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Mudwhelks and mangroves: The evolutionary history of an ecological association (Gastropoda: Potamididae)

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Abstract

Most of the 29 living species of Potamididae show a close association with mangroves. The trees provide the snails with shelter, protection from predators, a solid substrate and sometimes food. Using sequences from three genes (nuclear 18S rRNA and 28S rRNA, mitochondrial COI) we derive a molecular phylogeny and recognize six living genera (*Terebralia*, *Telescopium*, *Tympanotonos*, *Cerithidea*, *Cerithideopsis*, *Cerithideopsilla*). The oldest modern genera (*Terebralia*, *Cerithideopsis*) appeared in the Tethyan realm in the Middle Eocene, shortly after the origin of mangrove trees. Whereas most potamidid genera are now restricted to either the Indo-West Pacific (IWP) or to the eastern Pacific plus Atlantic (EPA), sister clades of *Cerithideopsis* survive in both realms. Based on a reinterpretation of the fossil record (particularly of the monotypic *Tympanotonos* and extinct *Potamides*), and parsimonious reconstruction of ancestral habitats, we suggest that the living potamidids are an adaptive radiation that has always been closely associated with mangroves. The specialized tree-climbing groups *Cerithidea* and *Cerithideopsis* were independently derived from mud-dwelling ancestors. *Cerithideopsilla cingulata* (a species complex in the IWP) and '*Potamides*' *conicus* (in the Mediterranean and Indian Ocean) form a single clade within the genus *Cerithideopsilla*. This refutes the hypothesis that '*P.*' *conicus* is the sole relict of the Tethyan *Potamides* that has occurred in the Mediterranean region since the Palaeocene. Instead, the phylogeny and fossil record suggest that an ancestor of *Cerithideopsilla conica* with planktotrophic larvae dispersed from the IWP to the Mediterranean in the Middle Miocene, that its direct development evolved in the Mediterranean during the Pliocene, and that it reinvaded the Indian Ocean during the Plio-Pleistocene.

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Keywords: Adaptive radiation; Tethys; *Cerithidea*; *Potamides*; Ribosomal RNA; COI

1. Introduction

The mangrove ecosystem has an ancient history. From the record of macrofossils and pollen, the earliest appearance of a modern mangrove genus, the palm *Nypa*, has been documented in the Late Cretaceous, and most genera of the Rhizophoraceae are known by the Early Eocene (about 50 Ma). By the Middle to Late Eocene most modern mangrove genera showed a worldwide tropical and subtropical distribution, centred on the Tethyan Seaway (Elli-

son et al., 1999; Plaziat et al., 2001). This continuous distribution was disrupted by the closure of the seaways in the Middle East at the end of the Early Miocene (16–18 Ma, Harzhauser et al., 2002), leading to the present separation between the Atlantic plus Eastern Pacific (AEP), and the Indo-West Pacific (IWP) biogeographic regions (McCoy and Heck, 1976; Ellison et al., 1999). Plaziat et al. (2001) have suggested that the separation of the mangroves of the AEP from those of the IWP began much earlier, with the global cooling of the early Oligocene, followed by aridity in Europe in the early Miocene, which combined to reduce the mangroves of the Tethyan Seaway to isolated stands of *Avicennia* alone (but see Herman and Marquet, 2007 and Doutrelepon, 2007 for a probable brief

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reimmigration of Rhizophoraceae in Belgium during the Middle Miocene). At the present time the species richness of mangroves in the IWP province exceeds 30 in the central diversity focus, whereas it is less than 10 anywhere in the AEP (Ellison et al., 1999; Ellison, 2002).

Although the Tethyan origin and vicariant history of mangroves are understood in broad terms, the factors contributing to their diversity gradient are not. This has led to calls for comparative study of their associated fauna (Ellison, 2002). Of this fauna, the molluscs have the best fossil record, and are taxonomically relatively well understood. The marine mangrove-associated molluscs are not very diverse, perhaps because of the unfavourable combination of heavy sediment load, acidic and anoxic soil, deep shade (restricting algal productivity) and intense crushing predation. Nevertheless, at least in the IWP there exists a suite of mangrove-associated molluscs sufficiently characteristic that their occurrence in the fossil record is indicative of marine palaeomangrove environments (Oyama, 1950; Plaziat, 1984, 1995). (Included as mangrove environments are the tropical ‘saltwort associations’ of *Arthrocnemum*, *Sesuvium* and halophytic grasses that replace mangroves in regions of low input of freshwater or high evaporation, e.g. Macnae, 1968, and share many molluscan species in common.) The mangrove-associated molluscs of the IWP include one or two species each of the gastropods *Nerita* and *Cerithium*, both of which are genera otherwise found on rocky substrates in shallow-water and intertidal environments. At a higher taxonomic level, the bivalve genera *Geloina* and *Enigmonia*, and the gastropods *Littoraria* (Littorinidae), *Rhizophorimurex* (Muricidae), *Cassidula* and *Ellobium* (Ellobiidae) are largely restricted to mangrove environments. However, only a single molluscan family, the Potamididae (mudwhelks or mud creepers), is found almost exclusively among mangroves and in their suite of associated tidal habitats. Potamidids are among the most specialized molluscan inhabitants of this ecosystem, and a long evolutionary association between mudwhelks and mangroves has been hypothesized (Glaubrecht, 1996, 1997, 1999).

Traditionally, the Potamididae included two subfamilies, Potamidinae and Batillariinae (e.g. Thiele, 1929; Wenz, 1938). However, data on sperm ultrastructure (Healy, 1983), anatomy (Houbrick, 1988; Glaubrecht, 1996) and DNA sequences (Lydeard et al., 2002) have shown that these should be ranked as distinct families that are not sister taxa within the Cerithioidea. Shell forms can be similar, so that some differences persist in the classification of fossil members of these families; for example, we assign *Granulolabium* to the Batillariidae (Lozouet, 1986; Lozouet et al., 2001; Harzhauser, 2004) while others still retain it in Potamididae (Kadolsky, 1995; Kowalke, 1998, 2003). As presently understood, the Potamididae consist of five living genera: *Potamides*, *Cerithidea*, *Terebralia*, *Telescopium* and *Tympanotonos*. These each occupy a distinct range of microhabitats within mangrove forests, among saltworts, in saltmarsh and on adjacent tidal flats

and saltpans. As reviewed below, all but *Cerithidea* are of low taxonomic diversity and now show restricted biogeographic range, although a long Tertiary fossil record in the Tethys Sea has been claimed for all of them.

Potamides, type genus of the family, is based on the fossil *P. lamarkii* from the Oligocene of Europe. During the Miocene and Pliocene it became diverse in the European Tethys and Paratethys (Lozouet, 1986; Kowalke, 2001a, 2003). Only a single extant species is attributed to the genus, distributed from the Mediterranean to the Red Sea, Arabia and the western Indian Ocean. Not only does it extend into higher latitudes (40°N) than other potamidids, but unlike most of them it does not have an obligate association with the mangrove habitat, occurring in brackish and hypersaline lagoons, in saline lakes, at the fringes of saltpans and on mudflats adjacent to mangroves (Lozouet, 1986; Plaziat, 1993; Kowalke, 2001a). Its shell is highly variable, and neither its anatomy nor relationships have been studied.

Three subgenera have been recognized within *Cerithidea sensu lato*, based on the morphology of the shell and radula, and this division corresponds with differences of habitat and biogeographic distribution (Houbrick, 1984). Members of *Cerithidea sensu stricto* are restricted to the IWP, living attached to roots and trunks of mangrove trees, anchored by mucus when dry, and sometimes migrating to the mud below to feed during low tide (Berry, 1972; Ohtaki et al., 2002; Vannini et al., 2006). This tree-climbing behaviour is apparently connected both with escape from predatory fish and crabs that enter the forest at high tide and with avoidance of physiological stress (McGuinness, 1994; Vannini et al., 2006). At least ten species can be distinguished by their shells (Brandt, 1974; Wilson, 1993; Brown, 1994; Hasegawa, 2000; Ma, 2004), but there has been no critical taxonomic revision. The subgenus *Cerithideopsis* is distributed in warm temperate and tropical latitudes of the AEP. Species occur in dense populations on estuarine mudflats, and most climb on or shelter beneath mangroves, saltworts and (outside the latitudinal limits of mangroves) saltmarsh grasses (Keen, 1971; Race, 1981; Houbrick, 1984; Plaziat, 1984). Three species are recognized in the western Atlantic (Bequaert, 1942) and five in the eastern Pacific (Keen, 1971; Abbott, 1974), although distinctions among the latter are not well defined. In the tropical IWP four species of the subgenus *Cerithideopsilla* occur (Van Regteren Altena, 1940; Brandt, 1974); *C. cingulata* lives in dense aggregations on open mudflats of sheltered bays and lagoons that are often, but not necessarily, fringed by mangroves (Vohra, 1970; Balaparameswara Rao and Sukumar, 1982; Maki et al., 2002), while the others are usually found on the mud in the shade of mangrove trees (Van Benthem Jutting, 1956; Wells, 1985; Maki et al., 2002; DGR, unpublished). In addition, the uncommon and enigmatic species *C. largillierti* has been placed in *Cerithidea*, although Houbrick (1984) suggested that a new genus was more appropriate; it has been recorded from eastern Asia and Australia (Wilson, 1993;

Hasegawa, 2000) and is found on mud beneath mangroves and saltworts. There is no confirmed fossil record of *Cerithidea* species earlier than the Miocene of the IWP (Houbrick, 1984), although the name has been used for species in the Eocene of Europe (Cossmann and Pissarro, 1910–1913; Glibert, 1962).

The remaining potamidid genera, *Tympanotonos*, *Telescopium* and *Terebralia*, are large, ground-dwelling mudwhelks, often exceeding 80 mm in length, which resist the intense crushing predation in mangrove habitats by means of their heavy, armoured shells (Sälgeback and Savazzi, 2006). Numerous fossil species in the Tethys and North America, extending back to the Eocene, have been classified as *Tympanotonos* (e.g. Squires, 1999; Lozouet et al., 2001; Kowalke, 2001b, 2003; Harzhauser, 2004). However, the type of the genus and only living species is the West African *Tympanotonus fuscatus*, found on estuarine mudflats and beneath mangroves, with an ecophenotypically variable shell (Plaziat, 1977, 1984; Brown, 1994; Bandel and Kowalke, 1999). The classification of fossil *Tympanotonos* is in doubt; Lozouet (1986) pointed out a resemblance to *Potamides*, whereas Kadolsky (1995) placed some in the genus *Mesohalina*. The genus *Telescopium* also contains a single living species, and together with three species of *Terebralia* is abundant among mangroves and on adjacent mudflats in the central IWP (Houbrick, 1991). There is some separation by microhabitat and diet; a combination of consistency of the mud substrate, tidal level and shade from the tree canopy determines the relative distributions of these species (Wells, 1980; Houbrick, 1991; Crowe and McMahon, 1997). Only the smallest of them, *Terebralia sulcata*, occasionally climbs onto mangrove roots (Sälgeback and Savazzi, 2006), and in some areas may gain protection from predatory rays by living among pneumatophores of *Avicennia* trees (Wells, 1986). Whereas most are algal-detritivores like other potamidids, adult *Terebralia palustris* are unique in consuming freshly fallen *Rhizophora* leaves (Fratini et al., 2001), although this diet is not obligatory (Feulner, 2000). The fossil record of *Telescopium* has not been confirmed before the Miocene; convergence with members of Campaniloidea casts doubt on older claims (Houbrick, 1991). However, shells of *Terebralia* are distinctive, and have been reliably identified in the Eocene of Europe (Kowalke, 2001b) and throughout the tropics in the Miocene (Houbrick, 1991).

In general, therefore, those living potamidids that are restricted to mangrove habitats appear to depend upon the trees for substrate, shelter or food. Some species climb on the trees or live among roots in order to escape predation (*Cerithidea sensu stricto*, some *Cerithideopsis*, *T. sulcata*). Spawning has been observed in a minority of species, but egg strings are commonly attached to hard substrates including mangrove bark (Houbrick, 1984, 1991; Bandel and Kowalke, 1999). Some large mudwhelks actively seek the shade and humidity beneath the trees (*Terebralia*). Only *T. palustris* feeds on mangrove litter, but the remainder are all algal feeders and detritivores

(Houbrick, 1984, 1991) and even those that inhabit open mudflats presumably benefit from the high primary productivity of adjacent mangrove forests and saltmarshes.

As reviewed above, the morphology and ecology of many living potamidids are well known and their alpha taxonomy is mainly uncontroversial (with the exception of some species groups of *Cerithidea*). The family has a rich fossil record but, owing to marked intraspecific variation, morphological convergence and lack of consistent diagnoses of genera (and even of the family itself), the fossil record is difficult to interpret. Several subfamilial classification schemes have been proposed for living and fossil species (Bouniol, 1981; Lozouet, 1986; Bandel, 2006), implying phylogenetic relationships among genera, but the formal phylogeny of the family remains largely unknown. Based on a parsimony analysis of morphological characters, Houbrick (1984) suggested that *Cerithidea* was a monophyletic group, and in a wider cladistic analysis of the superfamily Cerithioidea raised this genus to family level (Cerithioidea; Houbrick, 1988), as the sister of Potamidoidea. This suggestion was later revoked (Houbrick, 1991). Four potamidid species (two *Cerithidea s. s.*, a *Terebralia* and *Telescopium*) were included in a molecular phylogenetic analysis of the superfamily Cerithioidea using the mitochondrial 16S rRNA gene and the monophyly of the family was moderately supported (Lydeard et al., 2002). The population structure of six taxonomic species of *Cerithidea* in Japan has been studied using haplotypes of the mitochondrial cytochrome *c* oxidase subunit I (COI), but the monophyly of the genus was not tested (Kojima et al., 2006).

In the present study we aim firstly to examine the molecular phylogeny of the Potamidoidea using a much larger sampling of taxa (including representatives of all generic and subgeneric groups, and 19 of the 29 nominal species), a combination of three genes (18S rRNA, 28S rRNA, COI) and a range of appropriate cerithioidean outgroups. This has enabled us to test the monophyly of the family and of the ecologically and taxonomically diverse genus *Cerithidea*, and the hypothesis (implied by the subfamilial classification of Bandel, 2006) that the enigmatic monospecific *Potamides* is sister to all other potamidids.

Our second aim is to integrate the molecular phylogeny of living Potamidoidea with their extensive fossil record and geographical distributions, to develop an historical biogeographic hypothesis. In the absence of any comprehensive survey of potamidid fossils, it has first been necessary to establish a taxonomic framework and to review the extensive primary literature.

The nature of the remarkable ecological dependence of living mudwhelks on mangrove environments has been well documented. Using a molecular phylogeny, and habitat information for living and fossil species, our third aim is to test the hypothesis that the diversification of extant potamidids was contemporary with that of mangroves in the Early Eocene, and that specialization to the mangrove environment is a plesiomorphic feature. This would strengthen the case for using fossil potamidids as indicators

of palaeomangrove environments (Plaziat, 1995), and for using the family as a model for diversification of the mangroves themselves (Ellison et al., 1999; Ellison, 2002). This hypothesis would be falsified if the basal potamidids were sediment-dwellers without an obligate mangrove association (such as *Potamides* and *Cerithidea* (*Cerithideopsisilla*) *cingulata*), as implied by one classification scheme (Bandel, 2006).

2. Materials and methods

2.1. Sampling of taxa

The ingroup consisted of 19 species of Potamididae, including representatives of each of the recognized genera and subgenera (65% of the 29 taxonomic morphospecies, as reviewed above) (Table 1). Where possible, two specimens of each species were sampled from widely separated localities, and up to six individuals for particularly widespread or variable taxa. Nine outgroup taxa were used, representing the cerithioidean families Thiaridae, Batillariidae (genera *Batillaria*, *Lampanella*, *Zeacumantus*, *Pyrazus*), Modulidae and Cerithiidae (Table 1). One of these, Modulidae, has been identified as the sister taxon of Potamididae by a morphological cladistic analysis (Glaubrecht, 1996), a relationship neither contradicted nor supported by the only available molecular phylogeny of the Cerithioidea (Lydeard et al., 2002). Identifications were based on the most recent taxonomic accounts (reviewed above).

2.2. DNA extraction, amplification and sequencing

DNA was extracted from mantle or foot tissue of ethanol-preserved material using a DNeasy Blood and Tissue Kit (Qiagen) following the manufacturers' instructions. Genomic DNA was eluted from the columns in 400 μ l of elution buffer. Potamidid DNA required further purification prior to PCR amplification to remove inhibitors. This was achieved by adding 62.5 μ l of 5 M NaCl to the DNA, followed by 50 μ l of hexadecyltrimethyl ammonium bromide (CTAB) (10% v/v) in 0.7 M NaCl solution. This was incubated for 10 min at 68 °C and then extracted with equal volumes of chloroform: iso-amyl alcohol (24:1) and phenol: chloroform (1:1). The DNA was precipitated with an equal volume of isopropanol, washed with 70% ethanol and dried and resuspended in 100 μ l of 10 mM Tris-HCl pH 8.

Portions of three genes were amplified and sequenced: the nuclear 18S rRNA and 28S rRNA genes, and the mitochondrial COI gene. Polymerase chain reactions (PCR) were used to amplify approximately 1000 bp of 18S rRNA, 1500 bp of 28S rRNA and 700 bp of COI. Reactions contained 0.1 μ M of a forward and reverse PCR primer (Table 2), 200 μ M of each dNTP, a gene-dependent concentration of magnesium chloride (Table 2), 2.5 U of Qiagen DNA polymerase (50 μ l reaction), one-fifth volume of 'Q solution' and one-tenth volume of Qiagen buffer (10 \times). Thermal cycling was performed with an initial denaturation

for 3 min at 95 °C, followed by 40 cycles of 45 s at 94 °C, 45 s at a gene-specific annealing temperature (Table 2), 2 min at 72 °C, with a final extension of 10 min at 72 °C. All temperature changes were ramped 1 °C/s. Sequence reactions were performed directly on purified PCR products using a BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyser automated capillary sequencer.

Sequences were verified by forward and reverse comparisons. Some 18S rRNA and 28S rRNA sequences showed intra-individual variation (heterozygous bases) as has also been found in other molluscs (Stothard et al., 2000; Bonnaud et al., 2002; Williams and Reid, 2004; Williams et al., 2003, 2004; Armbruster and Korte, 2006). In such cases, two peaks were clearly observed in both forward and reverse chromatograms and were scored as intra-individual polymorphism. All sequences have been deposited in GenBank (accession numbers 28S rRNA: AM932690–AM932749; COI: AM932750–AM932809; 18S rRNA: AM932810–AM932872).

2.3. Sequence analysis and phylogeny reconstruction

Sequences were edited using Sequencher (v4.5, Gene Codes Corporation, Ann Arbor, Michigan). Sequences of ribosomal genes were aligned using Clustal X (Thompson et al., 1994, 1997) ('delay divergent sequence' = 95%, gap-opening penalty = 20, gap-extension penalty = 5) with minor adjustments made by eye in MacClade (v4.06 OSX; Maddison and Maddison, 2003). Poorly aligned sites were identified using Gblocks (0.19b, Castresana, 2000) and removed from analyses with parameters set as in Williams and Ozawa (2006). After removal of these ambiguous blocks of data, a total of 971 bp of sequence from 18S rRNA remained to be used in phylogenetic analyses (94% of 1030 bp in the original alignment) and 1448 bp of 28S rRNA (97% of 1485 bp in the original alignment).

Two different methods were used to assess incongruence among gene partitions. Firstly posterior probabilities (PP) were compared between trees, with strongly supported (PP \geq 95%) clades that conflicted seen as evidence of incongruence (Wiens, 1998; Reeder, 2003; Williams and Reid, 2004). This relies on the argument that weakly supported clades (PP < 95%) in conflict may be the result of stochastic error, rather than different phylogenetic histories (Wiens, 1998). Secondly, the partition homogeneity test in Paup was used to test for incongruence between genes. One hundred replicates of the ILD were conducted using a heuristic search with tree bisection-reconnection branch swapping (TBR), random addition of taxa with 10 replicates and the maximum number of trees constrained to 10,000. All characters were weighted equally, gaps were treated as fifth characters, and multiple states (in 18S and 28S) were treated as polymorphism. The ILD test showed no significant incongruence among gene partitions ($P = 0.01$), but there were examples of conflict among well-supported (PP \geq 95%) basal nodes among trees based

Table 1
Species of Potamididae (ingroup) and nine outgroup taxa (Thiaridae, Batillariidae, Cerithiidae, Modulidae) used in this study, with geographical ranges, localities of samples, and deposition of voucher material

Species	Range	Sample location and code	Voucher material
Outgroups			
<i>Thiara cf. amarula</i> (Linnaeus, 1758)	IWP, Freshwater	1: Obi, Maluku Utara, Indonesia	ZMB 191.489
<i>Lampanella minima</i> (Gmelin, 1791)	W Atlantic	1: Punta Rassa, Florida, USA	BMNH 20070368
<i>Batillaria zonalis</i> (Bruguière, 1792)	NW Pacific	1: St Johns I., Singapore	BMNH 20070371
<i>Pyrasus ebeninus</i> (Bruguière, 1792)	E Australia	1: Sandy Point, S of Mooan, Fraser I., Queensland, Australia	AMS C411801
<i>Zeacumantus lutulentus</i> (Kiener, 1841)	New Zealand	1: Kulim Park, Otumoetai, Tauranga Harbour, New Zealand	MNZ M.181413
<i>Cerithium coralium</i> Kiener, 1841	Central IWP	1: Lampia, S of Malili, S Sulawesi, Indonesia	ZMB 191.634
<i>Cerithium nodulosum</i> Bruguière, 1792	IWP	1: Panglao, Philippines	MNHN M3/BC128
<i>Cerithium echinatum</i> Lamarck, 1822	IWP	1: Panglao, Philippines	MNHN R14/BC266
<i>Modulus modulus</i> (Linnaeus, 1758)	W Atlantic	1: Bocas del Toro, Panama	BMNH 20050723
Potamididae			
<i>Potamides conicus</i> (Blainville, 1829)	Mediterranean, Indian O.	1: Khor Zawra, Ajman, United Arab Emirates 2: Ibo I., Cabo Delgado Prov., Mozambique	BMNH 20070406 BMNH 20070407
<i>Cerithidea (Cerithidea) anticipata</i> Iredale, 1929	N and NE Australia	1: Thirsty Sound, Porters Creek, just S of Plum Tree, Queensland, Australia. 2: Ludmilla Creek, Darwin Harbour, Northern Territory, Australia 3: Sandy Creek, Casuarina Beach, Darwin Harbour, Northern Territory, Australia	AMS C418805 ZMB 103.156 BMNH 20070372
<i>Cerithidea (Cerithidea) decollata</i> (Linnaeus, 1758)	W Indian O.	1: Ibo I., Cabo Delgado Prov., Mozambique 2: SE Pemba Bay, Cabo Delgado Prov., Mozambique	BMNH 20070374 BMNH 20070375
<i>Cerithidea (Cerithidea) obtusa</i> (Lamarck, 1822)*	Indo-Malaya	1: Mekong Delta, Vietnam	BMNH 20070377
<i>Cerithidea (Cerithidea) ornata</i> A. Adams, 1863	W Pacific O.	1: Mouth of Hikawa River, Hikawa Town, Yatsushiro-gun, Kumamoto Prefecture, Kyushu, Japan 2: Sai Kung, Hong Kong 3: Sandbyakken, Otsuka, Nakatsu City, Oita Pref., Kyushu, Japan	BMNH 20070378 BMNH 20070380 BMNH 20070379
<i>Cerithidea (Cerithidea) quadrata</i> Sowerby, 1866	Indo-Malaya	4: Panglao, Philippines 1: Panglao, Philippines 2: Panglao, Philippines 3: Middle Kung Kraben Bay, Chantaburi Prov., SE Thailand 4: Ninh Phu, 25 km N of Nha Trang, Vietnam	MNHN M29/BC1656 MNHN M31/BC1745 MNHN M49/BC2153 BMNH 20070385 BMNH 20070386
<i>Cerithidea (Cerithidea) rhizophorarum</i> A. Adams, 1855	NW Pacific	1: Mouth of Tamshui River, Bali, N Taiwan 2: Makiya, Okinawa, Japan 3: Sai Kung, Hong Kong	BMNH 20070387 BMNH 20070388 BMNH 20070389
<i>Cerithidea (Cerithideopsis) montagnei</i> (d'Orbigny, 1839)	Tropical E Pacific	1: Playa Pochote, Nicoya Peninsula, Costa Rica	BMNH 20070413
<i>Cerithidea (Cerithideopsis) valida</i> (C.B. Adams, 1852)	Tropical E Pacific	1: Shore opposite Isla Damas, Quepos, Costa Rica	BMNH 20070414
<i>Cerithidea (Cerithideopsis) alata</i> (Philippi, 1849)	Indo-Malaya	1: Middle Kung Kraben Bay, Chantaburi Prov., SE Thailand	BMNH 20070391

<i>Cerithidea (Cerithideopsilla) cingulata</i> (Gmelin, 1791)*	IWP	1: Mouth of Tamshui River, Bali, N Taiwan 2: Sandbyakken, Otsuka, Nakatsu City, Oita Pref., Kyushu, Japan 3: Khor Zawra, Ajman, United Arab Emirates 4: St Johns I., Singapore 5: Thirsty Sound, Plum Tree, Queensland, Australia 6: Lake Alexander, East Point, Darwin Harbour, Northern Territory, Australia	BMNH 20070398 BMNH 20070401 BMNH 20070395 BMNH 20070397 AMS C419621 BMNH 20070402
<i>Cerithidea (Cerithideopsilla) djadjariensis</i> (K. Martin, 1899)	W Pacific	1: Middle Kung Kraben Bay, Chantaburi Prov., SE Thailand 2: Kiire, Kagoshima Pref., Japan 3: Sai Kung, Hong Kong 4: Ninh Phu, 25 km N of Nha Trang, Vietnam	BMNH 20070404 ZMB 112.772 BMNH 20070405 BMNH 20070393
<i>Cerithidea (Cerithideopsilla) microptera</i> (Kiener, 1842)	Indo-Malaya	1: Panglao, Philippines	MNHN M27/BC/675
<i>Cerithidea largillierti</i> (Philippi, 1848)	Japan to Australia	1: River mouth of Jiksocheon, Bulmu-dong, Daehang-ri, Byeonsan-myeon, Buan-gun, Jeonrabuk-do, South Korea 2: Lower reaches of Ushitsu River, Nagata, Ashikari Town, Ogi City, Saga Prefecture, Kyushu, Japan. 3: Plum Tree, Thirsty Sound, Queensland, Australia 4: East Arm, Darwin Harbour, Northern Territory, Australia	BMNH 20070408 BMNH 20070410 AMS C419622 BMNH 20070412
<i>Tympanotonos fuscatus</i> (Linnaeus, 1758)*	W Africa	1: Ankobra River, 70 km W of Takoradi, Ghana 2: Old Ningo, 30 km E of Accra, Ghana 3: Garta, Gambia R., Gambia	BMNH 20070430 BMNH 20070431 ZMB 106.173 ZMB 200.319
<i>Telescopium telescopium</i> (Linnaeus, 1758)*	Central IWP	1: Panjim, Goa, India 2: Middle Kung Kraben Bay, Chantaburi Prov., SE Thailand 3: Panglao, Philippines 4: Great Sandy Strait, Urangan Sandflats at mouth of Pulgul Creek, Queensland, Australia 5: Ludmilla Creek, Darwin Harbour, Northern Territory, Australia	BMNH 20070415 MNHN M30/BC1774 AMS C411505 BMNH 20070416
<i>Terebralia palustris</i> (Linnaeus, 1767)*	IWP	1: Middle Kung Kraben Bay, Chantaburi Prov., SE Thailand 2: Kunduchi Creek, 40 km N Dar es Salaam, Tanzania 3: Ludmilla Creek, Darwin Harbour, Northern Territory, Australia	BMNH 20070417 BMNH 20070419 BMNH 20070421
<i>Terebralia semistriata</i> (Mörch, 1852)	N Australia	1: Great Sandy Strait, Urangan Sandflats at mouth of Pulgul Creek, Queensland, Australia 2: Ludmilla Creek, Darwin Harbour, Northern Territory, Australia 3: Cockle Bay, Magnetic I., Queensland, Australia	AMS C448572 ZMB 103.158 AMS C448382
<i>Terebralia sulcata</i> (Born, 1778)	Central IWP	1: Channel I., Middle Arm, Darwin Harbour, Northern Territory, Australia 2: St Johns I., Singapore 3: Panglao, Philippines 4: Panglao, Philippines	BMNH 20070425 BMNH 20070424 MNHN M6/BC151 MNHN M44/BC2117

Taxonomy and ranges from Keen (1971), Abbott (1974), Brandt (1974), Brown (1994), Houbrick (1984, 1991), Kowalke (1998), Lozouet (1986), Wilson (1993), Hasegawa (2000) and Ma (2004). Abbreviations: AMS, Australian Museum, Sydney; BMNH, Natural History Museum, London; IWP, Indo-West Pacific; MNHN, Muséum National d'Histoire Naturelle, Paris; MNZ, Museum of New Zealand Te Papa Tongarewa; ZMB, Museum für Naturkunde, Berlin. Type species of potamidid genera and subgenera are indicated by asterisks.

Table 2

Forward (F) and reverse (R) PCR primers (also used in sequencing), and forward (FS) and reverse (RS) internal sequencing primers

Name	Sequence 5'-3'	Annealing temp. (°C)	MgCl ₂ conc. (mM)	Source
18S rRNA		54	3.0	
18S-5' (F)	CTG GTT GAT YCT GCC AGT			Winnepenninckx et al. (1998)
18S1100R (R)	CTT CGA ACC TCT GAC TTT CG			Williams and Reid (2004)
18S600F (FS)	GGT GCC AGC AGC CGC GGT			Reverse of 18S600R
18S600R (RS)	ACC GCG GCT GCT GGC ACC			Modified from Littlewood et al. (2000)
28S rRNA		52	2.5	
LSU5 (F)	TAG GTC GAC CCG CTG AAY TTA AGC A			Littlewood et al. (2000)
LSU1600R (R)	AGC GCC ATC CAT TTT CAG G			Williams et al. (2003)
900F (FS)	CCG TCT TGA AAC ACG GAC CAA G			Reverse of ECD2S
ECD2S (RS)	CTT GGT CCG TGT TTC AAG ACG G			Modified from Littlewood et al. (2000)
LSU330F (FS)	CAA GTA CCG TGA GGG AAA GTT G			Williams and Ozawa (2006)
COI		50	3.0	
LCO1490 (F)	GGT CAA CAA ATC ATA AAG ATA TTG G			Folmer et al. (1994)
HCO2198 (R)	TTA ACT TCA GGG TGA CCA AAA AAT CA			Modified from Folmer et al. (1994)

Annealing temperatures and concentration of magnesium chloride (MgCl₂) used in 50 µl polymerase chain reactions.

on single gene datasets (Fig. 1; see Results). Nevertheless, all three genes were concatenated and analysed in a combined dataset.

Phylogenies were constructed for each gene-sequence dataset and for the combined dataset, using Bayesian methods implemented by MrBayes (v3.1.2, [Huelsenbeck and](#)

[Ronquist, 2001](#)). Models to be used in Bayesian analyses were determined by MrModelTest (v2.1, J. Nylander, www.ebc.uu.se/systzoo/staff/nylander.html). In addition, the COI dataset was tested to see whether variation across codon positions would result in an improved likelihood. The best model for 18S rRNA was SYM + I + G and for

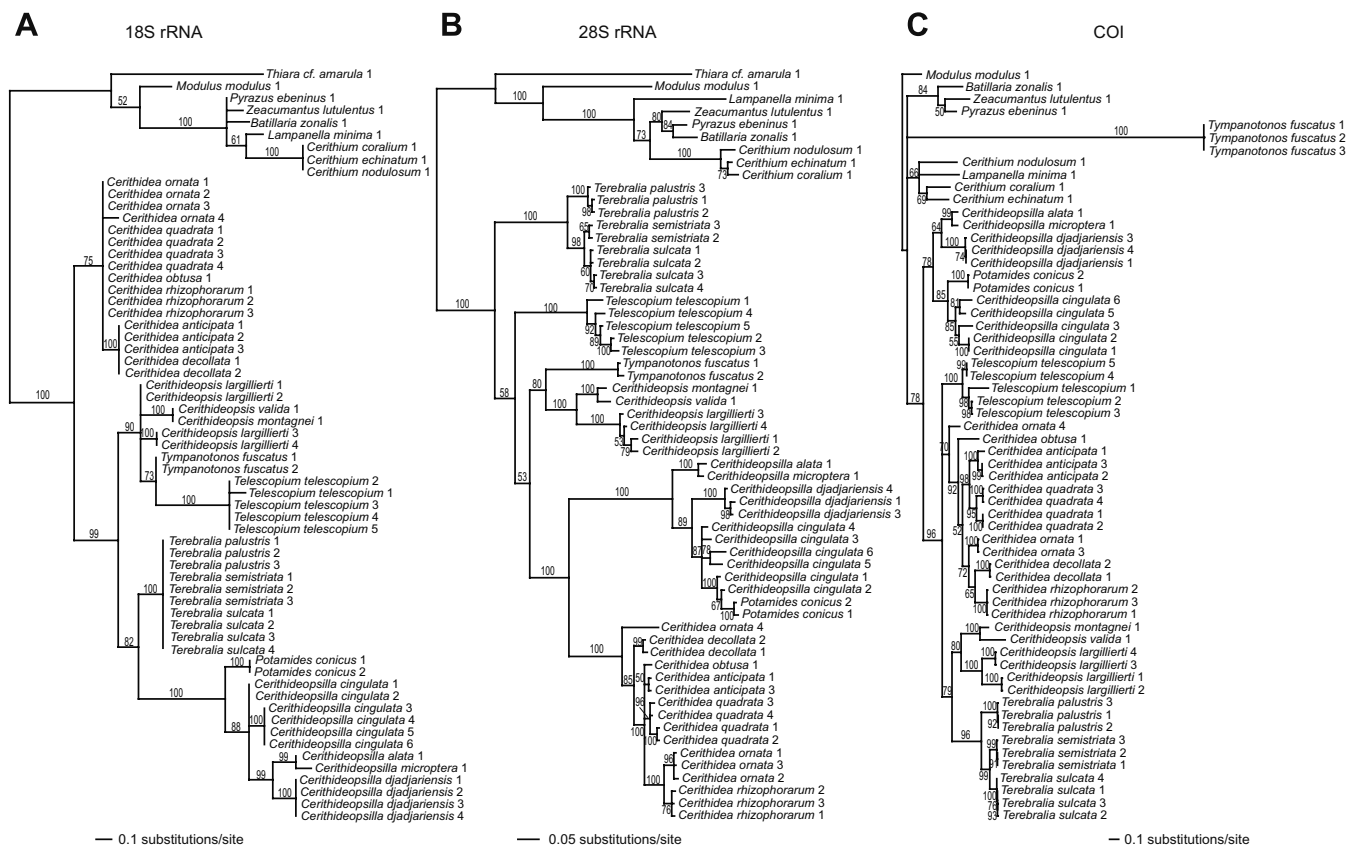


Fig. 1. Molecular phylogenies of Potamidae produced by Bayesian analysis of datasets from individual genes, the nuclear 18S rRNA (A), 28S rRNA (B) and mitochondrial COI (C). The taxonomy follows the traditional arrangement (Table 1), except that the three subgenera of *Cerithidea* (*Cerithidea s. s.*, *Cerithideopsis*, *Cerithideopsilla*; [Houbrick, 1984](#)) are raised to genus rank, and *Cerithidea largillierti* is assigned to *Cerithideopsis*. The outgroups are members of Thiariidae, Modulidae, Batillariidae and Cerithiidae (Table 1). Support values are Bayesian posterior probabilities.

all other datasets the best model was GTR + I + G, using either the hierarchical log-likelihood ratio test or Akaike's Information Criterion (AIC).

These models were used in all Bayesian analyses, with all parameters free to vary. In the combined Bayesian analyses, variation was partitioned among genes and gene-specific model parameters were used (with all parameters free to vary independently within each partition). In addition, each gene was allowed to evolve at a different rate. The analysis for each data set was run for 3,500,000 generations, with a sample frequency of 100. The first 15,001 trees were discarded, so that 20,000 trees were accepted after likelihood values had reached a plateau. The datasets were analysed in two independent runs, and the final tree was computed from the combination of accepted trees from each run (a total of 40,000 trees). Convergence between the two runs was tested by examining the potential scale reduction factors (PSRF) produced by the 'sump' command in MrBayes. Support for nodes was determined using posterior probabilities (calculated by MrBayes).

3. Results

Phylogenetic trees constructed from the separate gene datasets are shown in Fig. 1. Monophyly of the family Potamididae was highly supported (posterior probability PP = 100%) in the trees from both nuclear genes, but not in the COI tree. The 18S rRNA data (Fig. 1A) resolved all the genera and most of the subgenera of *Cerithidea*, although often with low support (i.e. PP < 95%). *Cerithidea s. s.* was excluded from a major clade of all the remaining potamidid species (PP = 99%). Sequences of 18S rRNA were highly conserved within each clade and many species shared identical sequences (only one of each shared sequence was included in the phylogenetic analyses of this gene and the additional species were added to the tree in Fig. 1A after the analysis).

The 28S rRNA tree showed higher resolution (Fig. 1B). All recognized generic and subgeneric groups were resolved with 100% support, with one exception. *Potamides conicus* clustered within *Cerithidea* (*Cerithideopsilla*) (PP = 100%; in the 18S rRNA tree these two taxa formed a clade but their relationships were unresolved). The subgenus *Cerithideopsis* was sister to *Cerithidea largillierti* (subgenus previously unspecified; Houbriick, 1984), and *Cerithidea s. s.* and *Cerithideopsilla* + *Potamides* formed a clade with 100% support. Other relationships among clades were not resolved.

The COI data provided finer resolution at shallow nodes (Fig. 1C). *Tympanotonos* appeared on a long branch in the COI tree (but not in either of the nuclear gene trees), and long-branch attraction (Bergsten, 2005) probably accounts for the placement of *Tympanotonos* among the outgroup taxa. *Potamides conicus* again fell within *Cerithidea* (*Cerithideopsilla*), but without significant support (PP = 78%). This clade was excluded from a large clade of all the remaining potamidids (except *Tympanotonos*;

PP = 96%). Elsewhere, the same generic and subgeneric clades were retrieved as in the nuclear gene trees, but sometimes with low support. At the specific level, almost all taxonomic species were monophyletic with high support (PP = 99–100%). Five individuals of *Cerithidea* (*Cerithideopsilla*) *cingulata* formed a clade with only 85% support. *Cerithidea* (*Cerithidea*) *ornata* was not monophyletic (PP = 92%).

In the analysis of the dataset of the three genes combined, all generic and subgeneric clades recognized in single-gene analyses were retrieved with maximum support, together with the sister relationship between *Cerithidea s. s.* and subgenus *Cerithideopsilla* + *Potamides conicus*, and between the subgenus *Cerithideopsis* and *Cerithidea largillierti* (Fig. 2). Other basal relationships among genera were not well resolved. In contrast to single-gene analyses *Terebralia* was excluded from a large clade containing all the remaining potamidids, but support was marginal (PP = 93%). Maximum support was achieved for *P. conicus* falling within the *Cerithideopsilla* clade, and in a subclade with *C. cingulata*. Monophyly of each of the two nominal species *C. cingulata* and *Cerithidea ornata* was not supported. The long branch of *Tympanotonos* in the COI tree did not adversely affect its placement in the three-gene tree; in a Bayesian analysis of the two nuclear genes alone (not shown) *Tympanotonos* appeared in the same position, as sister to *Cerithideopsis* plus *Cerithidea largillierti*, again without significant support (PP = 53%).

Relationships between clades within the outgroup cannot be tested, but the topology was consistent with monophyly of the families Cerithiidae and Batillariidae (Fig. 2).

4. Discussion

4.1. Phylogeny and classification of the Recent Potamididae

The Potamididae formed a monophyletic group in all but one of the analyses (clustering of the potamidid *Tympanotonos* with outgroup taxa in the COI tree appears to be an artefact of long-branch attraction). This is consistent with both anatomical (Healy, 1983; Houbriick, 1988; Ponder, 1991; Glaubrecht, 1996) and molecular (Lydeard et al., 2002) evidence separating the family from the superficially similar Batillariidae, here falling well within the outgroup. Shell characters distinguishing these families have not yet been rigorously defined; they include the twisted columellar base and more rounded aperture of Potamididae and the secondary spiral sculpture of Batillariidae (used by Lozouet, 1986, to distinguish *Potamides* from the batillariid *Granulolabium*), whereas protoconch characters are not known to be diagnostic (cf. Lozouet, 1986; Kowalke, 1998; Bandel, 2006).

Within the Potamididae, our molecular phylogenetic hypothesis shows each of the traditional genera *Terebralia*, *Telescopium* and *Tympanotonos* (Houbriick, 1991) to be monophyletic, and also supports two of the three subgenera of *Cerithidea* (*Cerithidea s. s.* and *Cerithideopsis*; Hou-

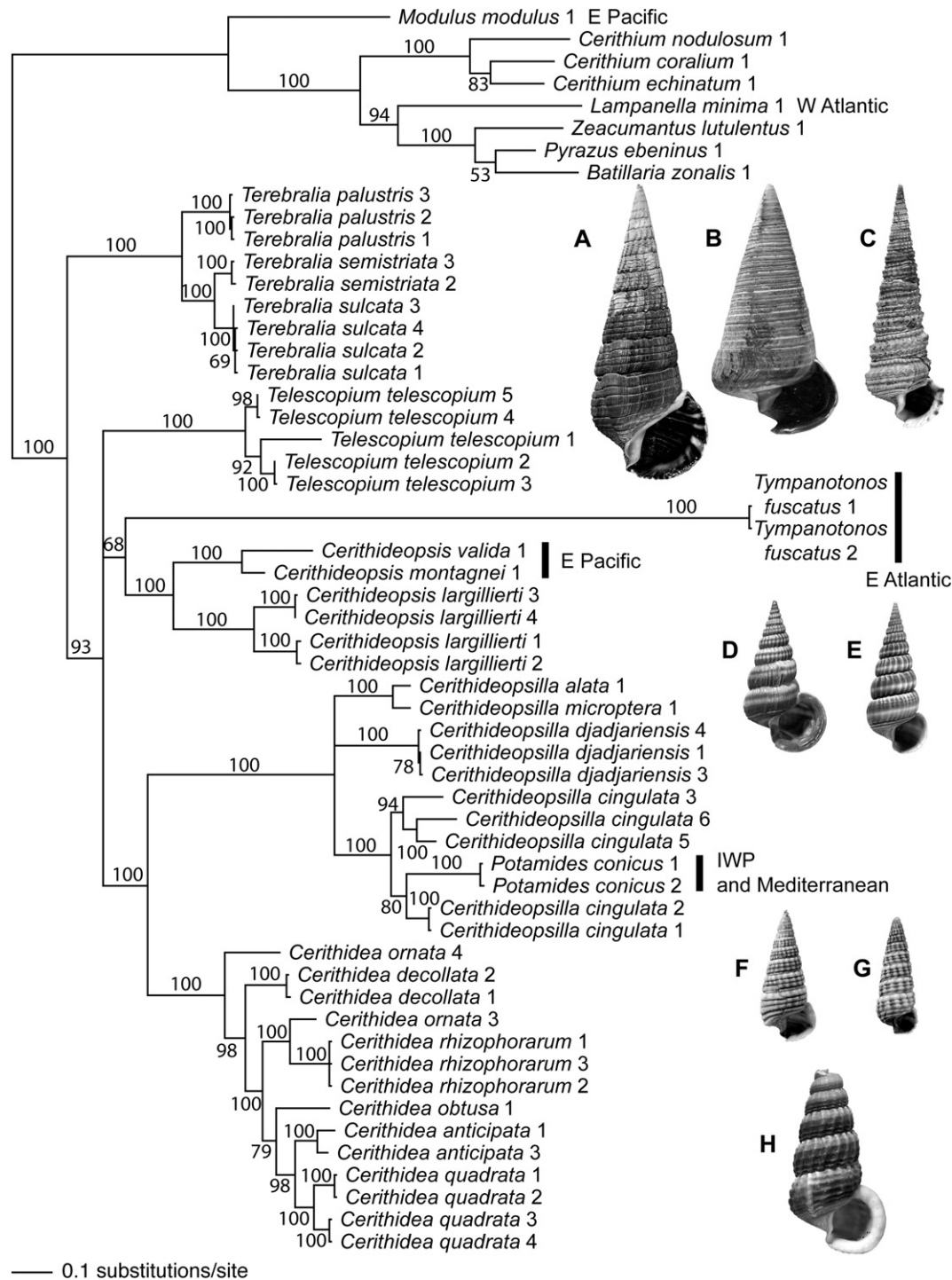


Fig. 2. Molecular phylogeny of Potamididae produced by Bayesian analysis of combined dataset from concatenated sequences of the nuclear 18S rRNA and 28S rRNA genes and mitochondrial COI gene. The taxonomy follows the traditional arrangement (Table 1), except that the three subgenera of *Cerithidea* (*Cerithidea s. s.*, *Cerithideopsis*, *Cerithideopsilla*; Houbrick, 1984) are raised to genus rank, and *Cerithidea largillierti* is assigned to *Cerithideopsis*. The outgroups are members of Thiaridae, Modulidae, Batillariidae and Cerithiidae (Table 1). Support values are Bayesian posterior probabilities. Geographical ranges are indicated; those species without a range occur only in the Indo-West Pacific (IWP) region. Shells: A, *Terebralia palustris*; B, *Telescopium telescopium*; C, *Tympanotonos fuscatus*; D, *Cerithideopsis montagnei*; E, *Cerithideopsis largillierti*; F, *Cerithideopsilla cingulata*; G, *Potamides conicus* (*Cerithideopsilla conica* herein); H, *Cerithidea obtusa*.

brick, 1984). However, there is no agreement with any previous schemes of phylogenetic relationship or subfamilial classification of these living genera. Based on a parsimony analysis of morphological characters, Houbrick (1984) sug-

gested that *Cerithidea* was a monophyletic group of three subgenera, of which *Cerithideopsis* and *Cerithidea s. s.* were sister taxa. Houbrick (1988) named this group as a separate family, Cerithideidae, sister to the remaining Potamididae,

but subsequently reversed this decision, recognizing their anatomical similarity (Houbrick, 1991). In the present analysis the two subgenera *Cerithidea s. s.* and *Cerithideopsilla* (with the inclusion of *P. conicus*) are sister taxa, and there is no support for the addition of *Cerithideopsis* to this group, these basal relationships being unresolved. Modifying an earlier scheme of Bouniol (1981) based on similarity of shells, Lozouet (1986) removed *Terebralia* from the remaining Potamididae, allying it with genera now recognized as batillariid (*Zeacumantus* and the fossil *Granulolabium*). This distinction of *Terebralia* has a parallel in its marginally supported basal position within Potamididae in the analysis of the combined-gene dataset, but Batillariidae are unrelated. Bandel (2006) recognized two subfamilies, Potamidinae and Telescopiinae, the latter including all living potamidids except *Potamides*. If *P. conicus* is accepted as a representative of the former subfamily, then our molecular results contradict this scheme; if not, then the placement of all living potamidids into a single group has no implication for the phylogenetic relationships among them. In the only previous molecular phylogenetic study of potamidid genera, Lydeard et al. (2002) reported moderate support (bootstrap 87%) for a sister relationship between *Telescopium* and *Terebralia*, to the exclusion of *Cerithidea s. s.* This is contradicted with marginal support (PP = 93%) in the present three-gene analysis.

The genus *Cerithidea sensu lato* contains 23 (79%) of the 29 nominal species of the Potamididae. There is no support for the monophyly of this large group in our analyses; instead, there are three well-supported and genetically divergent clades, two of which are relatively distant sister taxa (Fig. 2). We suggest that these relationships are best expressed by recognizing three genera, corresponding to the subgenera of Houbrick (1984). *Cerithidea s. s.* includes ten morphospecies (Brandt, 1974; Wilson, 1993; Brown, 1994; Hasegawa, 2000; Ma, 2004), all from the Indo-West Pacific (IWP), of which we sampled six (including the type species *C. obtusa*). Our analyses included all four morphospecies assigned to *Cerithideopsilla*, all from the IWP (Van Regteren Altena, 1940; Brandt, 1974), and to these we add '*Potamides*' *conicus*, hitherto the only recognized living species of its genus (Lozouet, 1986; Plaziat, 1993; Kowalke, 2001a). As discussed below, the generic name *Potamides* is based on a fossil that we consider unrelated to *Cerithideopsilla*. (The generic name *Pirenella* Gray, 1847 is based on *P. conicus*, and has priority over the name *Cerithideopsilla* Thiele, 1929; nomenclatural research might confirm that the former is the valid name for this genus, but would run counter to current usage.) Our sampling of *Cerithideopsis* is incomplete, including only two eastern Pacific species of the approximately eight in the eastern Pacific and Atlantic (EPA) provinces (Keen, 1971; Abbott, 1974). The shells of this group are closely similar, and we predict that further sampling will confirm their monophyly. We have also sampled the enigmatic '*Cerithidea*' *largillierti* from the IWP; this, according to Houbrick (1984), did not fit into any of his proposed subgenera. In our analyses

this species is retrieved with high support as sister to *Cerithideopsis* and there is a close resemblance between their shells (Table 3). We therefore transfer '*Cerithidea*' *largillierti* to *Cerithideopsis*. Diagnostic shell characters for *Cerithidea*, *Cerithideopsilla* and *Cerithideopsis* are summarized in Table 3, and these taxon names will be used at generic rank in the following discussion.

At the species level, our analyses support the classification of living *Terebralia* in three species (Houbrick, 1991). Three specimens of *Tympanotonos fuscatus* also showed little genetic difference. However, genetic structure was found in the nominal species *Telescopium telescopium*, with separation of specimens from the Philippines, Australia and India, and genetic distances (Kimura two-parameter K2P divergence in COI sequence) of up to 16%, so further investigation is required. K2P divergence between *Cerithideopsis largillierti* from Japan and from Australia averaged 15% and together with a disjunct distribution (DGR, unpublished) suggest that two species are involved. Within *C. cingulata* the K2P divergence between samples from Australia and Japan was 14%, suggesting that this widespread species may be a complex. The sample of *Cerithidea ornata* from the Philippines did not form a clade with those from Japan and Hong Kong in either 28S or COI trees, and therefore do not belong to the same phylogenetic species. Despite close morphological similarity, *Cerithidea anticipata* from Australia is distinct from *C. quadrata* from southeast Asia, judged by consistent phylogenetic separation and the average K2P distance for COI of 14%.

4.2. Phylogeny, historical biogeography and the fossil record of Potamididae

The Potamididae have a rich fossil record, but its interpretation is hampered by the lack of direct comparison between living and fossil representatives and absence of clear generic definitions. A comprehensive revision is beyond the scope of this work, but we have attempted to unify the classification of the living genera and those fossils that can confidently be assigned to the family (Table 3). Our classification is based on the six monophyletic groups distinguished in the molecular phylogeny and recognized as genera (see above). These have been diagnosed by characters of the shell (observations of all living species in Natural History Museum, London, by DGR) and mode of development, to provide a framework applicable also to fossil material. Detailed characters of the protoconch and early teleoconch sculpture may prove still more informative (e.g. Lozouet, 1986; Kadolsky, 1995; Kowalke, 1998), but remain unavailable for the majority of both living and fossil taxa. The poor basal resolution of the phylogeny of Potamididae, and uncertainty about its immediate sister group, prevent us from distinguishing apomorphic and plesiomorphic characters (but see discussion of developmental mode below). We have made an extensive survey of the fossil literature and have also examined specimens (in Natural

Table 3
Revised classification of the Potamididae, with principal synonyms and subgroups, and diagnostic shell characters

Genus	Subgenera or synonyms	Shell characters
<i>Terebralia</i> Swainson, 1840	^a <i>Gravesicerithium</i> ^b Charpiat, 1923 ^a ^a <i>Cerithideops</i> Pilsbry and Harbison, 1933	Development: planktotrophic (Houbrick, 1991; Kowalke, 1998, 2001b, 2006a,b; Harzhauser and Kowalke, 2001) Spire whorls: 4 or more spiral ribs ^c ; axial folds, becoming weak; scattered varices with internal teeth; usually a columella fold (absent in <i>Cerithideops</i> see Pilsbry and Harbison, 1933, weak in <i>T. subcorrugata</i> see Lozouet, 1986) Ventrolateral varix: present Aperture: flared; shoulder sinus weak or absent; basal projection may enclose anterior canal
<i>Telescopium</i> Montfort, 1810		Development: planktotrophic (Houbrick, 1991) Spire whorls: 3 spiral ribs plus intercalated riblet on shoulder; no axial sculpture except for beading on posterior rib of early whorls; no varices; columella fold Ventrolateral varix absent Aperture: unmodified; indeterminate growth; broad shallow shoulder sinus; basal projection; anterior canal short
<i>Tympanotonos</i> Schumacher, 1817		Development: planktotrophic (Egonmwan and Odiete, 1983; Bandel and Kowalke, 1999 illustrated the protoconch of a species of Cerithiopsidae in error) Spire whorls: 3 spiral ribs strongly beaded by axial folds; 1 riblet intercalated between two anterior ribs and another between anterior rib and suture; shoulder rib enlarged or spinose; scattered varices with internal teeth; small columella fold Ventrolateral varix: absent Aperture: flared; broad shallow shoulder sinus; basal projection
^a <i>Potamides</i> Brongniart, 1810	^a <i>Ptychopotamides</i> Saccho, 1895 ^a <i>Mesohalina</i> Wittibschlager, 1983 ^a <i>Vicarya</i> d'Archiac and Haime, 1854 ^a <i>Vicaryella</i> Yabe and Hatai, 1938 ^a <i>Eotympanotonos</i> Chavan, 1952	Development: mostly non-planktotrophic (Lozouet, 1986; Kadolsky, 1995; Harzhauser and Kowalke, 2002; lecithotrophic reported by Kowalke, 2001a,b, 2006a,b); 2 reports of planktotrophic development (Reichenbacher et al., 2004) Spire whorls: 3 spiral ribs, sometimes with intercalated riblets; ribs usually granular or tubercular; posterior rib may be enlarged or spinose; no varices; columella fold present or absent Ventrolateral varix: absent Aperture: usually flared and thickened; strong shoulder sinus, sometimes very deep (<i>Vicarya</i>); posterior canal, sometimes expanded and callused
^a <i>Campanilopsis</i> Chavan, 1949		Development: unknown. Spire whorls: 4 spiral ribs, finely granular; posterior rib enlarged, spinose in adult; columella fold Aperture: not flared
^a <i>Potamidopsis</i> Munier-Chalmas, 1900		Development: planktotrophic and non-planktotrophic (PL, unpublished). Spire whorls: 3 granulose spiral ribs; anterior rib enlarged, carinate or spinose; no varices; columella fold? Ventrolateral varix: absent Aperture: flared and thickened; strong shoulder sinus
<i>Cerithideopsis</i> Thiele, 1929	^a <i>Harrisianella</i> Olsson, 1929 ^a <i>Lagunitis</i> Olsson, 1929	Development: lecithotrophic (Houbrick, 1984) or planktotrophic (<i>C. douvillei</i> , PL, unpublished; <i>Harrisianella vulcani</i> , Kowalke, 2001a,b) Spire whorls: 2–3 spiral ribs on earliest whorls, usually becoming obsolete, sometimes increasing to 5; numerous axial folds, terminating at strong spiral rib demarcating the base; scattered varices; no columella fold (present in <i>H. peruwiana</i> Olsson, 1929) Ventrolateral varix: absent Aperture: slightly or strongly flared and thickened; peristome weakly sinuous or planar; slight anterior canal
<i>Cerithideopsilla</i> Thiele, 1929	<i>Pirenella</i> Gray, 1847 ^d	Development: planktotrophic (<i>C. cingulata</i> and <i>C. djadjariensis</i> , Houbrick, 1984) or non-planktotrophic (<i>C. conica</i> , Lozouet, 1986; Kowalke, 2001a) Spire whorls: 3 spiral ribs; numerous axial folds; no varices; no columella fold Ventrolateral varix: present (except <i>C. conica</i>) Aperture: slightly or strongly flared and thickened; peristome weakly sinuous or planar; basal projection defining anterior canal; posterior canal, sometimes forming wing-like projection
<i>Cerithidea</i> Swainson, 1840		Development: <i>C. rhizophorarum</i> probably non-planktotrophic (Houbrick, 1984) Spire whorls: earliest whorls decollate; 0–18 spiral ribs on adult whorls; numerous axial folds; no varices; no columella fold Ventrolateral varix: present Aperture: flared and thickened; peristome planar; slight anterior canal

^a Exclusively fossil genera.

^b According to Lozouet (1986).

^c Not counting rib to which succeeding whorl is attached.

^d Synonymy based on molecular results; type species is *Cerithium mamillatum* Philippi = *Pirenella conica*; *Pirenella* has priority over *Cerithideopsilla*; see text.

[?] Indicates doubtful generic assignment.

History Museum, London, by DGR; in Muséum National d'Histoire Naturelle, Paris, by PL). As a result, we propose new synonymies and diagnoses for some fossil genera and question the assignment of some fossils to Recent groups (Tables 3 and 4), as briefly discussed below.

The earliest fossils that have been assigned to the Potamididae include the genera *Echinobathra*, *Hadraxon* and *Terebraliopsis* (Bandel and Riedel, 1994; Kowalke and Bandel, 1996; Kowalke, 2003) from the Late Cretaceous. However, without a clear diagnosis of the family and with

Table 4
Outline of the fossil record of the Potamididae

Taxa	Age	Geographical range	References
<i>Echinobathra</i> , <i>Hadraxon</i> , <i>Terebraliopsis</i>	L Cret: Maastrichtian	Alps, Pyrenees	Bandel and Riedel (1994); Kowalke and Bandel (1996); Kowalke (2003)
Genus <i>Terebralia</i>			
? <i>T. pathani</i> Iqbal, 1969	E Eoc	Pakistan	Iqbal (1969)
<i>T. subcorvina</i> (Oppenheim, 1894)	M Eoc: Lutetian	Hungary, Italy	Kowalke (1998, 2001b)
<i>T. bonellii</i> (Deshayes, 1833)	M Eoc: Lutetian	France	Cossmann and Pissarro (1902, 1910–1913)
<i>T. vielensis</i> Belliard et al., 2006	M Eoc	France	Belliard et al. (2006)
<i>T. bidentata</i> (Defrance in Grateloup, 1832)	L Olig–M Mioc	France to Pakistan, Paratethys	Vredenburg (1925); Harzhauser and Kowalke (2001, 2002); Lozouet et al. (2001); Harzhauser (2004)
<i>T. rahti</i> (Braun, 1851)	L Olig–E Mioc	Mainz Basin, Aquitaine Basin	Kadolsky (1995)
<i>T. dentilabris</i> (Gabb, 1873)	E Mioc	Panama, Florida	Woodring (1959); Hoerle (1972)
<i>T. shibatai</i> Taguchi, 1992	Mioc	Japan	Taguchi (1992)
<i>Cerithidea</i> (<i>Cerithideops</i>) <i>insulaemaris</i> Pilsbry and Harbison, 1933	Mioc	Eastern USA	Pilsbry and Harbison (1933)
<i>T. palustris</i> (Linnaeus, 1767)	E Mioc–Rec	IWP; Italy (L Mioc)	Van Regteren Altena (1942); Houbrick (1991)
Genus <i>Telescopium</i>			
<i>T. schencki</i> Hatai and Nishiyama, 1949	L/M Mioc	Japan	Oyama (1950); Shimizu and Kaneko (1992)
<i>T. telescopium</i> (Linnaeus, 1758)	M Mioc–Rec	W Pacific	Van Regteren Altena (1942); Houbrick (1991); Inoue (2007)
Genus <i>Tympanotonos</i>			
<i>T. fuscatus</i> (Linnaeus, 1758)	Rec	W Africa	Bandel and Kowalke (1999); Kowalke (2001b)
Genus <i>Potamides</i>			
? <i>Terebralia juliana</i> Dailey and Popenoe, 1966	L Cret	California	Dailey and Popenoe (1966)
<i>P. (Eotympanotonos ?)</i> n. sp.	E Palaeo	Oise, France	Bouniol (1981)
? <i>Tympanotonos varians</i> (Briart and Cornet, 1873)	E Palaeo	Belgium	Glibert (1973)
<i>P. (Ptychopotamides) cinctus</i> (Bruguière, 1792)	M Eoc	Paris Basin	Cossmann and Pissarro (1910–1913)
<i>Tympanotonos conarius</i> (Bayan, 1873)	M Eoc	Paris Basin	Cossmann and Pissarro (1910–1913)
<i>Tympanotonos calcaratus</i> (Brongniart, 1823)	M Eoc	Hungary	Kowalke (2001b)
<i>Vicaryella</i> spp.	Eoc	Pakistan, Indonesia, Japan	Kanno (1986)
<i>Potamides</i> spp.	M Eoc–Plioc	Europe	Lozouet (1986); Nury (1998); Kowalke (2001a); Harzhauser and Kowalke (2002)
<i>P. lamarkii</i> (Brongniart, 1810)	E Olig	Paris Basin	Lozouet (1986)
<i>P. suprasulcatus</i> (Gabb, 1873)	L Olig–M Mioc	Peru–Florida	Woodring (1959); Hoerle (1972)
<i>Tympanotonos margaritaceus</i> (Brocchi, 1814)	L Olig–E Mioc	Mainz Basin, France, Greece, Iran,	Kadolsky (1995) (as <i>Mesohalina</i>); Lozouet et al. (2001); Harzhauser (2004)
<i>Vicarya</i> spp.	Mioc	Pakistan, W Pacific, Japan	Kanno (1986)
Genus <i>Potamidopsis</i>			
<i>Potamides (Potamidopsis) tricarinatus</i> (Lamarck, 1804)	M Eoc	Paris Basin	Cossmann and Pissarro (1910–1913)
<i>Potamides (Potamidopsis) californica</i> Squires, 1991	M Eoc	California	Squires (1991)
<i>Tympanotonos trochlearis</i> (Lamarck, 1804)	E Olig	Paris Basin	Gitton et al. (1986)
Genus <i>Campanilopsis</i>			
<i>Telescopium lemniscatum</i> (Brongniart, 1823)	M Eoc–E Olig	Europe	Cossmann (1906); Lozouet (1986)
Genus <i>Cerithideopsis</i>			
<i>Cerithidea (Harrisianella) vulcani</i> (Brongniart, 1823)	M Eoc	Italy, Hungary	Kowalke (2001b)
? <i>Tympanotonos californicus</i> Squires, 1999	M Eoc	California	Squires (1999)
<i>Potamides (Cerithidea) subpunctatus</i> (Deshayes, 1833)	M Eoc	Paris Basin	Cossmann and Pissarro (1910–1913)
<i>Potamides (Cerithidea) dowillei</i> (Vasseur, 1882)	M Eoc	Cotentin, Loire	Cossmann and Pissarro (1902); Cossmann (1906)
? <i>Harrisianella peruwiana</i> Olsson, 1929	L Eoc	Peru	Olsson (1929)
? <i>Lagunitus peruvianus</i> Woods, 1922	L Eoc	Peru	Woods (1922); Olsson (1929)

(continued on next page)

Table 4 (continued)

Taxa	Age	Geographical range	References
<i>Cerithidea</i> (<i>Cerithideopsis</i>) <i>pliculosa</i> (Menke, 1828)	Plioc	Florida	Olsson and Harbison (1953)
Genus <i>Cerithideopsis</i>			
<i>Cerithidea</i> (<i>Cerithideopsis</i>) <i>cingulata</i> (Gmelin, 1791)	M Mioc–Rec	Indonesia, W Pacific	Van Regteren Altena (1942); Houbriek (1984); Inoue (2007)
<i>Potamides</i> <i>graeus</i> (Deshayes, 1832)	M Mioc–Plioc	Mediterranean	Lozouet (1986); Kowalke (2001a)
Genus <i>Cerithidea</i>			
<i>Cerithidea</i> cf. <i>obtusa</i> (Lamarck, 1822)	Mioc	Saipan, W Pacific	Ladd (1972); Houbriek (1984)
<i>Cerithidea</i> (<i>Cerithidea</i>) <i>obtusa</i>	Plioc	Java	Van Regteren Altena (1942)
<i>Potamides</i> (<i>Cerithidea</i>) <i>babylonicus</i> Martin, 1884	Plioc	Java	Martin (1884)

The records are not complete, but attempt to list earliest reliable occurrences of all Recent and some fossil genera, and records demonstrating the full geographical range. Names are those used in the references quoted; revised generic assignment (bold) follows definitions in Table 3. ? Indicates uncertain generic placement. Abbreviations: Cret, Cretaceous (65.5–145.5 Ma); E, Early; Eoc, Eocene (34–56 Ma); L, Late; M, Middle; Mioc, Miocene (5–23 Ma); Olig, Oligocene (23–34 Ma); Palaeo, Palaeocene (56–65.5 Ma); Plioc, Pliocene (1.8–5 Ma).

no obvious similarity to Recent genera, their relationships cannot yet be assessed.

Of the Recent genera, *Terebralia* is large and distinctive, and has the most complete fossil record (Table 4). The earliest unquestioned member is *T. subcorvina* from the Middle Eocene of Europe (Kowalke, 2001b). A poorly preserved, doubtful species has been described from the Lower Eocene of Pakistan (Iqbal, 1969), but older species from California do not conform to our generic definition (Dailey and Popenoe, 1966; Squires and Kennedy, 1998). The genus did occur reliably in the Americas during the Miocene, persisted in Europe until the Late Miocene, and occurred in the IWP from the Miocene onwards (Table 4).

The type species of the genus *Tympanotonos* is the living *T. fuscatus*, but the generic name has been widely applied to fossil species. So too has *Potamides*, with the Oligocene fossil *P. lamarkii* as type species. Lozouet (1986) first pointed out that these could not be separated as distinct groups, and included *Eotympanotonos* and *Ptychopotamides* as subgenera. However, significant sculptural differences (the single largest and sometimes spinose ribs are not homologous, and varices are present only in *T. fuscatus*) suggest that Recent and fossil ‘*Tympanotonos*’ are not congeneric, leading Wittibschlager (1983; see also Kadolsky, 1995) to propose *Mesohalina* for the Oligocene ‘*Tympanotonos*’ *margaritaceus*. Although this has not been followed by most recent authors (Lozouet, 1986; Lozouet et al., 2001; Harzhauser and Kowalke, 2001; Kowalke, 2003; Harzhauser, 2004), we support this distinction, restricting *Tympanotonos* to the Recent species and using *Potamides* for the fossils. A possible early member of *Potamides* is ‘*Terebralia*’ *juliana* from the Late Cretaceous of California (Dailey and Popenoe, 1966). The subgenus *Eotympanotonos* may have been present in Europe as early as the Early Palaeocene (Bouniol, 1981) and by the Eocene was widespread in the Tethyan realm (Table 4). Contemporaneous shells from the western Pacific have been classified as *Vicaryella*, apparently based on geographical criteria rather than morphological difference. The Miocene genus *Vicarya* from the same region is superficially distinctive, but differs only in the more enlarged spines of the posterior rib and a more expanded aperture (Kanno, 1986). Detailed

comparative study may reveal that some of these groups should be recognized as genera, but we believe that they form a group more closely related to each other than to any Recent potamidids (Table 3). Those species of *Potamides* for which protoconchs have been described were mainly non-planktotrophic (Table 3). This is an additional distinction from the Recent *Tympanotonos*, which is planktotrophic (Egonmwan and Odiete, 1983). *Potamides* became extinct in the western Pacific (as *Vicarya*, Kanno, 1986) and in North America (Hoerle, 1972) in the Middle Miocene, but in Europe continued until the Pliocene (e.g. *P. granosus*; Lozouet, 1986). No Recent members of this group are known (see discussion of ‘*P.*’ *conicus* below). We retain *Potamidopsis* as a distinct genus (Lozouet, 1986; but listed as a synonym of ‘*Tympanotonos*’ by Kowalke, 2003), with a range from the Middle Eocene to the Early Oligocene (Table 4) and a possible relationship to *Potamides*. We also consider the enigmatic Tethyan *Campanilopsis* to be a distinct genus (as subgenus of *Telescopium* in Lozouet, 1986; listed as a synonym of ‘*Tympanotonos*’ by Kowalke, 2003).

Of the remaining potamidid genera, the Recent *Telescopium*, *Cerithidea* and *Cerithideopsis* are all known no earlier than the Miocene and only from the IWP. *Cerithideopsis* has an older fossil record, one of the earliest being *C. douvillei* from the Middle Eocene of the Paris Basin, here assigned to this genus for the first time (shell characters as in Table 3; protoconch indicates planktotrophic development; PL, unpublished). The contemporaneous *Harrisianella vulcani* also appears to belong to *Cerithideopsis*, and Kowalke (2001b) earlier noted this resemblance. It remains unclear whether the type species of *Harrisianella* from the Upper Eocene of Peru (Olsson, 1929) can also be classified in *Cerithideopsis*, and an Oligocene species of *Harrisianella* (Glibert, 1973) is considered an unlikely member. After the Eocene, no fossil *Cerithideopsis* are known until the Pliocene, in the western Atlantic (Olsson and Harbison, 1953; Houbriek, 1984).

To summarize, the oldest undoubted members of Recent potamidid genera are from the Middle Eocene, when both *Terebralia* and *Cerithideopsis* occurred in the European Tethyan realm (sensu Harzhauser et al., 2002), and the lat-

ter genus perhaps also in the Americas. Because the basal branches of the molecular phylogeny are not resolved, this fossil evidence is consistent with the origin of all the Recent genera (and of the clade *Cerithidea* plus *Cerithideopsis*) at or before this time. *Terebralia* persisted in Europe, and reached the western Atlantic in the Early Miocene, when a well-documented migration across the Atlantic took place (Harzhauser et al., 2002). During the Late Miocene *Terebralia* became extinct in both the Americas and Europe, and survived only in the IWP. A similar pattern of widespread distribution followed by restriction to the IWP is common in molluscs and other marine groups (Pau-lay, 1997; Vermeij, 2001; Williams, 2007). For *Cerithideopsis* the combination of phylogenetic and fossil evidence suggests a different history. It may have been widespread in both the Tethyan realm and the Americas (if identifications in Table 4 are correct) by the Middle Eocene, when other trans-Atlantic similarities are also recognized (Vermeij, 2001; Harzhauser et al., 2002). *Cerithideopsis* now survives in the AEP and IWP. Our finding of a sister relationship between the radiation of *Cerithideopsis* in the AEP and *C. largillierti* in the IWP suggests historical vicariance. Possible causes include global cooling at the end of the Eocene or early Miocene aridity, which restricted the mangroves of the Tethyan realm (Plaziat et al., 2001) or the final closure of the Tethyan corridor at the end of the Early Miocene (Harzhauser et al., 2002). A more fully resolved phylogeny and better fossil record might distinguish among these alternatives. Although the living West African *Tympanotonos fuscatus* has been considered the sole relict of a formerly pantropical genus (e.g. Kowalke, 2001a,b, 2003), we have found no evidence of this genus in the European fossil record. This is surprising, in view of faunistic similarities between Europe and West Africa in the Miocene (Brébion, 1974; Lozouet and Gourgues, 1995). For the remaining Recent genera (*Telescopium*, *Cerithideopsis*, *Cerithidea*) the limited fossil evidence is consistent with origin and radiation within the IWP and (as in *Terebralia*) appearance of living species in the Miocene, but the modern restriction of these groups to the IWP might also be the product of extinction elsewhere.

The relationships of the extinct genera *Potamides*, *Potamidopsis* and *Campanilopsis* to each other and to the Recent potamidid genera remain unclear. The limited evidence available suggests that most *Potamides* species were characterized by non-planktotrophic development (Table 3). Based on the topology of the phylogeny constructed from three genes (Fig. 2), the known developmental modes of some of the living species (Table 3), and the preponderance of planktotrophic development in other marine cerithiidean families (e.g. Scaliolidae, Cerithiidae, Modulidae; Kowalke, 1998; Bandel, 2006) that are appropriate for outgroup comparison, it can be argued that the ancestor of the living potamidids had planktotrophic development. Given that poecilogony (alternative modes of larval development; Ellingson and Krug, 2006) and evolutionary reacquisition of feeding larvae (Kowalke,

2001a; but see Collin et al., 2007) are rare in gastropods, we exclude a non-planktotrophic member of *Potamides* from the ancestry of the living potamidids. This, and the older fossil record of *Potamides* than of Recent genera, suggests the hypothesis that the extinct genera may be sister to (or paraphyletic to) the monophyletic radiation of the extant Potamididae. This recalls the separation of the two subfamilies (Potamidinae and Telescopiinae) advocated by Bandel (2006). More detailed study of the fossil taxa is required to test this suggestion.

4.3. Origin and relationships of '*Potamides*' *conicus*

In several respects '*Potamides*' *conicus* (as *Pirenella conica* before Kadolsky, 1984 and Lozouet, 1986) stands out as an unusual member of the Potamididae, and has therefore been a focus of interest. It extends further north than most other potamidids (to 40°N in the Mediterranean); it is not associated with mangrove habitats, but occupies marine lagoons and saline lakes; it is remarkably euryhaline (5–280‰); development is direct (Lozouet, 1986; Plaziat, 1993). In keeping with its isolated populations in extreme environments, it shows remarkable shell variation, yet the consensus is that there is only a single species distributed in the western Indian Ocean and eastern Mediterranean (Lozouet, 1986; Plaziat, 1993; Kowalke, 2001a). (Our samples were from Mozambique and Arabia; protoconchs were not present, but we have confirmed that other Arabian specimens do have protoconchs like those described from the Mediterranean by Kowalke, 2001a, indicating direct development.) Several hypotheses have been proposed to explain this unusual distribution. Por (1978) considered *Pirenella conica* to be a recent (but still 'pre-Lessepsian') migrant from the Red Sea, which was able by virtue of its physiological tolerance to disperse northward through the hypersaline lakes that were present during the Quaternary before the construction of the Suez Canal. In contrast, Lozouet (1986) identified the species as the sole extant member of the genus *Potamides*, proposing a line of descent from the Oligocene *P. lamarkii* to Miocene *P. theodiscus* to Pliocene *P. graecus* to Recent *P. conicus*, entirely within the Tethyan and Mediterranean region. The presence of *P. conicus* in the Indian Ocean was considered most likely the result of Quaternary dispersal, perhaps by birds, through the hypersaline lakes of Suez, but in a southward direction. By implication, the ancestors of *P. conicus* likewise had direct development and were similarly euryhaline, enabling them to survive in the Mediterranean through the Messinian salinity crises during the Late Miocene. Kowalke (2001a) described the protoconchs of the supposed ancestors of *P. conicus*, and argued that the lecithotrophic (i.e. brief planktonic but non-feeding) development of *P. theodiscus* precluded it from direct ancestry of the planktotrophic *P. graecus*. He did not, however, question the Tethyan–Mediterranean origin of *P. conicus*, its recent spread to the Indian Ocean (said to be due to human agency) or its membership of *Potamides*.

The molecular phylogeny, in combination with the fossil record, supports an entirely different hypothesis. '*Potamides*' *conicus* is a member of the otherwise exclusively IWP *Cerithideopsilla* clade and, in the three-gene tree, clusters with *C. cingulata* (internal relationships not resolved, Fig. 2). A parsimony argument (see above and Table 3) suggests that the common ancestor of these two species was a planktotrophic inhabitant of the IWP (like *C. cingulata*; Houbrick, 1984). Our new interpretation of the fossil record is that *P. theodiscus* was the last of the direct-developing *P. lamarkii*–*P. theodiscus* lineage in the Mediterranean, becoming extinct in the Paratethys during the Late Miocene. Although it would be most parsimonious to conclude that '*P.*' *conicus* arose in the IWP and dispersed northward to the Mediterranean, the fossil record suggests otherwise. '*Potamides*' *graecus* is a candidate for the planktotrophic ancestor of '*P.*' *conicus*; the latter must therefore have originated in the Mediterranean, and both should be classified as *Cerithideopsilla*. In support of this reclassification, *C. graeca* shows a weak ventrolateral varix (PL, unpublished), present in IWP *Cerithideopsilla* but absent in all *Potamides* (Table 3), suggesting how this was reduced and lost in *C. conica*, resulting in the convergence of the latter with *Potamides* species. *Cerithideopsilla graeca* was planktotrophic and thus likely to have been a species of marine or brackish habitats like IWP *Cerithideopsilla* (the salinity tolerance of *C. cingulata* is 1.5–50‰, Vohra, 1970; Plaziat and Younis, 2005). We therefore suggest that *C. graeca* reached the Mediterranean either before the closure of the Tethyan–Indian Ocean connection at the end of the Early Miocene (late Burdigalian) or during the intermittent connections of the Middle Miocene (Harzhauser et al., 2002). The earliest record of *C. graeca* is from the Late Miocene of Greece (Tortonian; Kowalke, 2001a), suggesting the latter alternative. (The taxonomy and relationships of the fossil *Cerithideopsilla* require reexamination; some Pliocene examples of *C. graeca* from Tunisia have non-planktotrophic development, PL unpublished, emphasizing the likely descent of *C. conica*. Furthermore, Lozouet, 1986, mentioned another *Cerithideopsilla*-like Pliocene species, '*Potamides*' *etruscum*, from Italy.) It is possible that the evolution of direct development in *C. conica* (or its *graeca*-like ancestor) was linked to the environmental crises (hypersalinity and cooling) in the Mediterranean during the Late Miocene. Whether this species maintained a continuous presence in the Mediterranean throughout the climatic fluctuations of the Pleistocene, or survived glacial intervals in an Indian Ocean refuge, is not known (Lozouet, 1986). In either case, we agree with Lozouet (1986) that spread of *C. conica* to the Indian Ocean was recent, some time in the Quaternary, that it was facilitated by direct development and euryhalinity, and that transport may have been effected by birds (see also Plaziat, 1993). The present distribution of *C. cingulata* is centred in the western Pacific, but it is sympatric with *C. conica* in the northern Indian Ocean (e.g. Plaziat and Younis, 2005), where the two remain distinct.

Retention of the morphological hypothesis of descent of '*Potamides*' *conicus* from *P. lamarkii*, in the light of the molecular hypothesis, would require parallel gain of the ventrolateral varix in *Cerithidea* and in two to four lineages of *Cerithideopsilla*, as well as multiple invasion of the IWP (or multiple extinction in the Mediterranean) to produce the biogeographic pattern (Fig. 2). We consider this untenable. Nevertheless, our hypothesis remains to be fully tested by a more detailed study of the fossil record, and by molecular sampling of *C. conica* from the Mediterranean to confirm that it is conspecific with Indian Ocean populations.

4.4. Evolution of Potamididae and the mangrove habitat

It is a longstanding question whether mangrove forests have a characteristic fauna of species that show a strict association with this habitat (Plaziat, 1984; Glaubrecht, 1997; Plaziat et al., 2001). As reviewed above, all the living genera of Potamididae are associated with mangroves, using the trees for shelter, as a substrate, for food and protection from predators. A dietary specialization is shown by *Terebralia palustris*, which as an adult feeds on fallen *Rhizophora* leaves using a specially modified radula (Plaziat, 1977; Houbrick, 1991; Fratini et al., 2001), yet populations in Arabia exist without this food source and even survive in sheltered habitats without mangrove trees (Feulner, 2000). Similarly, although *Cerithidea* species typically climb mangrove trees, they can exist locally on saltwort vegetation and driftwood (DGR, unpublished). Nevertheless, it is true that most living potamidid species maintain their greatest numbers on or beneath mangrove trees and probably could not survive without them. There are at least three exceptions. In the IWP, *Cerithideopsilla cingulata* is abundant on sheltered, intertidal, muddy sandflats that are not necessarily adjacent to mangroves (Vohra, 1970; Balaparameswara Rao and Sukumar, 1982; Maki et al., 2002; Plaziat and Younis, 2005). In the Mediterranean and Indian Ocean, *C. conica* occupies a similar habitat and can also be found in shallow lagoons and saline lakes (Lozouet, 1986; Plaziat, 1993; Kowalke, 2001a). In California, *Cerithideopsis californica* occurs at high densities on intertidal mudflats and among saltmarsh plants (Race, 1981); this species is predicted to be a member of the eastern Pacific *Cerithideopsis* clade (Houbrick, 1984; Fig. 2). These three species occupy terminal positions in the molecular phylogeny (Fig. 2), so that their independence from mangroves is a derived condition. Parsimonious reconstruction of ancestral habitats therefore suggests that association with mangroves is plesiomorphic within the entire radiation of living potamidids. The common ancestor of *Cerithideopsilla cingulata* and *C. conica* is predicted to have shared the same non-mangrove habitat, and was therefore able to colonize the Mediterranean in the Middle or Late Miocene, where mangroves were reduced to *Avicennia* alone, and to survive the extinction of mangroves in the

Mediterranean at the close of the Miocene (Plaziat et al., 2001).

The specialized tree-climbing habit is found in two potamidid clades, *Cerithidea* (Houbrick, 1984; McGuinness, 1994; Ohtaki et al., 2002; Vannini et al., 2006) and *Cerithideopsis* (Keen, 1971; Plaziat, 1984; but not in all species, e.g. Race, 1981; Houbrick, 1984). The shells show parallel morphological adaptations of lightweight construction, flared and planar apertures and (in *Cerithidea*) decollate (shed) apices. Given the tree topology of Fig. 2, it is parsimonious to reconstruct independent acquisition of tree-climbing in these two groups (but reconstruction would be equivocal under alternative resolutions of the basal polytomy in Potamididae) from ground-dwelling ancestors. This contrasts with the other tree-dwelling clade of mangrove-associated gastropods, the genus *Littoraria*, which was derived from rock-dwelling ancestors (Reid, 1999; Williams et al., 2003). There is a parallel among tree-climbing crabs, of which the Sesarmidae had sediment-dwelling ancestors whereas Grapsidae were derived from rock-dwellers (Fratini et al., 2005).

For fossil potamidids it is far more difficult to determine their membership of mangrove ecosystems. Based on the ecology of their living species, some genera (*Telescopium*, *Terebralia*) have been used as indicators of fossil mangrove assemblages (Oyama, 1950; Plaziat, 1995). For extinct species this argument is unsound unless confirmed by fossil pollen or plant remains, and this evidence is seldom available. The three living species of *Terebralia* are closely associated with mangroves (with the exception noted above). During the Early and Middle Miocene, *Terebralia bidentata* was abundant in the Mediterranean and Paratethys, and has been found with probable mangrove plant debris (Harzhauser and Kowalke, 2001) and *Avicennia* pollen (Plaziat, 1995); however, it also extended beyond the likely northern limit of mangroves, so the association was not invariable (Plaziat, 1995; Plaziat et al., 2001). During the Late Oligocene *Terebralia rahti* occurred in the Mainz Basin under semiarid conditions unfavourable for mangroves (Kadolsky, 1988); the same species was common during the Early Miocene in the Aquitaine Basin in a lagoonal environment, with no evidence of association with mangroves (PL, unpublished). The Middle Eocene species *Terebralia subcorvina* has been found together with the remains of mangrove plants, as has *Cerithideopsis vulcani* (Kowalke, 2001b).

In contrast, many fossil members of *Potamides* are believed to have inhabited shallow lagoons with low or variable salinity (Lozouet, 1986; Kowalke, 2001a, 2006a; Harzhauser and Kowalke, 2002) and even saline inland lakes (Plaziat, 1993; Kowalke, 2006b). (This palaeoecological interpretation has been strengthened by comparison with *Cerithideopsis conica* in similar habitats, and the belief that it is the surviving representative of *Potamides*, but this is refuted above.) The larger members of *Potamides* have frequently been identified as ‘*Tympanotonos*’ and, by analogy with the Recent mangrove-associated *T. fuscatus*, have

been used as mangrove indicators (Harzhauser, 2004; Reichenbacher et al., 2004; Dominici and Kowalke, 2007). These ‘*Tympanotonos*’ have occasionally been found in deposits with mangrove plant fossils and with *Terebralia* (Middle Eocene of Hungary, Kowalke, 2001b), but in other cases ‘*Tympanotonos*’ and *Terebralia* occur in distinct facies (Kadolsky, 1988, 1995; Harzhauser and Kowalke, 2001). At least some fossil ‘*Tympanotonos*’ are believed to have inhabited shallow sublittoral, sandy, reef flats (Harzhauser, 2004). In the case of *Vicarya* (here considered a synonym of *Potamides*; Table 3) fossils may occur together with *Telescopium* and *Terebralia*, but it is not considered an indicator of mangrove habitats (Oyama, 1950; Shimizu and Kaneko, 1992; Taguchi, 1992, 2002). The acid soils of mangroves are not conducive to preservation of molluscan shells (Plaziat, 1995), so the abundance of *Potamides* (and, indeed, of some *Terebralia*) in the fossil record argues against a strict association with mangroves. At the least, therefore, *Potamides* had a far wider range of habitats than Recent potamidid genera, and the evidence for its association with mangroves is slight. Another extinct potamidid genus, *Potamidopsis*, is believed to have inhabited sandy sublittoral seagrass beds (Gitton et al., 1986, as ‘*Tympanotonos trochlearis*’) and lagoons of variable salinity (PL, unpublished).

In conclusion, the molecular phylogeny in combination with our survey of the fossil record, the ecology of Recent and fossil potamidids, and the history of mangroves themselves, suggests the following hypothesis. Diverse mangrove forests first appeared in the Tethyan realm during the Early Eocene (following a likely radiation in the Palaeocene; Ellison et al., 1999; Plaziat et al., 2001). The living members of the Potamididae are a monophyletic radiation, whose earliest certain representatives appeared in the Middle Eocene of the Tethys (Fig. 2, Table 4). This historical and geographical coincidence of Recent mangrove and potamidid genera has been noted before (Glaubrecht, 1996, 1997; Ellison et al., 1999; Kowalke, 2003). However, we go further, and suggest that the living potamidids (subfamily Telescopiinae Allan, 1950) are a single adaptive radiation that diversified in the new mangrove environment shortly after its appearance. The evolution of the potamidids has been intimately connected with that of the mangroves ever since, although a few species have lost this dependence (several species of *Cerithideopsis*, *Cerithideopsis*, *Terebralia*, noted above). The detailed biogeographic history of potamidids is not yet understood, but at least some genera (*Terebralia* and *Cerithideopsis*) formerly had a pantropical distribution and have become restricted (by extinction and vicariance, respectively), mirroring patterns in the mangrove genera, which in turn responded to global climatic and tectonic events (Plaziat et al., 2001). The modern pattern of potamidid diversity, with a focus in the central Indo-West Pacific, matches that of mangrove species (Ellison et al., 1999; Ellison, 2002). Only those potamidids that have lost their association with mangroves (e.g. *Cerithideopsis conica*) have been able to colonize temperate

coastlines where mangroves do not occur. Vegetated salt-marsh habitats existed before the appearance of the distinctive mangrove environment (Plaziat et al., 2001), and may have been inhabited by extinct potamidid genera (Bandel and Riedel, 1994; Kowalke and Bandel, 1996; Kowalke, 2003). The fossil Potamididae require much further study, but at present there is little evidence that either the large group here termed *Potamides* (Table 3) or the genus *Potamidopsis* were ecologically associated with mangroves, nor that they were the sister group of any one of the living genera.

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