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Diversity and ecology of extant and Quaternary Australian charophytes (Charales)

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Abstract — The Australian charophyte flora (62 species recorded) is characterized by a high proportion of taxa which are endemic (62%), dioecious (45%), and that do not develop gyrogonites (84%). In this study, charophytes (Charophyta, Charales) were collected from one hundred and fifty two localities and forty two species identified. Ecological factors were recorded, in particular, salinity and water depth because these are the main factors affecting charophyte distribution, and pertinent to increasing salinisation of some Australian water-bodies. The different species were recorded at salinities ranging between 0 g L^{-1} and 58 g L^{-1} and at depths between few cm of water up to 12 m. Data on salinity and water depth are summarized by salinity/species and water depth/species graphs. A temporal perspective is important to understand the modern species distribution and ecology, so available data from the Australian Quaternary record are incorporated, being two from the Late Pleistocene and one from the Holocene. The palaeolimnological methodology uses the modern environmental data to infer environmental changes.

Charophytes / diversity / ecology / salinity / depth / palaeolimnology / Quaternary / Australia

Résumé — Diversité et écologie des charophytes (Charales) actuelles et du Quaternaire d'Australie. La distribution biogéographique des charophytes d'Australie (62 espèces inventoriées) montre une grande proportion de taxons endémiques (62 %) et dioïques (45 %), ainsi que des espèces qui ne développent pas de gyrogonites (84 %). La présente étude s'appuie sur la récolte de charophytes (Charophyta, Charales) de cent cinquante-deux localités et quarante-deux taxons ont été identifiés. Des facteurs écologiques, en particulier la salinité et la profondeur d'eau, sont indiqués parce que ce sont les principaux facteurs pour la distribution des charophytes et qu'ils sont indicateurs d'une augmentation de la salinité dans certaines pièces d'eau en Australie. Les différentes espèces ont été rencontrées à des salinités entre 0 g L^{-1} et 58 g L^{-1} et à des profondeurs allant de quelques cm d'eau à 12 m. Les données sur la salinité et la profondeur d'eau sont résumées par des graphiques montrant les relations Salinité/Espèce et Profondeur/Espèce qui pourront être utiles pour modéliser des changements dans les pièces d'eau et pour retracer des séries paléo-écologiques à l'aide de matériel fossile. Pour comprendre la distribution et l'écologie de l'espèce actuelle, il nous paraît important d'inclure les données disponibles pour le Quaternaire australien qui se limitent à deux références sur le Pléistocène et une sur l'Holocène. La méthodologie paléolimnologique utilise les données de l'écologie actuelle pour en déduire les changements environnementaux.

Charophytes / diversité / écologie / salinité / profondeur / paléolimnologie / Quaternaire / Australie

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INTRODUCTION

Charophytes (Charales, Charophyta), commonly called stoneworts, are green algae that inhabit non-marine environments and are the sister group of land plants (Karol *et al.*, 2001). Charophytes are characterized by complex reproductive structures, the oospores and gyrogonites, which are useful for identification. Oospores and gyrogonites are also the link between the taxonomy of modern and fossil charophytes (the latter based almost exclusively on oospore and gyrogonite morphology). These structures are resistant to desiccation and maintain their viability for up to 40 years (Tanaka *et al.*, 2003), and are a seed bank available for regeneration.

Robert Brown (1810) produced the first paper on Australian charophytes, followed by Braun (1843, 1849), Nordstedt (1918), and Groves & Allen (1935). Zaneveld (1940) studied charophytes from Southeast Asia and Malaysia of particular interest to Australia since there are many taxa in common. Wood (1972) published a paper on Australian charophytes. Recent papers on the systematics of Australian charophytes are van Raam (1995); García (1998, 1999); Casanova *et al.* (2003b); García & Casanova (2003) and García & Chivas (2004).

This study analyses Australian charophyte diversity, biogeography, and ecology covering different climatic areas and different types of water-bodies, from both modern and Quaternary records. The descriptions of species are not included because this is not a taxonomic paper, though it is important to remark that plant, oospore and gyrogonite morphology have been used for the identification of the taxa.

Late Quaternary charophytes were studied from sediments collected from three distinct climate areas of Australia: from palaeo-Lake Eyre, arid central Australia, Late Pleistocene sediments (~ 65 ka); from two coastal lakes from New South Wales, temperate wet, Holocene sediments (< 6 ka); and from the Gulf of Carpentaria, tropical Australia, with the development of "Lake" Carpentaria during the Late Pleistocene, at ~ 40 ka and 14 ka.

MATERIAL AND METHODS

The original materials for this paper comprise charophytes collected since 1994 from more than 400 widely distributed Australian non-marine environments from all states and territories of mainland Australia (including Rottnest Island (WA), Elcho Island (NT), Mornington Island (Qld), and Kangaroo Island (SA)). This extensive sampling provides a preliminary basis to investigate Australian charophyte diversity and ecological factors affecting their distribution. We synthesised data from only 152 water-bodies (Fig. 1), selected because their charophytes were complete (i.e., both sexes present for the dioecious species) and thus for which unambiguous identification was possible. Charophytes were collected from water up to 2 m deep by hand or using a hook, or up to 4-12 m deep from a boat (only from selected places). Characteristics of the water (conductivity expressed as Total Dissolved Solids (TDS), depth, pH, and temperature) were measured at most of the sites. Accordingly, charophyte populations from fresh/saline, ephemeral/permanent water-bodies within arid, temperate and tropical areas were studied. The classification of waters by salinity proposed by Hammer (1986) and widely used by limnologists, is adopted here.

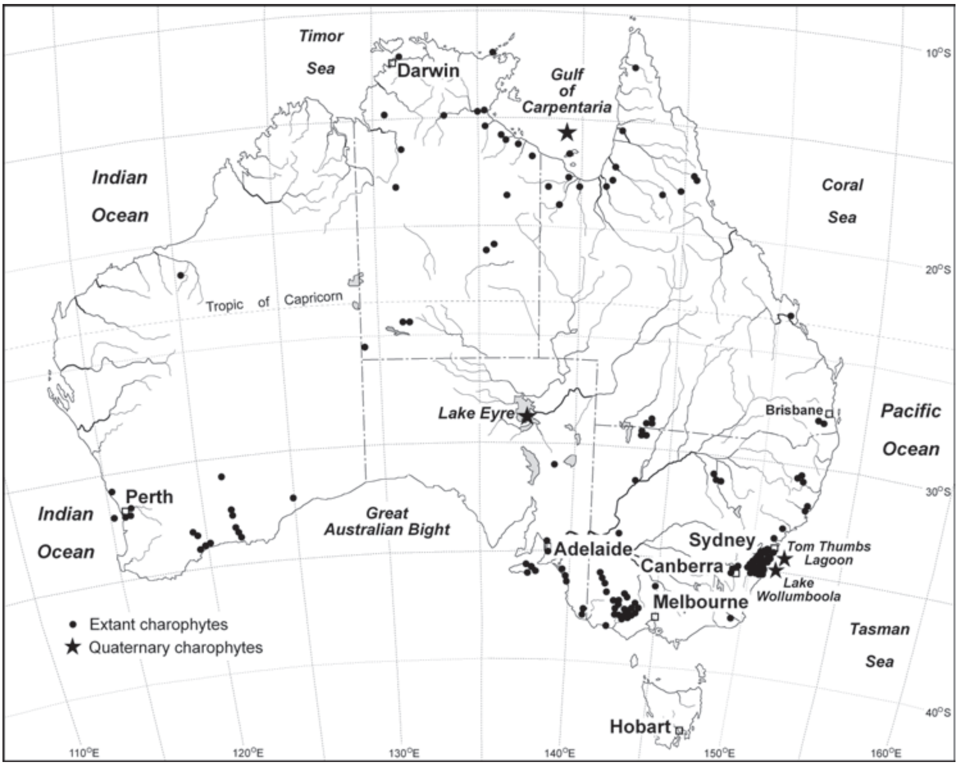

Fig. 1. Map of Australia showing the 152 localities with extant charophytes (black dots) included in this study. Charophytes are also recorded from Quaternary (black stars: Gulf of Carpentaria, Lake Eyre in northern South Australia, Tom Thumbs Lagoon and Lake Wollumboola south of Sydney).

Fossil charophytes were recovered from sediments using a 63-µm sieve and oven-dried at 60ºC. The microfossils were picked from these residues using a 00 brush under a Leica stereomicroscope. The collection of the host sediments followed a variety of coring and field techniques described in Chivas *et al.* (2001), García *et al.* (2002), and García & Chivas (2004). Extant and fossil specimens are stored in a personal collection at the University of Wollongong. Extant charophytes have been pressed (herbarium specimens) for storage at the Janet Cosh Herbarium, School of Biological Sciences, University of Wollongong, and fixed using 2-3% formalin and 70% alcohol.

RESULTS

Diversity of Australian charophytes

Wood & Imahori (1964-65), published a compendium of the world's charophytes, reducing the number of species from ~300 to 81, segregated in 21 subspecies, 101 varieties and 395 micro-species (= forms). This approach assumed that dioecy/monoecy; aulacanthous/ tylacanthous cortex; gymnophyllous/ with corticated branchlets; and sejoined/conjoined gametangia, are characters of infra-specific value, but later experiments demonstrated that these assumptions were not correct for most of the taxa (Grant & Proctor, 1972; Proctor, 1971, 1975, 1980). Based on the same original criteria, Wood (1972), in a study of Australian charophytes, listed 29 species. We provide here the analyses of Australian charophyte diversity based on a critical taxonomic approach and including observations on oospores and gyrogonites. The number of species of charophytes living in Australia is estimated to be at least 70. We list here 62 because *C. australis s. l.*, *C. fibrosa s. l.*, are under revision, and others are not yet formalised. It is important to note that the actual number of species may be much higher given the large size of Australia and its under-exploration, the opportunistic nature of some species, and the ephemeral nature of many Australian water-bodies.

Table 1 shows a list of 62 Australian charophytes compiled for this study, based on our collections plus species published by Nordstedt (1918), Groves & Allen (1935), Wood & Imahori (1964-65), Wood (1972), van Raam (1995), Hotchkiss & Imahori (1987), García (1998), García & Casanova (2003), and García & Chivas (2004). Current systematic studies include a revision of type specimens, and have focused on some of the species "complexes", e.g. the *Chara australis* Brown group, included by Wood within the macro-species *C. corallina* (Klein ex Willdenow) Wood, and the *C. fibrosa* (Agardh ex Bruzelius) Wood group, both highly diversified within Australia.

Characteristics and biogeography of the Australian charophyte flora: comparison with the world flora

Khan & Sarma (1984) and Khan (1991) analysed the distribution of the world charophyte flora based on cytological characteristics (e.g. chromosome number, dioecism/monoecism). They concluded that there are around 440 species, with *Chara* and *Nitella* being the more abundant species, ~62% are endemic, 77% are monoecious, 48% are monoecious endemic of particular zones, ~23 % are dioecious and ~14% are dioecious endemic. There are 195 species of *Chara*, 215 species of *Nitella*, 8 species of *Lamprothamnium*, 4 species of *Lychnothamnus*, 3 species of *Nitellopsis*, and 15 species of *Tolypella*). Khan (1991) established that the Australian zone shares with other parts of the world 62 species (~14% of taxa) (*Nitellopsis* being absent); with 24 species of *Chara* (~39%), 1 species of *Lamprothamnium* (~2% of taxa), 1 species of *Lychnothamnus* (~2%), 35 species of *Nitella* (~56%) and 1 species of *Tolypella* section *Tolypella* (~2% of taxa).

Our study also lists 62 species of charophytes, recording the presence of 20 species of *Chara*, 35 of *Nitella*, 4 species of *Lamprothamnium*, 1 species of *Lychnothamnus*, 1 species of genus *Tolypella* section *Rothia*, and 1 species of *Tolypella* section *Tolypella* (Table 1). Compared with Khan (1991), our analyses show that Australia has a greater diversity of species partially corticate/ecorticate of the genus *Chara*, the genus *Nitella*, the genus *Lamprothamnium*, and species that do not develop gyrogonites (~84% of the species). Endemism (~62% of the species), shows a similar percentage to that of the world-wide flora, whereas dioecism (~45% of the species instead 23 % world-wide) is much higher. The high number of dioecious and endemic taxa has been noted before (Wood, 1972; van Raam, 1995; Garcia, 1999). Figures 2 and 3 show in proportional terms the relationship of Australian charophyte flora and world-wide flora (based on Khan & Sarma, 1984; Khan, 1991; our data).

Table 1. List of the 62 charophyte species described from Australia (* species from the authors' collection), including characteristics of each species and its geographical distribution. The taxa are in alphabetical order and ranked as a function of host water salinity, listing the 152 localities. M: monoecy; D: dioecy; G: production of gyrogonite; COS: cosmopolitan or sub-cosmopolitan taxa; EN: Australian endemic taxa; Af: Africa; As: Asia; Aus: Australia; Eu: Europe; NZ: New Zealand; PNG: Papua New Guinea; SAm: South America; SP: South Pacific; ACT: Australian Capital Territory; NSW: New South Wales; NT: Northern Territory; Qld: Queensland; SA: South Australia; Tas: Tasmania; Vic: Victoria; WA: Western Australia; KI: Kangaroo Island; Arid: arid areas; Trop: tropical areas; L: Lake; R: River; Lg: Lagoon; Ck: Creek; Id: Island; St: Station.

Species	*Australian localities (this work)*
0-3 g L^{-1}: freshwater	
* *C. acanthopitys* Braun; M-NZ, Aus	L Leake, L Edward (SA)
* *C. australis* Brown; D-As?-Aus	Farm W of Newcastle, Killalea Lg, Hacking R (NSW)
* *C. australis* s.l; D-EN	L Purrumbete (VIC); L Barrine, Nicholson R., Mornington Id (Qld); Elcho Id, Kings Canyon, springs at Mataranka, Benmara St, Duck Pond, Arafura Swamp (NT)
* *C. braunii* Gmelin; M- COS	Yass R (NSW); Newman Rock (WA)
* *C. contraria* Br. ex Kütz.; M, G-COS	Port Fairy (Vic); close to Meadow Ck, Cooma Ck (NSW); Crossing Pool, Pilbara (WA)
* *C. fibrosa* Ag. ex Bruz.; M-COS (- Eu)	Yass R, Nattai R, Brooks Ck, Myall L (NSW); Elizabeth Ck (Qld); Crossing Pool, Pilbara (WA)
* *C. fibrosa* s.l.; M-EN	Brisbane Water National Park (at Woy Woy), Hacking R (NSW); Swan R (WA); Calvert R (NT)
* *C. fibrosa* s.l.; D-EN	Fitzmaurice R (NT)
* *C. globularis* Thuillier; M, G-COS	Meadow Ck, L Mungo (NSW); Wallace Ck (Qld); five springs on Werta Ck, Flinders Ranges, farm dam on KI (North Cape Road), farm pond on KI (Starr Road and Elsegood Road), Valley L, Hindmarsh Id (SA)
* *C. globularis* var. *virgata* (Kütz.) Wood; M, G-COS	Deep L, L Muirhead (VIC)
* *C. hookeri* Braun; D-EN	L Edward (SA)
* *C. leptopitys* Braun; D-EN (WA, SA)	Pond close to Naracoorte (SA)
C. mollusca Braun; D-EN (Tas)	(data from literature)
* *C. muelleri* Braun; M-EN	Black L, Killalea Lg (NSW)
C. myriophylla Müller ex Braun; M-EN (Tas)	(data from literature)
* *C. preissi* Braun; D-EN	L Muirhead, L Buninjon (Vic); The Morass (NSW); Blue L North, L Bulla (Qld); Swan R (WA); pond on KI (SA)
C. setosa Klein ex Willd.; M-EN (Trop)	(data from literature)
* *C. simplicissima* (Fil.) Wood; D-EN	Newman Rock (WA); Kings Canyon (NT)
* *C. submollusca* Nordstedt; D-EN (Trop)	L. Barrine (Qld)
* *Chara vulgaris* L.; M, G-COS	Hindmarsh Id (SA); Wallace Ck (Qld); Crossing Pool, Pilbara (WA)
* *C. zeylanica* Klein ex Willd.; M-COS (- EU)	Elizabeth Ck, Gilbert R, Flinders R, Bynoe R, Five Mile Ck (Qld); Mataranka reserve (NT); Crossing Pool, Pilbara (WA)
* *L. macropogon* (Br.) Ophel; M, G-NZ, Aus	L Muirhead (Vic); Lake Leake (SA)
* *"Protochara" inflata* Wom. & Ophel; M, G-EN (WA-SA)	Pond south of Kalgoorlie (WA)

Table 1. *(continued)*

Species	*Australian localities (this work)*
* *Lychnothamnus barbatus* (Meyen) Leonh.; M, G-As, Eu, PNG, Aus	Wallace Ck, Warrill R, Elizabeth Ck, Gilbert R (Qld)
* *Nitella acuminata* Br. ex Wallm.; M-COS (- Eu)	L Barrine, Nardellos Lg, Davis Ck (Qld)
N. australiensis (Bailey) van Raam; M-EN	(data from literature)
N. confusa (Wood) van Raam; M-EN (Tas)	(data from literature)
* *N. congesta* (R. Brown) A. Braun; D-EN	Valley L (SA)
* *N. cristata* Braun; D-NZ, Aus	Macquarie Marshes, Llangothlin Lg, Little Llangothlin Lg, Kellys Ck, Black Bobs Ck, Nattai R, Murrumbidgee R, Hacking R, Kara Ck, Frys Ck, Hyams Ck, Buttles Ck (NSW)
N. diffusa Braun; M-EN	(data from literature)
N. furcata Roxb. Ex Bruz.; M-COS	(data from literature)
* *N. gelatinifera* (Wood) Wood; D-EN	Shoalhaven R (NSW); Pinneys L, Canning R (WA)
N. gloeostachys Braun; D-EN	(data from literature)
N. haagenii van Raam; D-EN	(data from literature)
N. hookeri ? Braun; M-NZ, Aus	(data from literature)
N. hookeri var. *arthroglochin* Braun; M-EN?	(data from literature)
* *N. hyalina* (DC) Ag.; M-COS	Fitzgerald R, Killalea Lg, Myall L (NSW); Thorndon Park (SA); Roper R (NT); pond in Perth; Crossing Pool, Pilbara (WA)
* *N. ignescens* García; D-EN	L George (NSW); L Cooper, Green L (Vic)
* *N. leonhardii* Wood; M-EN	Badgerys Ck (NSW)
* *N. leptostachys* Braun; M-NZ, Aus	Deep Ck, Barrangarry Ck (NSW)
* *N. lhotzkyi* (A. Br.) A. Braun; D-SAm, Aus	Shoalhaven R (NSW); Hindmarsh Id (SA)
* *N.* cf. *Lhotzkyi*; D-EN	Rowles Lg (WA)
N. microteles Williams; D-EN	(data from literature)
N. monopodiata van Raam; D-EN (Tas)	(data from literature)
* *N. myriotricha* Br. ex Kütz.; D-EN	South Alice Ck (Qld)
N. partita Nordstedt; D-EN	(data from literature)
N. penicillata Braun; D-EN	(data from literature)
* *N. phauloteles* Groves; M-EN	Hacking R (NSW)
* *N. pseudoflabellata* Braun; M-As, SP, Af, NZ, Aus	Rose Lg, Hacking R (NSW)
N. remota; D-EN	(data from literature)
N. robertsonii; D-EN	(data from literature)
* *N. sonderi* Braun; D-EN	Paddys R; Budjong Ck (NSW)
* *N. stuartii* Braun; M-SAm, As, NZ,Aus	Molonglo R, Deep Ck (NSW)
* *N. subtilissima* Braun; D-EN	Budjong Ck, Snowy R, Hacking R (NSW); L Ginninderra (ACT); Cann R (Vic)
* *N. tasmanica* Müller ex Braun; D-SP, NZ?, Aus	Paddys R, Collector Ck (NSW)
* *N. tricellularis?* Nordstedt; M-EN	Kara Ck (NSW)
* *N. tumida* Nordstedt; D-EN	Spring close to Eulo (Qld)
* *N. woodii* ? Hotchkiss *et* Imahori; D-EN	Collector Ck (NSW)
* *T. intricata* (Trent. ex Roth) Leonh.; M-COS	Pond north of Naracoorte (SA)

Table 1. *(continued)*

Species	*Australian localities (this work)*
3-20 g L^{-1}: hyposaline	
* *C. contraria*	Port Fairy (Vic); close to Meadow Ck (NSW)
* *C. fibrosa* s.l.	Bobundara Ck (NSW); Elizabeth Ck, pond in Rockhampton (Qld); Crossing Pool, Pilbara, Swan R (WA); Salt Ck (NT)
* *C. globularis*	Meadow Ck, L Mungo, McLaughlin R (NSW); Wallace Ck (Qld)
* *C. preissi*	L Muirhead, L Buninjon (Vic); The Morass (NSW); Blue L North, L Bulla (Qld); Swan R (WA)
* *Chara vulgaris*	Hindmarsh Id (SA)
* *C. zeylanica*	Upper Swan R (WA)
* *N.* cf. *ignescens*	L Struan, L Coradgill, L Martin (Vic)
N. subtilissima	(data from literature)
N. tumida	(data from literature)
* *N. ungula* Garcia; D-EN	L Bathurst (NSW); L Muirhead (Vic)
* *N. verticillata* (Fil. *et* Allen ex Fil.) Wood; D-EN	L Wollumboola, Swan L (NSW); Windabout L (WA)
* *L. heraldii* García *et* Casanova; D, G-EN (Arid)	L Gidgee, Lower Bell L, Palaeo L (NSW) , Blue L North, Mid Blue L, L Bulla (Qld)
* *L. macropogon*	16 localities from Victoria (García, 1999); Discovery L, Lashmar Lg, Murray Lg, Eleanora R, White L (KI, SA)
* *L.* cf. *macropogon*	5 lakes in Coorong (SA); Gordon R, Hamersley R, Jerdacattup R, Windabout L, L Warden, Avon R, Woody L, 3 lakes on Rottnest Id (WA)
* *L. succinctum* (Braun in Asch.) Wood; M, G-COS	L Wollumboola, Swan L, L Illawarra, Wallis L (NSW); Port Fairy coastal channels (Vic)
* *"Protochara" inflata*	Pond south of Kalgoorlie (WA)
* *Tolypella glomerata* (Desv. in Lois.-Desl.) Leonh.; M-COS	Pond at Port Fairy (Vic)
20-50 g L^{-1}: mesosaline	
* *C. preissi*	The Morass (NSW); Blue L North, L Bulla (Qld); Swan R (WA)
* *N. ungula*	L Bathurst (NSW)
* *L. heraldii*	L Gidgee, Lower Bell L, Palaeo L (NSW), Blue L North, Mid Blue L, L Bulla (Qld)
* *L. macropogon*	4 localities from Victoria (García, 1999); Discovery L, Lashmar Lg (SA)
* *L.* cf. *macropogon*	Gordon R, Hamersley R, Jerdacattup R, Windabout L, L Parkeyerrang, L Dumbleyung (WA)
* *L. succinctum*	L Wollumboola, Swan L, L Illawarra, Wallis L (NSW); Port Fairy coastal channels (Vic)
> 50 g L^{-1}: hypersaline	
* *L. macropogon*	3 localities from Victoria (García, 1999); Discovery L, Lashmar Lg (KI, SA)
* *L.* cf. *macropogon*	Gordon R, Hamersley R, Jerdacattup R, Windabout L (WA)
* *L. succinctum*	L Wollumboola, Swan L, L Illawarra, Wallis L (NSW)

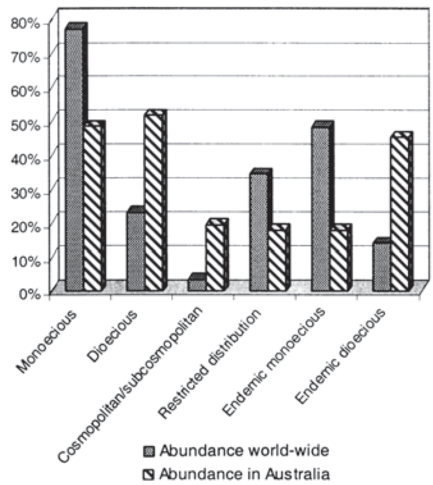

Fig. 2. Comparison of the relative abundance of monoecy/dioecy, distribution and endemism of charophytes world-wide (Khan, 1991) and in Australia (this study).

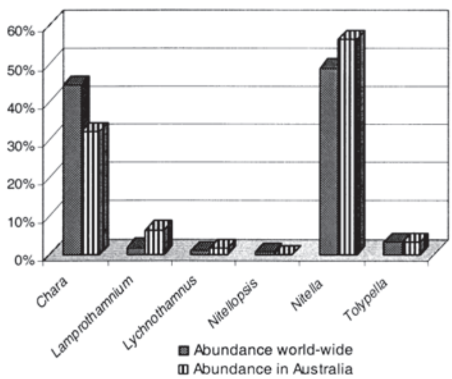

Fig. 3. Comparison of the relative abundance of the 6 genera of charophytes world-wide (Khan, 1991) and in Australia (this study).

The high endemism and distinctive dioecism have had about 80 million years (Ma) of isolation to become established. The break-up of Gondwana beginning in the Early Cretaceous finally completely isolated the Australian land mass from about 50 Ma until it reached the tropics in the Miocene (Müller *et al.*, 2000). Since collision with Southeast Asia, during the Late Miocene, interchange of species between Asia and Australia has been more active, enhanced when land bridges developed between them during low-stands of sea level, something that repeatedly happened during the Quaternary. Dry conditions have been a feature of central Australia since the Miocene, as indicated by falling groundwater tables (18 to 8 Ma) near Coober Pedy, central Australia (Bird *et al.*, 1990) and continuing aridity is documented for the past 500 thousand years (Bowler, 1978), producing a high number of short lived water-bodies. Patchiness and disconnection of water-bodies are the likely bases for speciation and endemism.

The high number of charophyte species that do not develop gyrogonites is probably due to Australia's poor soils. Australia has a very old weathered landscape with predominance of lateritic and duricrust soils, and silica sand-sheets and dunes, which are commonly impoverished in carbonates (except for the calcretes in southern Australia). At a regional level, García (1999) indicated the predominance of lakes of volcanic (basaltic) origin, where magnesium is more abundant than calcium, as a possible reason for the lack of calcification of charophytes collected in southwestern Victoria and southeastern South Australia.

The biogeographical pattern is here summarized (based on Table 1), showing:

62% of charophyte species are endemic to Australia;

13% of species are cosmopolitan or sub-cosmopolitan (only excluded from Europe) (*Chara globularis, C. vulgaris, C. contraria, C. braunii, C. zeylanica, C. fibrosa, Nitella furcata* Roxb. ex Bruz. and *N. hyalina* (DC.) Ag., all of them monoecious)

11% are only found in Australia and New Zealand;

7% have been recorded also in Africa, Southeast Asia and the South Pacific area;

4% have an exclusive distribution in Australia and the South Pacific region, and

1% is present in Australia and South America.

Ecology of Australian charophytes

From an ecological perspective, charophytes play an important role within fresh and saline coastal and terrestrial aquatic ecosystems, and from the macrophyte commonly with the highest biomass. Charophytes are important as primary producers, in providing protection for zoobenthos, food for fish and aquatic birds; supporting epiphytes that are in turn food or zoobenthos; in keeping the water clear by retention of previously suspended sediments, constraining the re-suspension of sediments from the water-body-floor, and inhibiting the blooms of micro-organisms (clear water versus a turbid state as shown by Scheffer, 1998; van den Berg & Coops, 1999). The importance of charophytes within Australian environments is shown in this study. Their distribution within a given water-body can be sparse (e.g. Yass River, NSW), or more commonly cover areas of 5 to 30 m^2 in creeks and rivers (e.g. Gordon River, WA; Barrangarry Ck., NSW) and up to 75 % in lakes (~4,000 m^2 in Lake Wollumboola, NSW and ~63,000 m^2 in Myall Lake, NSW (personal observations; Redden *et al.*, 2004), and they are the only macrophyte growing at water depths greater than 3-4 m (recorded between 6-12 m in Lake Purrumbete, Victoria). Although charophytes are present in almost every water-body, there are no previous studies in Australia relating their distribution to ecological factors. This work reports the effect that salinity and depth have on Australian charophytes, filling a gap in the knowledge of species tolerance to salinity (e.g. the Australian Nature Conservation Agency (1996), indicated that information on which "plant or invertebrate species tolerate different salinities is sparse").

Salinity, temperature, depth, water chemistry, pH, water regime, and substrate, are some of the more important factors affecting charophyte distribution, and previous studies of Australian charophytes (Groves & Allen, 1935; Wood, 1972; Brock & Casanova, 1991; van Raam, 1995) do not provide precise information about salinity or other ecological parameters from the collection sites. The first and only list of Australian charophyte species distribution as a function of salinity was provided by García (1999), who studied fourteen species from 55 lakes and creeks from South Australia and Victoria.

Salinity

Salinity appears to be one of the strongest factors governing the presence or absence of charophytes and species distribution (Tab. 1, Fig. 4). Tribe Chareae has taxa living from fresh to hypersaline, ~70 g L^{-1} TDS, whereas Tribe Nitelleae has taxa living mostly in freshwater, some tolerating mesosaline conditions of ~20 g L^{-1} TDS, and some exceptionally in salinities up to 25 g L^{-1}. In Australia, the genus *Chara* inhabits usually fresh to low subsaline environments, i.e. *C. australis* s. l., *C. fibrosa* (monoecious), *C. muelleri* and *C. braunii.* Taxa tolerating increasing salinity are *C. globularis, C. contraria, C. preissii, C. zeylanica*, and some species of the *C. fibrosa group*, found in water bodies with salinity up to ~10 to 20 g L^{-1} TDS. The only species of *Lychnothamnus*,

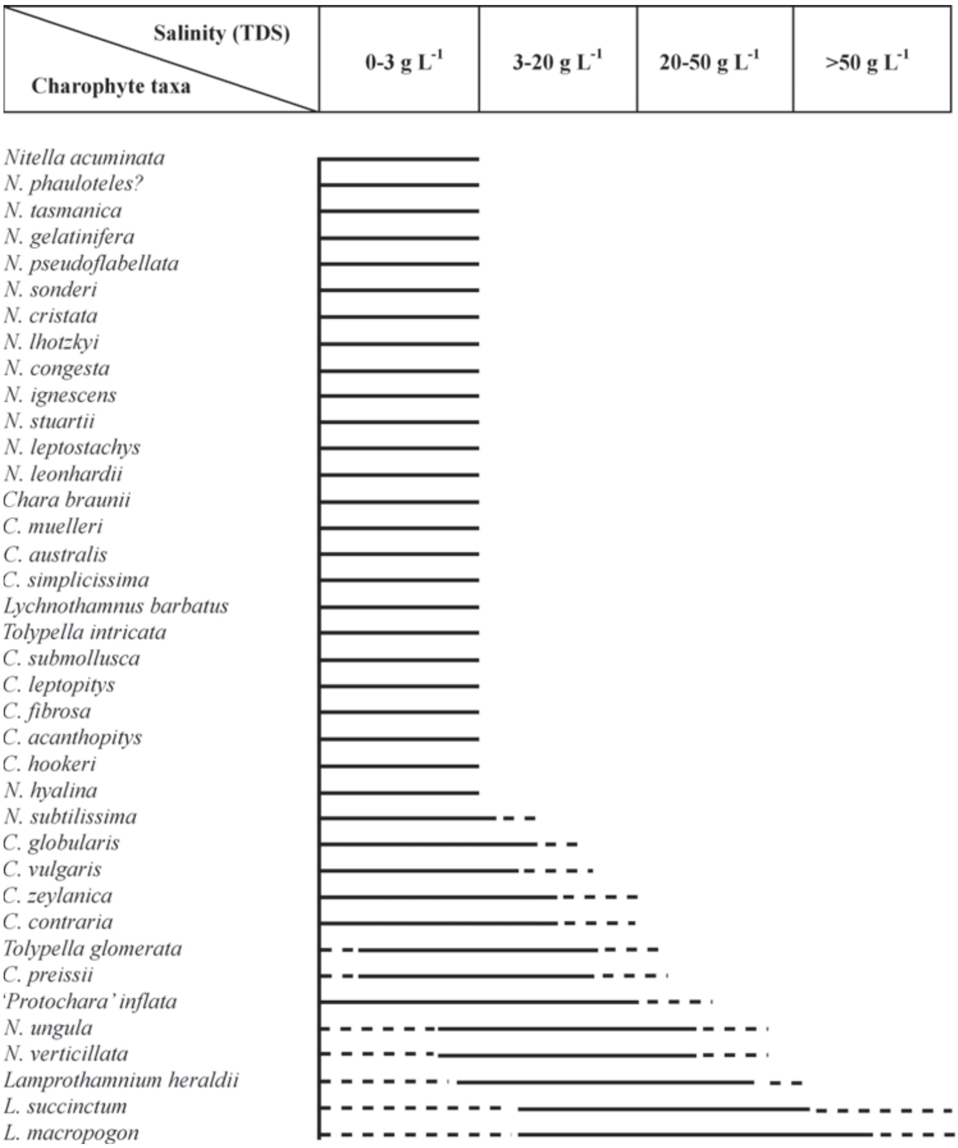

Fig. 4. Distribution of selected Australian charophytes as a function of host-water salinity, based on observations and salinity measurements of more than 152 water-bodies. Dashed lines indicate the extreme tolerable ranges in salinity.

L. barbatus, is typical of freshwater. The genus *Lamprothamnium* is the only euryhaline genus within the charophytes, adapted to sudden changes in salinity and able to tolerate hypersaline conditions. Soulié-Märsche (1998) indicated that in particular *L. papulosum* needs changes in salinity, in her study of Holocene African inland lakes. Therefore, *Lamprothamnium* is distributed in both inland

and ocean-marginal water bodies, subjected to fluctuations in salinity by evaporation or sea-water connections (García, 1999; García *et al.*, 2002; García & Chivas, 2004).

All species of the genus *Nitella* are adapted to freshwater bodies, with few taxa tolerating hyposaline to mesosaline conditions, i.e. *N. hyalina*, *N. ungula* García and *N. verticillata* (Filarszky & Allen ex Filarszky) Wood living at ~20 g L^{-1} TDS. *Tolypella* section *Rothia* with its only species *T. intricata*, is an exclusive inhabitant of freshwater habitats, whereas the species of *Tolypella* section *Tolypella* tolerate increasing salinity, such as *T. glomerata* which prefers subsaline to mesosaline conditions.

Temperature

Temperature affects every aspect of the charophyte life cycle from germination to death (Zaneveld, 1940; Corillion, 1957; García, 1994). Australian perennial charophytes survive temperatures as low as 0ºC in temperate areas, whereas the thalli of annual species disappear during winter and re-grow during spring, from oospores or bulbills. Within Tribe Chareae, examples of *Chara* tolerating winter months are *C. globularis* and *Chara fibrosa*, the latter found fertile during July in the Yass River, N.S.W., whereas *C. leptostachys* is a typical annual taxon. *C. australis* is a perennial species, surviving the winter months and producing reproductive structures at least in the temperate areas. The genus *Lamprothamnium* is perennial, with *L. succinctum* found fertile throughout the year in coastal saline water bodies of temperate Australia, and *L. macropogon* in Victorian inland lakes. *Lychnothamnus* is only found in tropical/subtropical areas, where the lowest mean annual temperature is ~15ºC.

Within the Tribe Nitelleae, species of *Tolypella* are annual. It is interesting that both *T. glomerata* and *T. intricata* have been found only in southern temperate Australia, in Victoria and South Australia respectively. *Nitella ungula, N. stuartii, N. sonderi* and *N. tasmanica*, are perennial species, whereas *N. woodii* Hotchkiss & Imahori (and probably *N. cristata*) "die" during winter when only the turions (long bulbills) are found.

The effect of temperature on reproduction has been established for some species, for example with germination at 20-25ºC for *C. contraria, C. zeylanica* and *C. globularis* (Forsberg, 1965).

Water depth, light and energy

Water depth is one of the factors that strongly affects charophyte distribution, producing species zonation in deep lakes (Corillion, 1957; García, 1990). Factors such as light intensity, energy of the water, and temperature are closely related to water depth (García, 1994). Clear-water lakes, where light penetration is high, allow the growth of charophytes at up to 40 m depth, e.g. *N. opaca* Braun from Europe (Corillion, 1957). García (1994) described the presence of *C. globularis* in lakes from the Cordillera de los Andes, growing at 10-15 m deep (García, 1987), and the American taxon *C. bulbillifera* (Donterberg) García growing in water depths up to 14 m in northern Patagonia (García, 1990).

Figure 5 summarises the distribution of some Australian charophytes as a function of water depth. Within Tribe Chareae, species of *Chara* are able to grow in a few centimetres of water up to 9-12 m. In some cases, the same species with a more short or elongate habit, may be found at different depths, i.e. *C. contraria, C. zeylanica* and *C. australis* recorded from 0.1 m to 1.5 m depth,

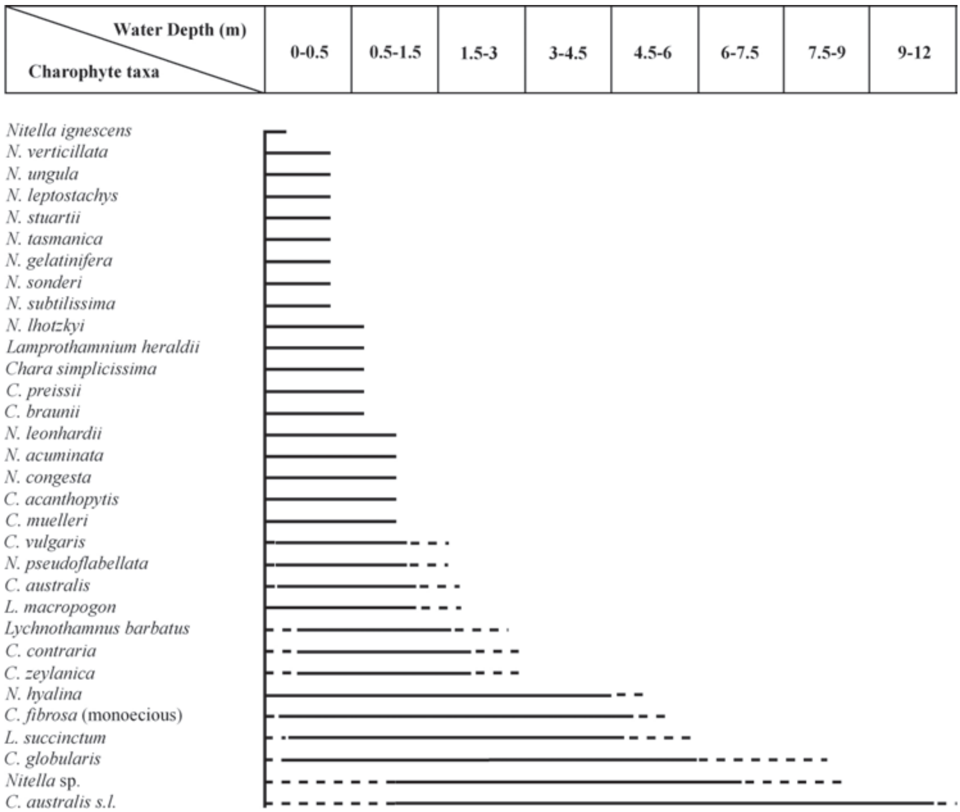

Fig. 5. Distribution of selected Australian charophytes as a function of water depth based on observations of more than 152 water-bodies. The maximum depth where the samples were collected was 12 m. Dashed lines indicate the extreme tolerable ranges in depth.

C. fibrosa and *C. globularis* from 0.1 m to 4 m depth, and *C. australis* s.l. collected at depths up 6 m to 12 m at Lake Purrumbete (Vic). *Lamprothamnium* is a typical heliophilic genus inhabiting shallow water bodies (Guerlesquin, 1992; García, 1993, for *L. papulosum* and *L. haesseliae* Donterberg respectively). *Lamprothamnium* in Australia has been recorded between the shoreline and 2 m depth, in particular for *L. macropogon* (García & Chivas, 2004), whereas in deeper lakes it can reach to ~4 m water depth, e.g. *L. succinctum* from Lake Wollumboola, NSW. *Lychnothamnus barbatus* has not been found in depths less than ~0.2 m, displaying its distinctive habit at 0.4-0.6 m depth, probably due to the large size of its whorls.

Within the Tribe Nitelleae, the species of *Tolypella* collected in Australia, *T. glomerata* and *T. intricata*, grow in depths of 0.3-0.5 m, whereas *Nitella* shows a more variable range. *N. ignescens* for example lives strictly at the shoreline, semi-exposed to the air and the action of waves from 0-0.03 m depth (García, 1998). *N. hyalina* has been found in up to 3 m water and as shallow as 0.1 m depth, in which latter case its upper whorls commonly reach the surface of the water. For both species in shallow water, a thick mucus protects the upper whorls from desiccation, being the younger and commonly reproductive part of the plant. *N. pseudoflabellata* grows in depths of 0.3 m to 2 m, while most of the species of *Nitella*, e.g. *N. stuartii*, *N. leptostachys*, *N. lhotzkyi, N. leonhardi, N. cristata, N. subtilissima* and *N. ungula* are found in 0.1 m to 0. 5 m of water. A particular example is *Nitella* sp. which was collected up to 9 m depth from Lake Purrumbete (Victoria).

pH and chemistry

Charophytes commonly inhabit waters with a neutral or higher pH. There are some examples of species tolerating pH of 5 to 6, and they commonly belong to *Nitella. Lamprothamnium* species have been found in Australian waters with a pH from 7-9, with one locality of pH 6, probably representing a brief environmental perturbation (García, 1999). It has long been known that the solute chemistry of most of Australian lakes is dominated by Na and Cl, although some have significant minor HCO_3^- contents (Bayly & Williams, 1973; Chivas *et al.*, 1986).

Historical perspective

The knowledge of environmental changes occurring during the Quaternary is necessary to interpret present conditions and rationalise natural versus induced changes. Three cases of Quaternary charophytes from arid, temperate and tropical Australia are discussed from Lake Eyre, some coastal lakes from NSW and the Gulf of Carpentaria, respectively.

Lake Eyre, South Australia

Lake Eyre (Fig. 1) is a large, temporary saline lake in central Australia, filled intermittently from northern rivers. The ephemeral nature and land-use sensitivity of Lake Eyre and other water bodies within its basin led Williams (2002) to include the area and its biota in his work on saline lakes, and their conservation and management. Magee *et al.* (1995) investigated the palaeo-hydrology of the last 130 ka for Lake Eyre, including the cliff exposure of Quaternary sediments at Williams Point, Madigan Gulf, Lake Eyre North. This 12-m high outcrop has aeolian sediments in the upper 5 m overlying a lacustrine sequence 7-m thick. García & Chivas (2004) analysed the charophytes of the lacustrine facies, and the species *Lamprothamnium williamsii* García & Chivas (named for Professor Bill Williams) was described from a population from the upper layer dating to ~65 ka. *L. williamsii* was the only charophyte described that has not been found yet in modern environments. Thus, we know this species only based on its gyrogonite. Charophytes are present through the whole lacustrine series indicating a succession of ephemeral lakes between 65-92 ka ago.

The presence of successive populations of *Lamprothamnium* indicate that the Lake Eyre basin has undergone several dry-wet events from freshwater-low salinity to hyper-saline periods, and a history of wet-dry cycles, supported by the presence of gypsum layers. The “flood” times carrying fresher water to Lake Eyre can be related to periods of enhanced monsoon rains in northern tropical Australia (García & Chivas, 2004; Magee *et al.*, 2004) although a relationship with El Niño/La Niña events remains to be established.

Coastal lakes, New South Wales

The charophyte *Lamprothamnium succinctum* is living in Lake Illawarra, Lake Swan and Lake Wollumboola (Table 1) and has been found in sediments younger than 6 ka from Tom Thumbs Lagoon (García *et al.*, 2002) and Lake Wollumboola. The development of coastal barriers after the mid-Holocene high-stand of sea level, at ~6 ka for this area, interrupted the connection between these coastal water bodies and the ocean. Thus, a marine biota is replaced by charophytes towards the top of the core (García *et al.*, 2002).

Gulf of Carpentaria, northern Australia

The Gulf of Carpentaria (Fig. 1) is an epicontinental sea, ~70 m deep, which was disconnected from the Pacific and Indian Oceans during episodes of low sea-level in the Quaternary. Consequently, a palaeo-lake known as Lake Carpentaria was formed at the same time as the partial "land bridges" between Asia and Australia. In Carpentaria, *Chara vulgaris, C. zeylanica*, and *Lychnothamnus barbatus* have been found in two cores (MD-31 and MD-32), in the uppermost lacustrine facies underlying 0.65 and 0.40 m, respectively, of more recent marine sediments. This last non-marine/marine transition has been dated by radiocarbon methods to ~9.7 ka BP (Chivas *et al.*, 2001). *Chara vulgaris, C. zeylanica*, and *L. barbatus* are present between 3.30-4.30 m and 0.60-0.90 m in the former and latter cores, respectively. Another date of 72 ka was obtained by amino acid racemization at a depth of 5 m in core MD-32, showing that these species were living in the area during the late Pleistocene. As *L. barbatus* lives exclusively in freshwater, this indicates that at ~40 ka and ~14 ka, Lake Carpentaria was fresh, and this is supported by the presence of other biological remains such as ostracods (*Candona, Cyprinotus*).

Extant *C. vulgaris,* and *L. barbatus* have been found in Warrill R. and Wallace Creek, Qld; *C. zeylanica* and *L. barbatus* have been found in Elizabeth Ck. and Gilbert R., Qld. All these localities are freshwater. *C. zeylanica* has been collected also in the Upper Swan R., WA, whith a recorded salinity of 4 gL^{-1} (hyposaline range).

Within the "Lake" Carpentaria sequence, of particular importance is the presence of *Lychnothamnus* because *L. barbatus*, the only living representative of the genus, is currently in decline world-wide (Krause, 1997; Casanova *et al.*, 2003; García, 2003; Chou & Wang, this volume). *Lychnothamnus* is well-represented in the fossil record from Europe and Asia and has been reported since the Late Eocene, having a more widespread distribution during the Late Pliocene and Miocene (Bhatia *et al.*, 1998; Soulié-Märsche, 1989; Casanova *et al.*, 2003; Bhatia, this volume). The finding of *L. barbatus* in the Pleistocene of Lake Carpentaria confirms its introduction into Australia via Southeast Asia during a time of low sea level. Extant *L. barbatus* has been found in Europe, Asia, Papua New Guinea, and Australia. In Australia, *L. barbatus* was initially found in 1960 in Warrill Creek in Queensland by Wood, and re-discovered in 1997 (Casanova *et al.*, 2003; García, 2003) after a thorough search in its original locality and nearby catchments. McCourt *et al.* (1999) suggested the colonisation of Australia by *Lychnothamnus* via Southeast Asia, but there was also the possibility of its more recent incidental introduction from Europe, particularly as the area near Warrill Creek had seen significant immigration of people from Germany. The discovery in the Gulf of Carpentaria of Pleistocene *Lychnothamnus barbatus* supports its protection and declaration as an endangered species by providing a palaeogeographical validation for the hypothesis of an Asian route of colonisation. During the last few decades, *Lychnothamnus* has been absent from large parts of its previous distribution world-wide, and in Australia was listed as endangered by the Australian government in 2000 (García, 2003). A pre-requisite for formal protection is certainty that the taxon is "native" to Australia (i.e. demonstrably present in the continent prior to European colonisation) and this work demonstrates its true status.

DISCUSSION AND CONCLUSIONS

The conservation of biodiversity requires a comprehensive strategy. Species genetic diversity at local, regional and global level, their ecology and responses to ecological changes, biotic/abiotic inter-relationships, and taxa spatial distribution integrated within an historical framework are the basis of any attempt to understand and conserve biodiversity. To fully understand Australian species/genetic biodiversity, its conservation and management, a sound taxonomic/ecologic/biogeographic understanding is needed in conjunction with pre-European arrival records. Biological diversity in Australian saline water-bodies is higher than in other continents, and their ecological role is very important as they occur widely.

Australian charophytes are diversified and well adapted to changing salinity, with at least seven endemic salt tolerant species. It is important though, to remark on the need for the conservation of saline water-bodies and their biota as indicated by Brendonck & Williams (2000). Our new ecological data define those charophytes which are saline-tolerant or freshwater species; species living at the shorelines of water-bodies or at greater depth; species restricted to tropical/subtropical or temperate areas, and tolerant species not restricted by temperature. For example, *Chara vulgaris, C. contraria, C. globularis* and *C. zeylanica* are regarded as freshwater taxa that can tolerate temporary increases in salinity. *Lamprothamnium* is the only euryhaline genus and has species inhabiting coastal water bodies and inland saline water bodies. *Lychnothamnus* is exclusively freshwater, as are *Tolypella intricata* and most of the *Nitella* species, except *N. ungula, N. verticillata, N. subtilissima* (for the latter, datum from Wood, 1972), and probably *N. tumida*. Australian charophytes are characterised by endemism, as might be expected in a land-mass isolated from other continents for much of the past ~80 Ma, as well as by dioecism and a lack of gyrogonite development. Our environmental key diagrams (especially for salinity and water depth) will allow the use of charophytes to develop historical records for water bodies, even over the past 200 years, using materials recovered from sediment cores. This will assist with assessment of natural environmental variability, understanding the changes induced by past land-use practices, and future management.

The study of Quaternary material, based on oospores and gyrogonites, uses data from extant species as modern analogues to determine past environments. Particularly important are data obtained from modern populations of *Lamprothamnium* that allowed the identification of a new species in Lake Eyre at ~65 ka, *L. williamsii* (García & Chivas, 2004). In coastal lakes from New South Wales, charophytes indicate when lagoons became disconnected from the ocean. In tropical Australia, *Chara vulgaris, C. zeylanica* and *L. barbatus*, were discovered in Pleistocene sediments from Lake Carpentaria with ages of ~40 ka and ~14 ka. The modern ecology of the last two taxa, adapted to particular characteristics of tropical (rarely subtropical) Australia, allows a palaeo-environmental reconstruction relating their presence with times of enhanced monsoonal activity. In turn, their presence also confirms routes of colonisation as described for *L. barbatus* from Asia, and proves that the species was in Australia prior to European settlement.

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