocene (2.92 Ma)-Early Pleistocene (1.87 Ma) records are from the Kashmir valley in the Himalaya where the species is also present in Dal Lake. Late Pliocene records (2.8 ± 0.56 Ma) are also known further south from the Upper Siwalik of Jammu (Bhatia *et al.* (2001). The dispersal routes during the Pliocene were also in existence between Greece, Himalaya, Khazakistan and Tarim Basin in China as stated by Bhatia (2003) for *Chara rantzieni* (= *C. pappii*) and other charophytes. *L. barbatus* may also have been dispersed along this route from Greece to Himalaya during Pliocene times.

Later records (Late Pleistocene, 23 ka – 22 ka) of *L. barbatus* (which are still to be verified) are by Mathur (2001) from the lacustrine sediments of marginal plains, south of the Yamuna River. The species apparently dispersed to the southern part of the Ganga plain from the Himalayan foothills in the Late Pleistocene times and has continued to flourish through Late-Middle Holocene to recent times (this work and Pal *et al.*, 1962) in the Indo-Gangetic plain.

Interestingly, Kropelin & Soulié-Märsche (1991) suggested a dispersal route during Holocene between Central Europe and eastern Africa for the dispersal of *Nitellopsis obtusa* and *C. rantzieni* into north western Sudan. The same route may have been in existence for the dispersal of *L. barbatus* and *C. rantzieni* from Greece to Mali in Central Sahara during the Middle Holocene (7.5 ka).

The dispersal route during Late Pleistocene into Carpentaria is not clear as we do not yet have records of fossil occurrences between the Ganga plain and the Lake Carpentaria. One possible route may have been from China through Mayanamar, Malaysian peninsula and Indonesian archipelago as shown in Fig. 7. This possible alternative route is evident from the distribution pattern of the ostracod *Strandesia weberi* (= *S. spinifera*) from the Middle Holocene (8 ka) marls of Misa Tal in the Ganga plain to Malaysia, Java, Cambodia, Celebes and Phillipines (Bhatia, 1983; Keyser & Bhatia, 1989). The extant records in Papua New Guinea, south eastern Queensland and northern Queensland (new data García & Chivas, this volume), were probably routed through Lake Carpentaria which was an extensive freshwater lake prior to the final marine transgression around ~9.7 ka (Chivas *et al.*, 2001).

CONCLUSIONS

Based on the known ecological parameters and proxy evidence from the Middle Holocene fossil records of *Lychnothamnus barbatus* in the Ganga plain, it is postulated that the larger gyrogonites (*megalicarpus* type), may be ascribed to a combination of several ecological factors (oligotrophic water body, muddy and calcareous substrate and a deep bathymetry (≥ 6 m depth) and should not be considered as a subspecies of *L. barbatus*. The change in any of these ecological parameters may prohibit the production of large-sized gyrogonites. On the other hand, shallow depth and mesotrophic status favoured plants producing only the normal sized (*barbatus* type) gyrogonites, as was found in 3 of the studied sites. In the fourth locality studied, the basin morphometry with different types of substrates, shallower and deeper parts and oligotrophic status, favoured the growth of both types of populations and consequent post-mortem admixture (thanatocoenose) of large sized (in situ) and normal sized (exotic) gyrogonites.

The dispersal routes suggested in this work may need further refinement /correction when additional Quaternary fossil and extant records come to light from the eastern part of the Indo-Gangetic plain and countries in south-east Asia.

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