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LONG-TERM DYNAMICS OF A MEDITERRANEAN ALKALINE VERNAL POOL (RHONE DELTA, SOUTHERN FRANCE)

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Abstract: Mediterranean vernal pools are threatened habitats that support a number of endangered/rare plant and invertebrate species. Conservation management of these important habitats is limited by a lack of knowledge, especially concerning their past and present ecological dynamics. A multidisciplinary palaeoecological investigation was conducted on one of the last alkaline vernal pools of the Rhone delta (southern France). Results highlighted the value of a multidisciplinary approach based on several complementary methods, and provide direction for subsequent palaeoecological studies in temporary wetlands. Despite some degradation, fossil assemblages provides an accurate reconstruction of the past ecological dynamics of the vernal pool studied. The pool originated *c.* 1100 years ago from the infilling of an abandoned palaeochannel and its subsequent fragmentation. It may thus be considered as a legacy of past natural fluvial activity, which ended with the complete channelization and confinement of the River Rhone in 1869 AD. With natural processes disrupted, new pools may need to be artificially constructed in order to preserve the biological communities of alkaline vernal pools of the Rhone delta.

Key Words: Branchiopoda, Charophyta, conservation, Ostracoda, palaeoecology, pollen, temporary wetland

INTRODUCTION

Mediterranean vernal pools are defined as ephemeral rain-filled wetlands that form periodically in permanent depressions. They are subject to irregular, sometimes long-lasting dry stages during which the level of moisture is similar to that of the surrounding uplands (Anonymous 2002, Zedler 2003). They are recognized as being important and endangered biodiversity reservoirs, and many of the resident species have legal protections (Médail et al. 1998, Quézel 1998, Grillas et al. 2004). Compared to the relatively small surface area they occupy in the western Mediterranean basin, they house a significant part of the region's endangered flora (Médail and Quézel 1997, Médail et al. 1998). Directive 92/43/CEE (May 21, 1992) of the European Union, the so-called "Habitats Directive", distinguishes two main types of Mediterranean vernal pools with major conservatory interest: freshwater acidic pools, characterized by rare vascular cryptogams (*Isoetes*, *Marsilea*, *Ophioglossum*, and *Pilularia*), and calcareous, slightly brackish pools, whose flora also consists of endangered species belonging essentially to the genera *Ranunculus*, *Damasonium*, and *Lythrum*.

Despite their conservation importance, vernal pools are still poorly understood, especially as their past and present ecological dynamics are concerned. Their ecological significance is often ignored by the general public, who use them as car parks, fields for cultivation, dumps, or for sediment extraction (Rhazi et al. 2001). Their isolation, both in space and in time (Ebert and Balko 1987), makes them particularly sensitive to human disturbances. Human threats make the study of their past and present ecological dynamics urgent. However, temporal dynamics, including formation, ecological succession, and persistence can be directly evaluated only in the short-term by annually following the evolution of a site. To study longer-term trends, one could conduct either comparisons among pools of different ages (spatial approach) or sediment studies (temporal approach). To the best of our knowledge, only one palaeoecological study (Le Dantec et al. 1998) has focused on the past vegetation history of a vernal pool. Long-term dynamics of these ecosystems, as well as their longevity, are thus virtually unknown.

Studies by Dutil et al. (1959) and Le Dantec et al. (1998) found that a record of past ecological dynamics in vernal pools is trapped and conserved in biological remains. Due to their generally small size and to their location within Mediterranean meso-xerophilous plant formations, vernal pools are likely to provide palaeoecological records at a local scale that correspond to long-term dynamics of plant communities in and around the habitats. Here we present a multidisciplinary palaeoecological study designed to reconstruct past ecological dynamics of a vernal pool, located in the Rhone delta (Camargue, southern France). This work aims to 1) define the potential value and limits of palaeoecological methods in a temporary-habitat context, and 2) relate past ecological dynamics of a vernal pool to current problems of conservation management.

MATERIAL AND METHODS

Study Site

The vernal pool of Cerisières moyennes (43°29′77″ N, 04°40′52″ E, 0.5 m a.s.l.) is one of several pools located within the biological reserve of the Tour du Valat, in the Rhone delta (Camargue, southern France). It is situated on calcareous alluvial sediments of the Ulmet branch of the Rhone palaeochannel (Figure 1a), which was active from 6650–6480 cal. BP (5740 ± 40 BP, Vella et al. 2005) until its artificial separation from the Grand Rhone in 1440 AD (Rossiaud 1994). The first known Ulmet channel flowed from north to south, about 2.5 km west of the Cerisières. During that time, the Ulmet channel meandered through the deltaic plain, switching its channel to produce at least eight fluvial lobes (Arnaud-Fassetta 1998, Raccasi 2003, Vella et al. 2005). One of these lobes, still visible on aerial photographs, was located close to the Cerisières when it was abandoned around 2280 ± 65 BP. From the second century to the sixth century AD, several episodic secondary channels appeared in succession from east to west at the present-day location of the Cerisières pools (Raccasi 2003). In the middle of the fifteenth century, the study area was located a few km north of the seashore, and close to the Ulmet Abbey. It apparently remained undisturbed until the twentieth century, when a drainage ditch was constructed between the pools. It was then used as pasture land for livestock.

The vegetation surrounding the Cerisières moyennes (Figure 1b, Table 1) is composed of Chenopodiaceae salt scrublands (*Sarcocornia fruticosa*, *Halimione portulacoides*, *Salicornia europaea*), helophytic marshes (*Bolboschoenus maritimus*, *Juncus* spp., *Phragmites australis*, *Typha* spp.), and scattered shrubby patches of *Ulmus minor*, *Tamarix gallica*, and *Phillyrea angustifolia*. Plant communities of the vernal pool itself are Mediterranean annual

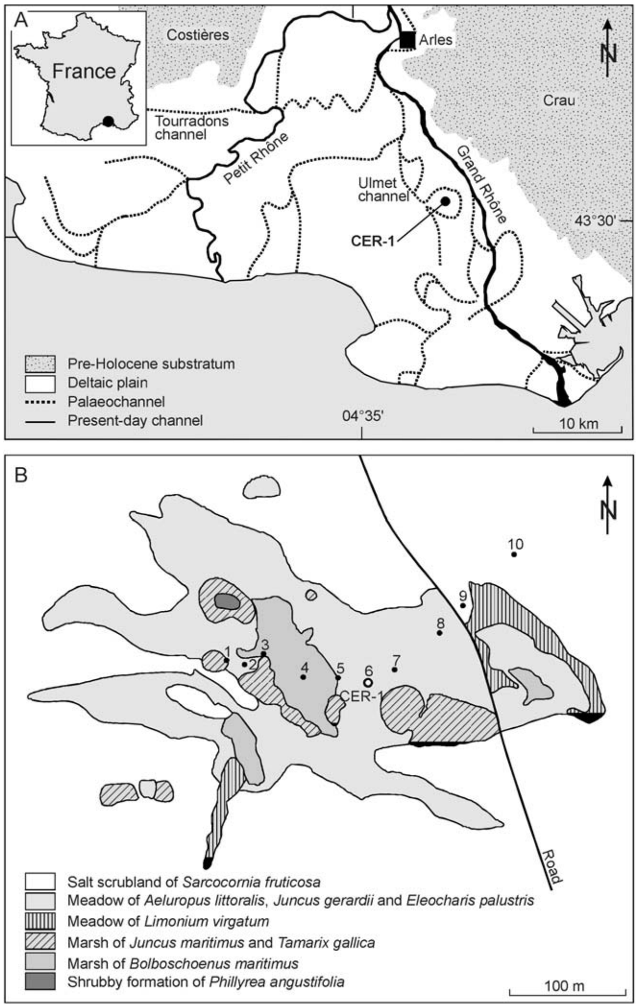

Figure 1. A) Palaeochannels of the Rhone delta and location of the study site. B) Distribution of plant communities on the vernal pool of Cerisières moyennes (grey zone) and location of surface samples and coring site.

amphibious grasslands (phytosociological order of Nanocyperetalia) (Gaudillat and Haury 2002). These communities are composed of endangered and rare plant species (e.g., *Cressa cretica*, *Damasonium polyspermum*, *Lythrum thymifolium*, *L. tribracteatum*, *Nitella opaca*, *Pulicaria sicula*; Table 1) and large Branchiopoda crustaceans (*Imnadia yeyetta*, *Tanymastix stagnalis*). Plants are organized in concentric belts, related to water depth and duration of submersion. The outer belt is characterized by patches of *Juncus maritimus* and *Tamarix gallica*, while the inner one is dominated by *Bolboschoenus maritimus*. Characteristic annual species of vernal pool occupy mainly the intermediary belt, free of helophytic species. Camargue cattle and wild boars regularly enter the pool, and can disturb the surface of the sediment, especially in the late spring when the pool is drying. However, measurements of footprints and wallow scrapes in the compact silty clay show that they generally affect only the top few centimeters and rarely penetrate > 10 cm depth.

Coring, Sedimentology, and Chronology

A 3 m-long sediment core (CER-1) was taken with a mechanized Russian corer (Jowsey 1966) midway between the edge of the pool and its deepest point, within a community of *Damasonium polyspermum* (Figure 1b, point 6). The upper 10–15 cm of the core showed evidence of disturbance, consistent with the similar depths of penetration of $^{210}Pb_{xs}$, ^{137}Cs, and $^{239,240}Pu$ reported by Miralles et al. (2004). This probably resulted from compaction by cattle or boars. Chronological control is based on measurements of short term rates of accretion (Hensel et al. 1998), on geochemical multitracer analyses (Miralles et al. 2004), and on one AMS radiocarbon date (Table 2). Archaeological artifacts found a few hundred meters away from the core site (C. Vella, cited in Miralles et al. 2004) have been used in order to support the local chronology. As discussed by Miralles et al. (2004), this combined evidence leads us to assume an almost constant sediment accumulation rate of 0.45 to 0.55 mm year^{-1} (Figure 2, dashed line).

Complementary information may be provided by sedimentological and geomorphological analyses. In order to determine the past channel hydrodynamics and the means of its infilling, sediment samples were taken along the core depending upon the appearance of sedimentary units; samples were analyzed with a laser granulometer (ISTEEM, Université Montpellier-2). Because no one channel was synchronous to another at Ulmet, and because each channel has been shown to function independently (Raccasi 2003, Rey 2006), no comparative data are available to refine the accumulation rate. Nevertheless, geomorphological information taken from aerial photographs (Raccasi 2003) suggests an increase in the sediment accumulation rate between the second and the sixth century AD, a time when the core site was occupied by episodic secondary channels oriented east-west (referred to earlier). The sedimentological analysis allows us to identify this period as being between 80 and 50 cm depths, and allows us to propose a more realistic age-depth model (Figure 2, continuous line).

Palaeoecological Analyses

We addressed the modern relationship between pollen and vegetation by studying surface samples taken along a transect through the various plant

Table 1. List of modern plants and Branchiopoda crustaceans of the vernal pool of Cerisières moyennes and correspondence of angiosperms with pollen taxa. Superscript numbers indicate the level of protection of rare and endangered species: ^{1}national protection, ^{2}regional protection, ^{3}red list, ^{4}none (Olivier et al. 1995, Grillas et al. 2004).

Family	Taxon	Pollen Taxon
PLANTS		
Alismataceae	*Baldellia ranunculoides* (L.) Parl.	*Alisma*-type
	Damasonium polyspermum Cosson (*D. alisma* subsp. *polyspermum*)^{1,3}	
Apiaceae	*Oenanthe lachenalii* C.C.Gmel.	Apiaceae
	Torilis nodosa (L.) Gaertn.	
Asteraceae	*Achillea ageratum* L.	Asteroideae
	Aster tripolium L.	
	Bellis annua L.	
	Pulicaria sicula (L.) Moris^{2}	
	Leontodon saxatilis Lam. subsp. *saxatilis* (*L. taraxacoides*)	Cichorioideae
Brassicaceae	*Lepidium squamatum* Forssk. (*Coronopus squamatus*)	Brassicaceae
Callitrichaceae	*Callitriche truncata* Guss.	*Callitriche*
	Callitriche sp.	
Caryophyllaceae	*Sagina apetala* Ard.	Caryophyllaceae
Chenopodiaceae	*Atriplex prostrata* Boucher ex DC. (*A. hastata* L.)	Chenopodiaceae
	Chenopodium urbicum L.	
	Halimione portulacoides (L.) Aellen	
	Salicornia europaea L.	
	Sarcocornia fruticosa (L.) A.J.Scott	
Convolvulaceae	*Cressa cretica* L.^{2}	*Cressa cretica*
Cucurbitaceae	*Ecballium elaterium* (L.) A.Rich	Cucurbitaceae
Cyperaceae	*Bolboschoenus maritimus* (L.) Palla (*Scirpus maritimus*)	Cyperaceae
	Carex divisa Huds. subsp. *chaetophylla* (Steud.) Nyman	
	Eleocharis palustris (L.) Roem. & Schult.	
Fabaceae	*Trifolium campestre* Schreb.	Fabaceae
	Trifolium nigrescens Viv.	
	Trifolium resupinatum L.	
	Trifolium sp.	
Gentianaceae	*Centaurium pulchellum* (Sw.) Druce	*Centaurium*
	Centaurium spicatum (L.) Fritsch ex Janch.	
Juncaceae	*Juncus gerardi* Loisel.	Juncaceae
	Juncus maritimus Lam.	
Lamiaceae	*Teucrium scordium* L. subsp. *scordioides* (Schreb.) Arcang.	Lamiaceae
Lythraceae	*Lythrum hyssopifolia* L.	*Lythrum*
	Lythrum thymifolium L.^{1,3}	
	Lythrum tribracteatum Salzm. ex Spreng.^{1,3}	
Oleaceae	*Phillyrea angustifolia* L.	*Phillyrea*
Plantaginaceae	*Plantago coronopus* L.	*Plantago lanceolata*-type
Plumbaginaceae	*Limonium narbonense* Mill.	*Limonium*
Poaceae	*Aeluropus littoralis* (Gouan) Parl.	Poaceae
	Agrostis gigantea Roth.	
	Alopecurus bulbosus Gouan	
	Brachypodium phoenicoides (L.) Roem. & Schult.	
	Bromus hordeaceus L.	
	Elytrigia campestris (Godr. & Gren.) Kerguélen ex Carreras	
	Hordeum marinum Huds.	
	Lolium perenne L.	
	Parapholis incurva (L.) C.E.Hubb.	
	Phragmites australis (Cav.) Steud.	
	Poa annua L.	
	Polypogon maritimus Willd.	
Polygonaceae	*Rumex crispus* L.	*Rumex*
Primulaceae	*Anagallis arvensis* L.	*Anagallis*

Table 1. Continued.

Family	Taxon	Pollen Taxon
Ranunculaceae	*Myosurus minimus* L.	*Ranunculus*-type
	Ranunculus peltatus Schrank subsp. *baudotii* (Godr.) Meikel ex C.D.K.Cook	
	Ranunculus sardous Crantz.	
Rosaceae	*Rubus fruticosus* L.	Rosaceae
Rubiaceae	*Galium palustre* L.	Rubiaceae
Tamaricaceae	*Tamarix gallica* L.	*Tamarix*
Ulmaceae	*Ulmus minor* Mill.	*Ulmus*
Zannichelliaceae	*Zannichellia palustris* L. subsp. *pedicellata* (Walhenb. & Rosén) Arcang.	*Zannichellia*
Characeae	*Chara aspera* Detharding ex Willd. / *galioides* DC.	
	Nitella opaca (Bruzelius) Agardh[4]	
	Tolypella glomerata (Desv. in Loisel) Leonh.	
	Tolypella hispanica Nordst.	
INVERTEBRATES		
Anostraca	*Branchipus schaefferi* Fisher	
	Chirocephalus diaphanus Prevost	
	Tanymastix stagnalis (Linnaeus)[4]	
Notostraca	*Triops cancriformis* (Bosc)	
Spinicaudata	*Imnadia yeyetta* Hertzog[4]	
Cladocera	*Ceriodaphnia reticulata* Jurine	
	Ceriodaphnia laticaudata P.E. Müller	
	Ceriodaphnia dubia (Richard)	
	Chydorus sphaericus (O.F. Müller)	
	Daphnia magna Straus	
	Daphnia curvirostris Eylmann	
	Scapholeberis rammneri Dumont & Pensaert	
	Simocephalus vetulus (O.F. Müller)	
	Simocephalus expinosus (Koch)	

communities of the vernal pool and the surrounding salt scrubland (Figure 1b). Pollen analyses were performed both on surface samples and on the sediment samples taken each 8 cm along the core. Pollen extraction was performed on sediment volumes of 1 cm^3, following the protocol of Faegri and Iversen (1989). Calculations of pollen percentages excluded Pteridophyta spores and aquatic plants because their dispersion and pollination modes could result in overrepresentations. The minimum pollen total was 500 grains for surface samples and 300 for sediment samples, unless microfossil recovery was so poor as to prevent achieving the minimum.

Samples for microfossils were taken every 5–8 cm between the surface and 158 cm depth. Ostracoda, Charophyta gyrogonites and oospores, Branchiopoda resting eggs, and Foraminifera were recovered after washing and sieving (125 µm diameter mesh), picked out with a brush, and then counted. The results are expressed as frequencies per 30 g of dried sediment. Identification of the Charophyta was accomplished by comparison with data from Soulié-Märsche (1989), and the identities of large Branchiopoda (Anostraca, Conchostraca, and Notostraca) and *Ceriodaphnia* ephippia (resting eggs) were based on Thiéry and Gasc (1991), Defaye et al. (1998), and Vandekerkhove et al. (2004). Two species of Foraminifera were also found. Among the microremains, Ostracoda valves were the most frequent, and with a few exceptions, were determined to species level. Some ostracod taxa present

Table 2. AMS radiocarbon dates performed on unidentified organic matter from core Cer-1, vernal pool of Cerisières moyennes. The calibrated age (cal. BP) was computed with the CALIB 5.0 program (Stuiver and Reimer 1993), using the calibration dataset INTCAL04.14c (Reimer et al. 2004). n.a.: not available.

Depth (cm)	Sample Code	Dating Method	^{14}C Age (BP)	Calibrated Age (cal. BP)	$\delta^{13}C$
69–70	Poz-13556	AMS	17150 ± 120	–	−2‰
157–158	Poz-13557	AMS	3275 ± 35	3400–3580	n.a.

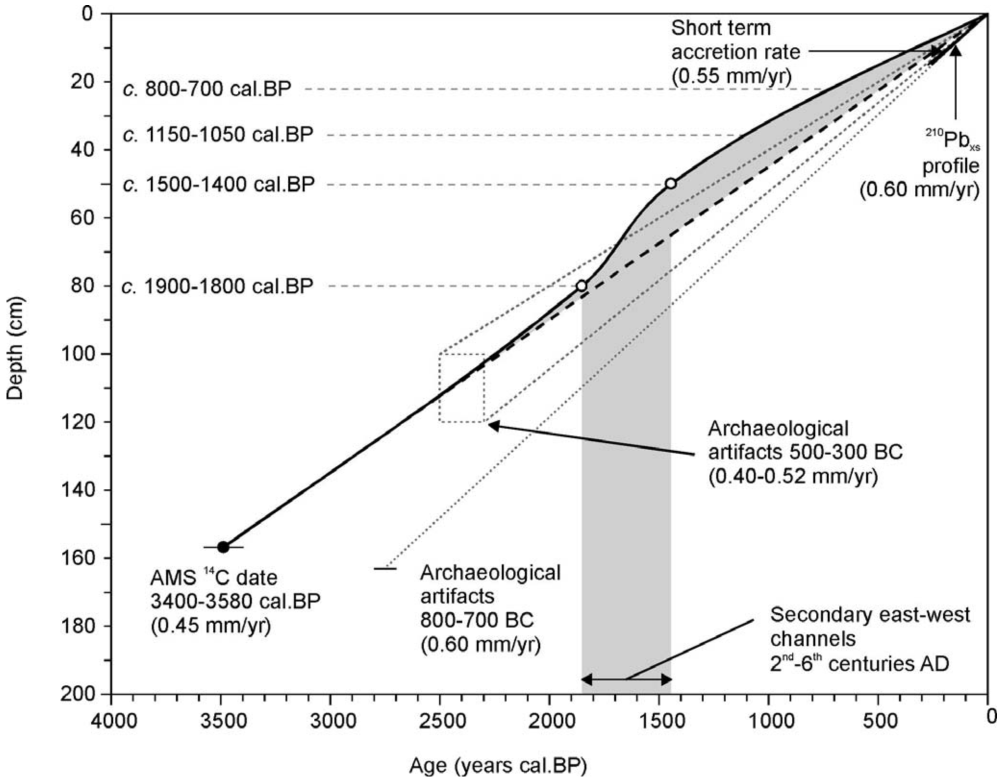

Figure 2. Chronological data available at and around the study site: short term rates of accretion at the Tour du Valat (Hensel et al. 1998), geomorphological features at the study site (Raccasi 2003), ^{210}Pb at the study site (Miralles et al. 2004), archaeological artifacts a few hundred meters away from the study site (Vella C., in Miralles et al. 2004), and radiocarbon date on the studied core (this study).

only in very small numbers or as juveniles were identified only to genus. Fragments of valves from the lower parts of the core section could not be identified, and were excluded from the total. Our ecological interpretation made use of previous studies of wetlands in the Camargue (Steger 1972, Bodergat 1983) as well as studies of the ostracod fauna from channels of the Rhone River (Marmonier and Creuze des Chatelliers 1992, Marmonier et al. 1994). Diagrams were prepared using the computer program GpalWin (Goeury 1997).

RESULTS

Calibration of Modern Samples

Pollen. Pollen spectra from the surface of the Cerisières moyennes were dominated largely by Chenopodiaceae (37%–75%), which dominate the surrounding salt scrublands (Figure 3). The record of these halophytic communities shows an obvious abundance gradient from the margins to the center of the pool. Moreover, zones of bare soils, near *Tamarix* groves and in *Damasonium* hollows, appear to record the surrounding vegetation better than zones of meadow and marsh.

The regional arboreal pollen input, constituting between 9% and 28% of the pollen assemblage, was represented by a meso-xerophilous Mediterranean flora that is comprised by *Pinus halepensis* Mill. on recently burned areas, *Pinus pinea* L. on the sandy coast, and *Quercus ilex* L. in the foot-hills. The riparian forests of the Rhone River (*Populus* spp., *Alnus glutinosa* (L.) Gaertn., *Fraxinus angustifolia* Vahl., *Ulmus minor* Mill., and *Salix* spp.) produced a weak pollen signal, consistent with their reduced geographical extent and low pollen production. We also noted a small but diverse long-distance component of *Abies*, *Betula*, *Carpinus*-*Ostrya*, *Cedrus*, *Corylus*, *Fagus*, Myrtaceae, and *Picea*, which are taxa characteristic of montane zones of the Massif Central and southern Alps.

Plant communities of the vernal pool itself, dominated by Asteroideae, Cyperaceae, and *Limonium*, represented 8%–28% of the pollen record. Among them, the characteristic taxa of the pool (*Alisma*-type, *Centaurium*, *Cressa cretica*, Juncaceae, *Lythrum*, *Ranunculus*-type, and *Zannichellia*) present numerically small but regular occurrences between 6% and 12%. In regards to its scarce distribution, *Plantago lanceolata*-type (locally represented by *P. coronopus*) had surprisingly high percentages (be-

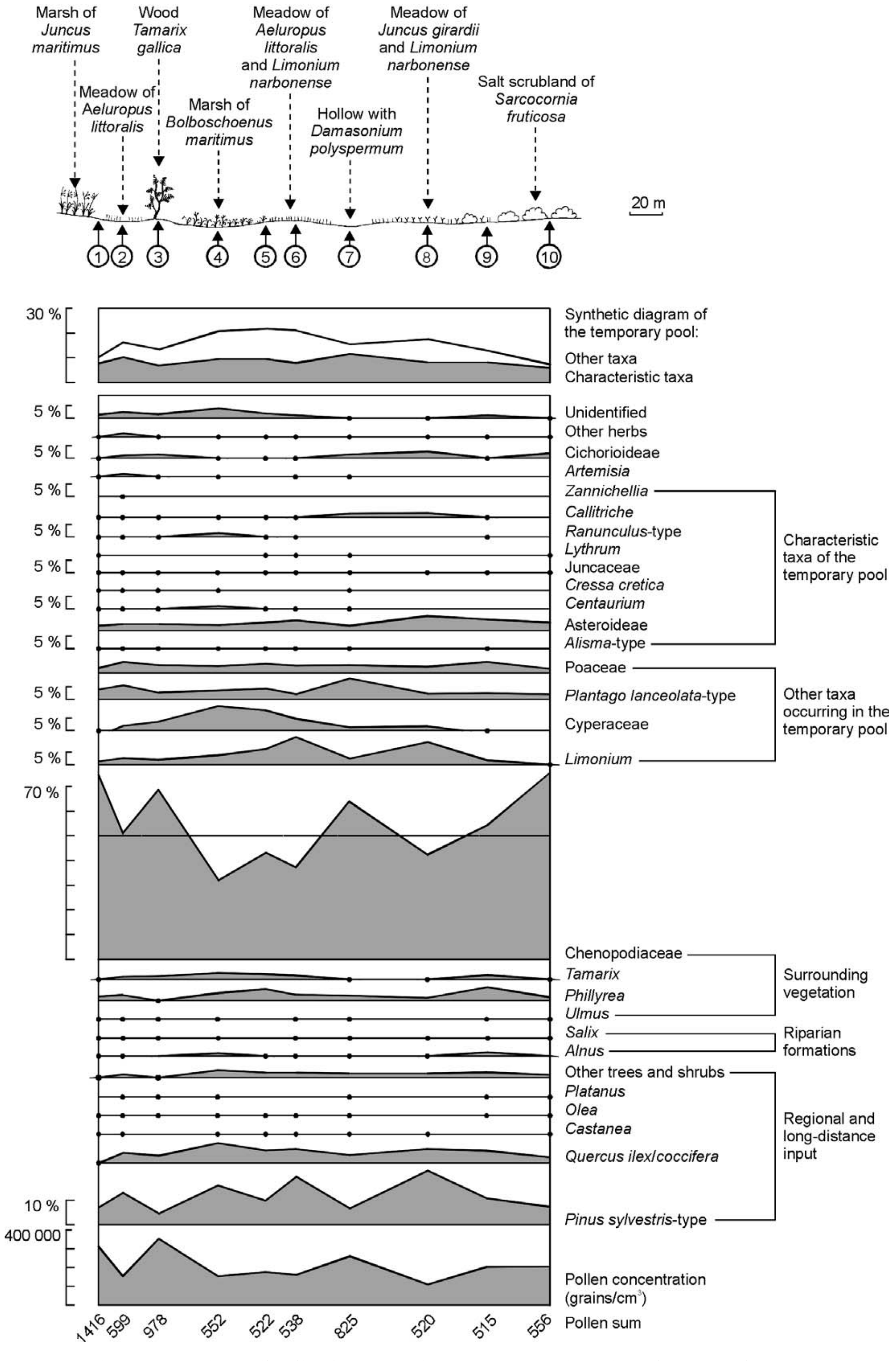

Figure 3. Transect of modern plant distribution (numbers correspond to location on Figure 1) and modern pollen spectra, Cerisières moyennes (analysis: S. D. Muller 2004). Dots represent < 1%.

tween 2% and 8.5%), which probably resulted from being wind-pollinated. Three woody taxa occur around and within the pool: *Ulmus* (three individuals) attained a pollen abundance of 0.9%; *Phillyrea* (a single grove) had relatively high pollen percentages (0.8%–5.4%); and *Tamarix*, which was scattered throughout the pool, was poorly represented (0.1%–2.7%). *Tamarix* pollen, while abundantly produced, is weakly dispersed and usually rare in sediments (Triat 1971).

Composition of modern pollen emphasized the very local character of the pollen record within the vernal pool of Cerisières moyennes, and showed how the pollen assemblages reflected the vegetation within a radius of a few hundred meters. If pollen is sufficiently preserved in the sediment, the fossil spectra can be used to reconstruct the past dynamics of both the surrounding (extra-local) and local plant communities.

Charophyta. Water depths in the vernal pool of Cerisières moyennes varies from temporal patterns of flooding and drying. Living aquatic species were described during 2000–2001. The coring site, located in the intermediary belt, was flooded to about 30 cm and the water soon subsided; only a few charophytes of the genus *Tolypella* germinated there. The main depression, which lies about 80 m to the south of the core site, remained inundated with water depths $>$ 1 m until early summer. The vernal charophyte species *Nitella opaca*, *Tolypella glomerata*, and *T. hispanica* developed there during winter and early spring, followed by species of the genus *Chara*. By May 2001, numerous individuals of the dioecious species *Chara aspera* and *C. galioides* were intermingled with the decayed remains of *Tolypella* in the central part of the pool.

Chara aspera and *C. galioides* are closely related species that are characterized by the size of their antheridia. These structures do not fossilize (Bonis et al. 1993), although some other morphological differences in the plants can be seen (Flor-Arnau et al. 2006). Both species show abundant fructification, including fully mature and calcified oospores, which provide fossil gyrogonites (Soulié-Märsche 2002). The oospores and gyrogonites of these taxa have very similar morphology and their dimensions largely overlap (Soulié-Märsche 1989); they could not be distinguished within the sediments of the core and are considered here as a species-complex, *C. aspera/galioides*. Based upon ecological characteristics observed in the pool, we inferred that the presence of gyrogonites of *C. aspera/galioides* in the core sediments was indicative of periods of long-lasting submersion, with water depths exceeding 1 m. On the other hand, places where only *Tolypella* species occurred corresponded to periods of shorter duration flooding (Grillas 1990).

Branchiopoda. A preliminary study reported five large branchiopod species from the vernal pool of Cerisières moyennes: three Anostraca (*Chirocephalus diaphanus*, *Tanymastix stagnalis*, and *Branchipus schaefferi*), one Notostraca (*Triops cancriformis*), and one Spinicaudata (*Imnadia yeyetta*) (Nourisson and Aguesse 1961). Only the two most abundant species of the pool, *T. stagnalis* and *I. yeyetta*, were recovered from the core. The others, locally rare, are probably poorly represented within the egg bank. Moreover, while all species are known to live in ephemeral ponds and to survive desiccation, *T. cancriformis* and *C. diaphanus* require longer wet phases to complete their life cycles. It was noteworthy that these two taxa were collected from the longer hydroperiod, southern portion of the pool of Cerisières moyennes during 2006–2007. As shown by Thiéry (1991, 1997), crustacean egg banks are not always uniformly distributed over pools and the distribution pattern of the resting eggs in a temporary pool differs from species to species. *Triops* and *Chirocephalus* in particular deposit their eggs in the peripheral parts of pools, corresponding to the highest water levels.

Past Sedimentary and Ecological Dynamics Inferred from Coring

The Depositional Environments. The lithological log (Figure 4) shows successive alluvial and stagnant sedimentary facies in the core. At the base of the sequence, extensive coarse sands with no foraminifers or shells correspond to the bottom sediments of an active channel. The zone between 230 and 210 cm marks a transition between the coarse sand facies and fine-grained silt and silt-clay deposits; these represent the abandonment of the channel by the Rhone River. This event occurred after the initiation of the Ulmet Rhone around 6650–6480 cal. BP (Vella et al. 2005), and may be dated around 4600–4200 cal. BP if we extrapolate the calculated mean sediment accumulation rate. These fine-grained clastics, including layers of fine to very fine sand, characterize the infilling of the abandoned channel, which continued to carry flood waters intermittently (Rey 2006). The deposits become essentially silt-clay above 80 cm, which probably represents the final abandonment of the channel around 1900–1800 cal. BP (Figure 2). The sediments that accumulated between 80 and 50 cm could be partially attributed to the presence of secondary east-west channels that

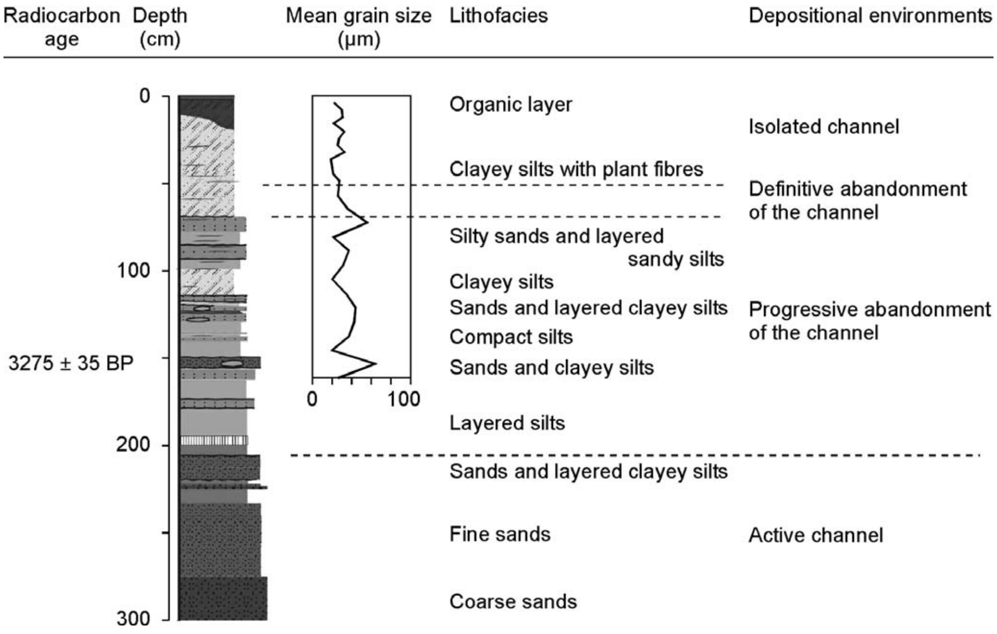

Figure 4. Sedimentology of core CER-1, Cerisières moyennes (analysis: T. Rey 2006).

flowed through the Cerisières area from the second to the sixth century AD (Raccasi 2003). The nature of sediments therefore attests to the episodic flooding of the core site up to the current time.

Ostracoda and Foraminifera. A lower one (zone 1, Figure 5a), between 157 and 56 cm depth, contained a scarce ostracod fauna with a fluctuating, sometimes high, diversity associated with a few lagoonal foraminifers (*Ammonia beccarii* and *Elphidium*). The abundance of ostracod valves is higher in the sandiest samples and lower in the siltiest ones. Two sterile levels, at 96 and 56 cm are very fine grained and show evidence of a slight pedogenesis such as a few ferruginous and calcareous concretions around root remains. Different associations appear mixed in the same samples. The lagoonal-estuarine species (*Cyprideis torrosa*, *Leptocythere* spp., *Loxoconcha elliptica*, *Cytheromorpha fuscata*) are always represented by small instars. Those valves as well as the foraminifers are never larger than the sand grains found in the corresponding sample and were probably transported from nearby lagoons into the coring site. The freshwater ostracods contain some ubiquitous species of the Rhone plains and channels (*Pseudocandona* cf. *albicans*, *Cypridopsis vidua*, *Potamocypris*), some permanent water species (*Darwinula stevensoni*, *Limnocythere* spp.), and some species that are restricted to interstitial waters within the sandy sediments of the river channels (*Pseudocandona zschokkei*, *Schellencandona triquetra*, *Fabaeformiscandona wegelini*). All these freshwater species form an association typical of the sandy infilling of the Rhone channels. They are represented by adults, which are larger and heavier than the sand grains, as well as immatures, and they characterize the *in situ* environment.

The upper zone (zone 2, Figure 5a), from 49 cm upwards, contains an increasingly abundant ostracod fauna with a stable but low diversity. The assemblages, dominated by *Ilyocypris* (*I. bradyi*, *I. gibba*), *Candona* (*C. neglecta*), and *Pseudocandona* (*P.* cf. *albicans*) species, are typical of today's oligohaline vernal pools of the Rhone delta. The most frequent *Ilyocypris* species was *I. bradyi*, while *I. gibba*, although more widespread in the Rhone delta, only appeared sporadically. *Ilyocypris bradyi* is often described as preferring, but not being exclusively confined to, slowly running waters; however, it also prefers biotopes with dense vegetation. *Ilyocypris gibba* is more of a stagnant water species and is also slightly more euryhaline and eurythermic. No lagoonal-marine species were found, which indicates that there was no connection between the sea or lagoons and the pond. Fluctuating numbers of *Heterocypris salina*, which is more tolerant of higher salinities, could suggest fluctuating total dissolved solid concentrations, a condition that probably developed from seasonal evaporation. Two subzones (2a and 2b, Figure 5a) could be distinguished. Between 49 and 21 cm, some of the most common species of the channel were present; some infrequent connection with a channel might still have occurred. The most euryhaline species of the assemblage (*I. gibba*, *H. salina*, *P.* cf. *albicans*) were also present. In the upper 20 cm, these species

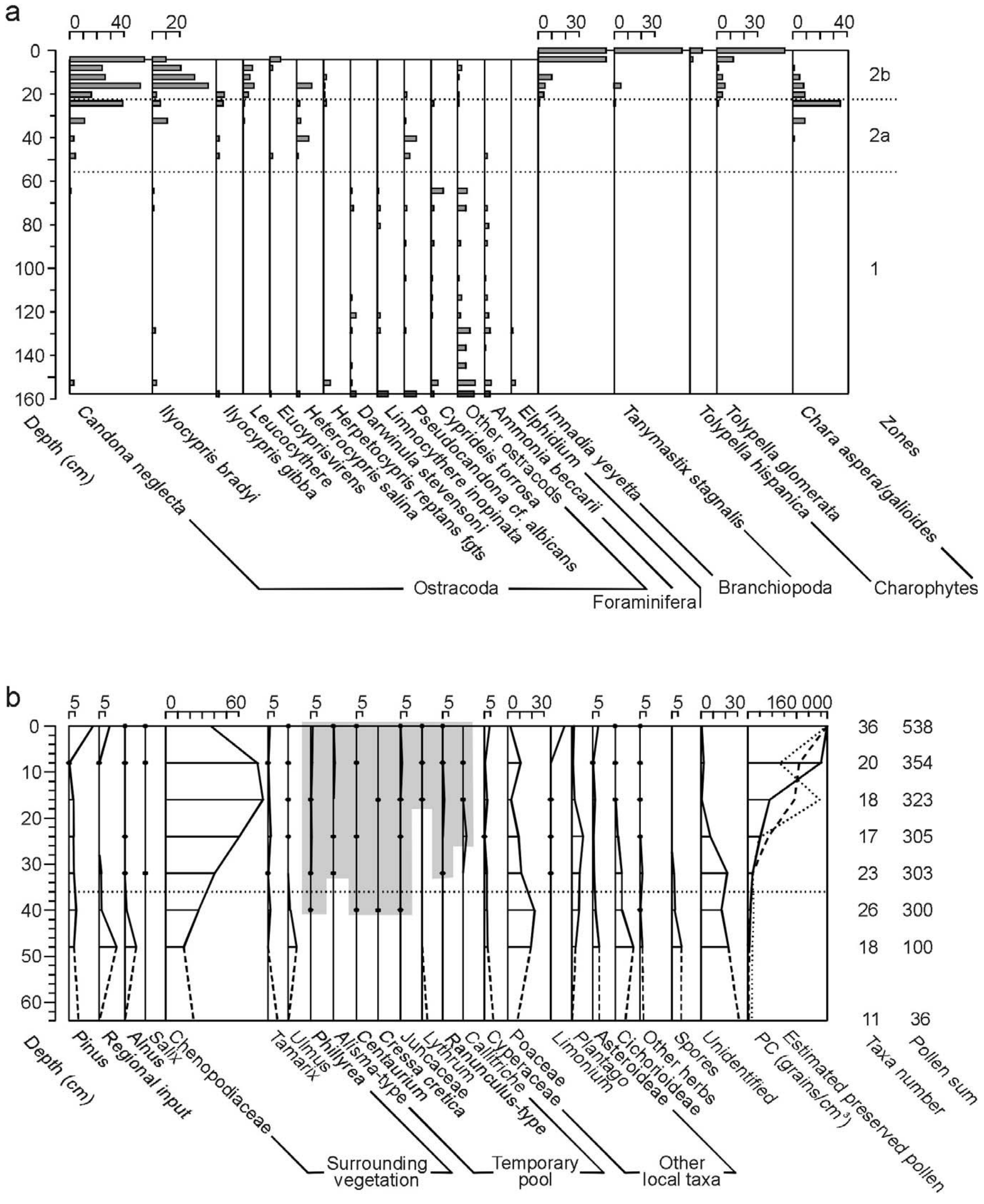

Figure 5. Simplified diagrams of core CER-1, Cerisières moyennes. A) Concentrations of ostracods, foraminifers, and charophytes (analysis: H. Bruneton, I. Soulié-Märsche and A. Thiéry, 2005–2007). The concentrations are expressed in number of remains (ostracod valves, gyrogonites or oospores) per 30 g of dry weight of sediment. B) Pollen percentages (analysis: S. D. Muller 2005). Dots represent $< 1\%$ occurrences. The line identified as PC includes pollen concentrations (continuous line) and the proportion of preserved pollen grains estimated from the mean percentage of Cichoriodeae and spores (dashed line) and from the percentage of unidentified grains (dotted line). Grey area represents the vernal pool taxa.

decline or disappear. High numbers of *I. bradyi* reveal the absence of floods and short submersion periods, with less fluctuating salinity and vegetation.

Females of one unidentified *Leucocythere* species were also found. The valves were well preserved and indicate an *in situ* population. This species closely resembles *L. mirabilis*, but the latter is an inhabitant of permanent water, and is a cold stenothermic species preferring oligohaline waters. It would be surprising to find a cytherid in a temporary eurythermic pond with a distribution following that of *I. bradyi* and other species tolerant of intermittent drying. One species of the genus, though, is known to be one of the two cytherid capable of producing desiccation resistant stages (Danielopol et al. 1989). This species, *L. algeriensis*, is very closely related to *L. mirabilis*, and might be the one found in the Cerisières pool. Its disappearance from samples in the upper core sample might indicate that it is not as tolerant of some ecological stresses as *Ilyocypris* and *Candona* species, including, possibly the duration of the dry season.

Branchiopoda. The short duration of present-day inundation is consistent with the abundance of resting eggs of the branchiopods *Imnadia yeyetta* and *Tanymastix stagnalis* in upper sediment layers (Figure 5a, Figure 6a–d). Both taxa live in vernal pools and have very short life cycles. In addition, the presence of ephippia of the cladoceran species *Ceriodaphnia* aff. *dubia* (which is common in all local temporary ponds) corroborates the short duration of the current hydroperiod in the site (Figure 6e). Because the deposition pattern of branchiopod resting eggs is species-specific (Thiéry and Gasc 1991), more cores would be necessary to reconstruct the complete spatial distribution of the water body.

Charophyta. Basal levels of the core, from 158 to 50 cm below the surface, did not contain any charophyte remains (gyrogonites, oospores; Figure 5a). A hydrological change occurred between 40 and 33 cm, accompanied by local development of charophyte populations dominated by *Chara aspera/galioides*. These taxa, which presently grow abundantly in the deepest part of the pond, characterize a temporary hydrological regime with inundation periods of about 5–7 months. The absence of gyrogonites in the upper 30 cm of the core suggests a significant lowering of the water depth after floods, and consequently a reduction of the size of the submerged area.

The increasing abundance of *Tolypella* oospores from 20 cm depth to the surface indicates that the duration of submersion periods decreased over time, rapidly becoming short, and even ephemeral. Both species present, *Tolypella glomerata* and *T. hispanica*, are typically residents of ephemeral vernal pools (Corillion 1957, 1961, Grillas 1990). Based upon assemblages above 12–13 cm depth, the local environment appears to have been similar to that of today, with a terrestrial stage of longer duration than the aquatic one. The core was located at the margin of the deeper zone of Cerisières moyennes, which is irregularly flooded and holds water for only a few months in winter.

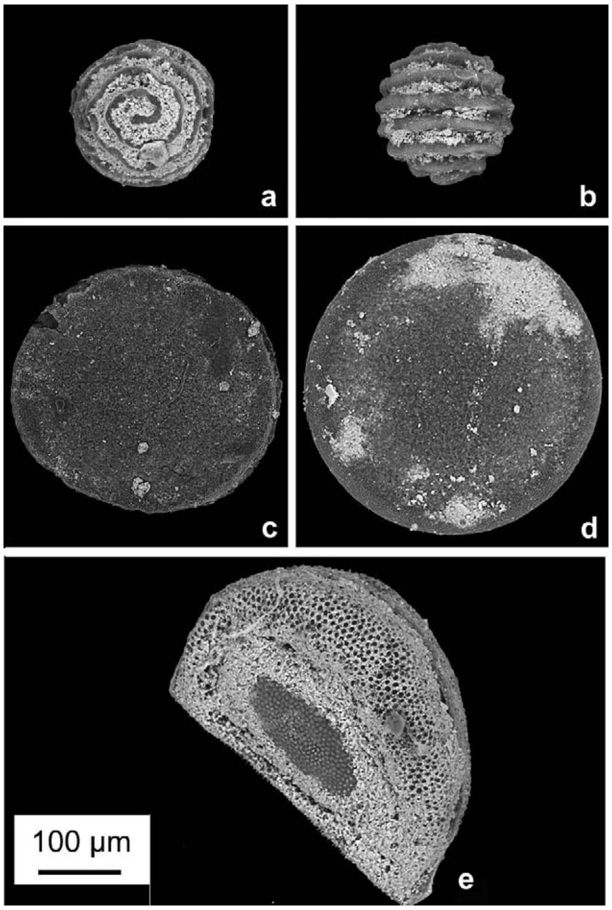

Figure 6. Resting eggs recovered from the sediments of core CER-1, Cerisières Moyennes, SEM photographs. A and B) *Imnadia yeyetta* (Branchiopoda), apical and lateral view. C and D) *Tanymastix stagnalis* (Branchiopoda), upper sides. E) Cladoceran ephippium of *Ceriodaphnia* aff. *dubia*. Scale bar 100 µm, common to all pictures (analysis: A. Thiéry 2006).

Pollen Data. Pollen was retrieved only from the upper 64 cm of the core. Pollen concentration decreases with depth, whereas unidentified grains, spores, and Cichorioideae increase. Our pollen diagram is subdivided into two zones (Figure 5b). The lower zone, below 36 cm, is characterized by relatively high percentages of regional pollen, *Alnus*, *Ulmus*, and Poaceae, while the upper one shows a strong increase in Chenopodiaceae percentages coinciding with the appearance of *Limonium* and vernal pool taxa. This points towards a major palaeoenvironmental change (Figure 2) as the surrounding landscape changed from a freshwater environment, favorable to riparian vegetation (*Alnus*, *Ulmus*) and helophytic communities (Poaceae), to salt-influenced Chenopodiaceae scrubland in a mosaic with vernal pools developed in shallow depressions. The lack of a pollen record for common riparian forest trees (*Populus*, *Fraxinus*) may result from poor preservation of their pollen grains in sediments (Triat-Laval 1979).

DISCUSSION

Interpretation of Pollen Spectra from Vernal Pool Sediments

Taphonomic processes are evident within the sediments of the vernal pool of Cerisières moyennes through the progressive decrease of pollen concentration with depth, and an increasing proportion of unidentified grains, spores, and Cichorioideae (Figure 5b). These features reveal a selective degradation of pollen assemblages, resulting in the over-representation of the most resistant pollen types, such as monolete spores and Cichorioideae (Cushing 1967, Bottema 1975, Coûteaux 1977, Reille 1978, Coles et al. 1989). Progressive destruction of pollen might be attributed to the calcareous nature of the sediments and to the temporary hydrological regime, which regularly exposed fossil assemblages to desiccation and oxidation. Three independent indicators may be useful for estimating the proportion of destroyed pollen along the sedimentary core: 1) pollen concentration, which should be relatively constant with a stable regional vegetation and consistent accumulation rate, 2) the proportion of Cichorioideae and monolete spores, which is generally below 5% in well-preserved recently deposited pollen (Triat-Laval 1979, Andrieu-Ponel et al. 2000a, 2000b, this study), and 3) the proportion of degraded, unidentifiable grains, which should reflect the progressive destruction of diagnostic features (Hall 1981). Despite some discrepancies among the three indicators in the upper part of the sequence, they all provided consistent results and estimated that $<$ 10% of the pollen assemblages were preserved at 32–40 cm depth, and only 1% to 3% in the deeper layers (48–64 cm).

Nevertheless, the pollen spectrum was similarly rich and diverse down to at least 48 cm below the surface, which could be attributed to two features. First, a high resistance to degradation by the main pollen types (Chenopodiaceae, *Alnus*, *Ulmus*, Cichorioideae, and spores) permitted recognition even in deep layers. Second, differential degradation appeared to affect pollen grains independently from taxonomy; the most abundant types had a wide range of degradation (e.g., Chenopodiaceae), and the most fragile types were observed even in the deepest layers (e.g., Cyperaceae, Poaceae). In comparison with the clearly degradation-related proportion of Cichorioideae and spores, and despite the reduced number of well-preserved taxa in the fossil pollen spectra, the unexpected trends of Chenopodiaceae, Cyperaceae, and Poaceae may reflect their actual past dynamics and thus allow reconstructing palaeoecological changes.

Origin of Salt Scrublands

Pollen assemblages (Figure 5b) revealed that between 48 and 33 cm depths, freshwater plant formations (riparian forests and helophytic marshes) were replaced by salt-influenced communities characterized by Chenopodiaceae and *Limonium*. This species replacement resulted from a major hydrological change related to the progressive abandonment of the Ulmet channel. Drought and salinization occurred as natural processes, corresponding to the evolution of abandoned channels to lagoon systems (Astier 1970, Pons et al. 1979, Rey 2006), and not as a human-induced phenomenon from the Rhone embankment. Similar environmental changes were observed around 4000–3000 cal. BP in the northwestern part of the Rhone delta during the abandonment of the Tourradons channel (Rey et al. 2006; Figure 1a). Thus the influence of salt waters extended far inland, and point to a situation very different from other deltas, such as the Danube, where freshwater flows limit marine influence to a narrow coastal belt.

Initiation and Development of the Vernal Pool

The palaeoecological and sedimentological data showed four successive phases of pool development since *c.* 3500 cal. BP (Figure 7). The first one (160–80 cm) corresponds to channel infilling while a fluvial freshwater feature from *c.* 3500 to 1900–1800 cal. BP. The sediments contained neither pollen nor charophytes. Analogous situations can be found in present-day abandoned channels in the delta, which generally have shallow water depths and high turbidity that hinders the development of aquatic plants. The occurrence of brackish water ostracods and foraminifers indicates proximity to a seashore

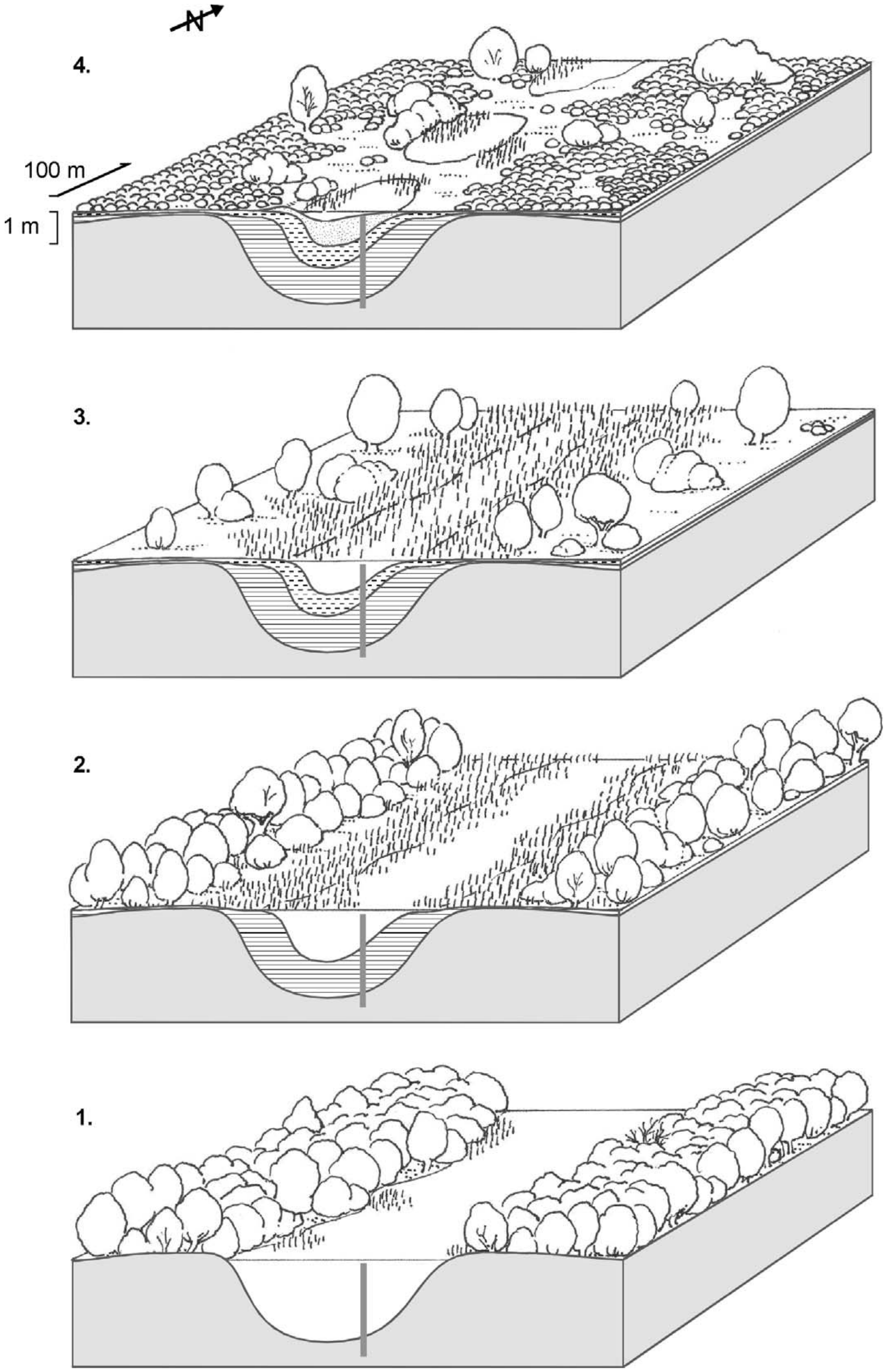

Figure 7. Schematic bloc diagrams illustrating four stages of the space-time evolution of the Cerisières moyennes palaeoenvironment. 1) Active channel, riparian forest (> *c.* 3500 cal. BP). 2) Partially abandoned channel, marshes and riparian forest (*c.* 2700–2600 cal. BP). 3) Abandoned channel, marshes and sparse trees (1500–1400 cal. BP). 4) Isolated temporary pools within salt scrublands (today). The vertical grey bar represents the core CER-1.

or lagoon, and confirms the close co-existence with brackish and fluvial environments.

Phase 2 (80–50 cm) corresponds to the final period of channel infilling, and represents a habitat that was probably fed sporadically by a series of secondary channels oriented east-west between 1900–1800 and 1500–1400 cal. BP. The diminishing number of channel ostracods in the assemblages indicates a disconnect from the active channel except during flood episodes. The presence of juvenile lagoonal ostracods shows that a downstream connection with lagoon areas still existed. The riparian communities at the top of this zone (Figure 2) supported populations of *Alnus glutinosa* and *Ulmus minor*, which are the only extant species of these genera growing in the French Mediterranean coastal plain. While *A. glutinosa* is presently rare in the Rhone delta, the historical record suggests it was abundant close to the seashore. Present-day riparian vegetation of the Rhone delta is restricted to some residual and highly degraded forests that are not representative of ancient conditions. The abundance of *Alnus* in the pollen record may result either from an over-representation of its pollen in fossil assemblages or to a recent decrease in abundance linked to declines of riparian forests.

Phase 3 (50–22 cm) corresponds to the initiation of a closed pool with a temporary hydrological regime between 1500–1400 to 800–700 cal. BP. The pollen of Poaceae and the fibers found in the sediments suggest that the first stage of the temporarily inundated channel was probably characterized by helophytic marshes of *Phragmites australis*, a species widespread today across the whole delta. *Heterocypris salina* and *Pseudocandona* cf. *albicans* ostracods also occurred, which were progressively replaced by *Candona neglecta* and *Ilyocypris bradyi*, indicating the onset of a typical vernal pool environment and decreasing salinity. The appearance of *Alisma*-type, *Centaurium*, *Cressa cretica*, *Ranunculus*-type, and *Callitriche* clearly marks the development of typical vernal pool macrophytic communities. The concentrations of gyrogonites and oospores during this phase indicate dense carpets of *Chara aspera*/*galioides*, which both require inundation periods of 5–7 months and oligohaline conditions. The progressive replacement of lagoonal ostracods by *Candona neglecta* and *Ilocypris bradyi* also indicates a lowering of salinity.

Phase 4 (22–0 cm) is characterized by an increasing presence of *Tolypella* oospores, indicating that submersion periods were rapidly becoming short and sporadic. Both species identified, *Tolypella glomerata* and *T. hispanica*, are typical of vernal pool development (Grillas 1990). Ripening of *T. glomerata* oospores occurs at a salinity ≤ 12‰ (Winter et al. 1996). This is also consistent with an abundance of resting eggs of the branchiopods *Imnadia yeyetta* and *Tanymastix stagnalis*, and with a late colonization by amphibious macrophytes (*Alisma*-type, *Lythrum*, and even Juncaceae) and the ostracod *Ilyocypris bradyi*. Above 12–13 cm depth, the local environment appears to have become similar to that of today, with a terrestrial stage of longer duration than the aquatic one. The decreasing duration of submersion may have caused the ostracod *Leucocythere* to disappear and favored very recent colonization of the pool margins by *Limonium narbonense*, a species that tolerates moderate salinity and short periods of inundation.

CONCLUSIONS

Our geomorphological and sedimentological surveys informed us about past changes in the physical context of the environment. Ostracod, foraminifer, branchiopod, and charophyte assemblages provided information on salt concentration, water depth, and hydroperiod. Pollen records allowed us to reconstruct past vegetation dynamics, despite the progressive degradation of fossil assemblages with depth. Concurrence of results among the different approaches enhanced overall reliability, and allowed us to better understand the long-term developmental history of the vernal pool. However, because our work was limited to a single core, it only provides a very localized perspective of the internal dynamics of the pool. A transect of cores from the margin to the center of the pool would be necessary to obtain a complete picture.

The Cerisières moyennes probably originated *c.* 1100 years ago from the infilling of an abandoned palaeochannel and its subsequent fragmentation (Figure 7). This process likely resulted in the formation of strings of pools, suggesting a past abundance of these ecosystems in fluvial systems with meandering channels. Abandoned channels at diverse stages of evolution probably existed. The vernal pools of the Natural Reserve of La Tour du Valat are relicts of habitats that were historically much more abundant, and therefore represent a valuable and endangered heritage of a past fluvial system. These habitats will disappear as remnant channels naturally evolve or are transformed by anthropogenic activity. Our results imply that present-day conservation measures might be ineffective without the artificial construction of new pools.

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