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New Records, Biogeography, and Habitat Protection Needs of Four Species of *Potamon* (Decapoda: Brachyura) in Greece

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ABSTRACT

Objectives are to determine the occurrence of species of *Potamon* in eastern Crete and the Aegean Islands (Chios, Naxos, Paros, Mykonos, Tinos and Andros); generate phylogenetic relationships among species to propose a biogeographic hypothesis relative to current distributions of the four species of the freshwater crab genus, *Potamon*, in Greece; and comment on the need to protect habitat suitable for the survival of species of *Potamon* in the country. Our collections, made in areas not previously sampled by researchers, indicate the presence of *Potamon fluviatile* on Tinos, Naxos, and Andros, and *Potamon potamios* from central to eastern Crete; and verified the presence of *Potamon ibericum* on Chios. Cladistic analyses resulted in a single parsimonious tree (CI=85, RI=75). *Potamon* in the Balkan peninsula and islands in the Mediterranean region is a monophyletic group composed of two main clades: Clade 1 (*P. fluviatile* and *Potamon algeriense*) and Clade 2 (*P. ibericum* and its sister group composed of *Potamon rhodium* and *Potamon potamios*). Vicariant events (e.g. marine transgression and regression, orogeny, volcanism) are hypothesized as major factors that have shaped current distributions of species of *Potamon* in the Balkan Peninsula, Asia Minor, and the islands of the North Aegean Sea, Eastern Sporades, the Cyclades, and Crete. We recommend an increase in environmental education and communication among older and younger generations, agriculturalists, politicians, policy writers, land developers and economists to create an understanding for the need to protect land and aquatic environments that harbor unique species and the potential benefits for economic activities such as ecotourism. We also recommend the creation of an action plan to develop ecotourism around conservation areas (e.g. from the source of existing springs downstream for about 200 m before the installation of water withdrawal equipment for irrigation and potable supplies) to generate revenue for funding protection initiatives and to promote green economic development that is ecologically and socio-culturally sustainable.

Keywords: *Potamon*, biogeography, habitat protection

INTRODUCTION

In response to the European Environmental Agency's (EEA) biodiversity initiative to inventory, identify, and describe aquatic and terrestrial species in European Union (EU) countries, Maurakis et al. (2004) provided an update to the distributions of freshwater crab species of *Potamon* (Decapoda: Brachyura) relative to lotic stream factors in Greece. Significant gaps in distributional records of both freshwater crabs and fishes and the absence of sampling in some areas (e.g. Aegean Islands and eastern Crete), however, have hampered the creation of the biodiversity inventories needed for determining candidate protection areas, conducting environmental impact studies, and understanding biogeographic mechanisms (Bobori et al., 2001; Maurakis et al., 2004; 2003). Additionally, climate change (hotter and drier conditions) and increased anthropogenic influences (i.e., surface water withdrawal and high rates of ground water pumping) over the past 40 years have decimated water resources and degraded remaining aquatic habitats in significant portions of Greece (Bobori et al., 2001). Water extraction has resulted in fragmented, polluted, and xeric aquatic habitats that have led to the extirpation of native fish and crab species in this Mediterranean country on the European fringe. Without a national action plan to monitor and manage aquatic resources (Economou et al., 2000; OECD, 2000), desertification, which already is increasing (Yassoglou and Kosmas, 2000), will accelerate and permanently alter the land towards a Middle Eastern environment.

Objectives of the study are to determine the occurrence of species of *Potamon* in eastern Crete and the Aegean Islands (Chios, Naxos, Paros, Mykonos, Tinos and Andros); generate phylogenetic relationships among species to propose a biogeographic hypothesis relative to current distributions of the four species of the freshwater crab genus, *Potamon*, in Greece; and comment on the need to protect habitat suitable for the survival of species of *Potamon* in the country.

Geologic, Tectonic, and Eustatic Descriptions of Study Area

In a relatively short amount of geologic time (58 my), a variety of events have taken place in the Balkan Peninsula and surrounding areas which make this area both fascinating and challenging for the study of the relationships among groups of organisms (Maurakis and Economidis, 2001; Maurakis et al., 2001). The following is a summation of the events, which have played an important role in shaping the study area as it occurs today, and the distributions of species of *Potamon* in the region.

During the Eocene and Oligocene (58-22 mya), the Afro-Arabian continent moved towards and collided with the Eurasian continent (=Alpine collision). During this collision, the Pindus thrust was initiated and led to the creation of the Pindus Mountain range in western Greece (Clews, 1989). Compressional forces were strong, and by the Miocene (22-5 mya) oceanic crust began to sink northward below the Aegean in a newly formed subduction zone, the Hellenic Trench. Many events precipitated in response to the opening of this subduction zone. Just north of the Hellenic Trench, formation of the non-volcanic Hellenic arc emerged due to the crust above the subduction zone arching upwards. Islands of Crete, Karpathos and Rhodes, the western edge of Peloponnesos, and southeastern Turkey form this Hellenic arc (Angelier, 1982). As the subducting ocean slab began to melt, the South Aegean volcanic arc, which spans from Corinth to the Dodecanese, formed and grew further north of the Hellenic arc (Higgins and Higgins, 1996). This volcanism, beginning about 5 mya, continues today in the Cyclades Islands of Milos and Thera (Higgins and Higgins, 1996). In response to subduction and volcanism, extensional forces developed and created a back-arc basin in the Aegean region. A series of horsts and graben structures, many with roughly NW/SE orientation, resulted from this Neogene extension. Several of the rivers (e.g. Nestos, Strymon, Axios, Loudias, and Aliakmon) in our study area presently flow down valleys formed by these grabens.

The North Aegean Trough, associated with the North Anatolian Fault Zone (FZ), is an important feature that developed during the Neogene extension. The North Aegean Trough is 1000-1500 m deep where surrounding basins (e.g. Thrace Basin, Strymon Basin) constitute the southern margin of the European plate (LePichon and Angelier, 1979). The North Aegean Trough runs in a NNW/SSE orientation from the Saros Trough in the east to Magnesia on mainland Greece in the West (Lyberis, 1996). The North Anatolian FZ, a prominent right lateral strike-slip fault, runs horizontally beneath the Sea of Marmara, the Gallipolis Peninsula north of the Dardanelles, and along the North Aegean Trough where it terminates near Skiathos near the Pelion Peninsula (Higgins and Higgins, 1996).

Along with these tectonic events, the Aegean region has experienced a handful of eustatic changes in sea level, which have set the stage for joining and severing ancient river drainage systems, and islands in the Aegean. Rising and lowering sea levels have been triggered by tectonic and climatic events (Rogel and Steininger, 1983). For example, the Alpine collision triggered a widespread regression 20 mya (Rogel and Steininger, 1983). During the Tortonian (10 mya), a major transgression followed by regression occurred. During the Messinian (5.1 mya), glaciation of the West Antarctic ice sheet increased, which led to worldwide regression (Bianco, 1990). Coupled with this lowering of sea level, Hsu (1983) believes the Mediterranean dried into a desert, "Messinian Salinity Crisis," leaving only a few isolated freshwater lakes in the region. Soon, the Atlantic Ocean broke through the Straits of Gibraltar and flooded the Mediterranean region with salt water (Hsu, 1983), a significant barrier to freshwater faunas. Since then glacial and interglacial periods have been the primary factor controlling regressions and transgressions of the region. At the peak of the last glaciations (20,000ya), sea level was about 120 m below present levels (Higgins and Higgins, 1996). During this time, the Black Sea and Sea of Marmara were freshwater lakes, which drained into the Dardanelle's valley. By 8000 BCE, sea level of the Mediterranean Sea began to rise rapidly to its present level, encroaching on the Dardanelles, Sea of Marmara, Black Sea and ancient river drainage systems. With sea levels and climatic conditions remaining relatively constant for the last 8000 years, the study area has endured much weathering and erosion. Coupled with this, movement along fault lines within both compressional and extensional regions and subsidence of basins have played roles in shaping and molding the landscape of the region.

MATERIALS AND METHODS

Specimens of *Potamon* collected by hand, seines and dip nets from sampling sites in stream and riparian habitats, were preserved in 95% ethanol and transported to the laboratory for identification (Appendix 1).

Two characters, terminal and subterminal segments of 1st pleopod in males presented in Brandis et al. (2000) and Pretzmann (1983, 1962) were used to identify male *Potamon* spp.:

P. fluviatile: flexible zone of male gonopod V-shaped, and subterminal segment of Pl.I S-shaped with inner lobe of terminal segment buldging strongly in a regular curve from base to just before tip;

P. ibericum: flexible zone of male gonopod broadened in its mesial part, and subterminal segment of Pl.I extended straight, length of terminal segment of Pl.I at most 0.4 x length of subterminal segment, greatest width at base, approximately spherical;

P. potamios: flexible zone of male gonopod symmetrically bilobed; subterminal segment of Pl.I extended straight, length of terminal segment of Pl.I rather less than 0.33 of length of subterminal segment, segment very seldom somewhat greater than 0.33, greatest width about middle, or distal to middle; and,

P. rhodium: flexible zone of male gonopod distinctly V-shaped where top of "V" is situated directly on the subterminal median bulge.

Ten morphological characters in Brandis et al. (2000) and Pretzmann (1983, 1962) for *P. fluviatile, P. ibericum, P. potamios*, and *P. rhodium* were identified and determined as primitive or derived by out-group comparison (Table 1). *Potamon* (*Orientopotamon*) *gedrosianum* distributed in Afghanistan and Pakistan was used as the out-group. The computer program *hennig86* (Farris, 1988; Lipscomb, 1994) was used to construct cladograms of species using the options *ie** which generates cladograms by an implicit enumeration algorithm and retains all parsimonious cladograms. The relative quality of results was judged using the consistency index (CI), a measure of the degree to which characters changes on the cladogram are minimal (see Kluge and Farris, 1969), and the retention index (RI), a measure of the amount of relatedness hypothesized by the presence of characters that is not in conflict with the final cladogram (Farris, 1989). Multiple equally fit hypotheses of relationships of the species were re-evaluated using successive weighting (command *xs w* in *hennig86*), a procedure that reanalyzes after down-weighting data that are in conflict with initial results (Farris, 1969; Carpenter, 1988). *Winclada* (Nixon, 1999) was used to plot characters and character states per node.

RESULTS AND DISCUSSION

With the exception of Paros, *P. fluviatile* was found on all Aegean islands sampled (Naxos, Tinos, and Andros)(Fig. 1). Our collections are new distribution records that extend the range of *P. fluviatile* to Tinos and Naxos, and confirm the continued presence of the species on Andros, where the species was last reported extant by Pretzmann in 1980. Our records of *P. potamios* in eastern Crete extend the range of the species from central Crete to the eastern and southeastern portion of the island, where freshwater habitats are scarce (Fig. 1). Previously, the easternmost record of *P. potamios* was in the Lasithi Plateau (Brandis et al., 2000). Our collections of adult male *P. ibericum* on Chios confirms the presence of the species on the island

TABLE 1. Characters and character states of *Potamon gedrosianum* (out-group) from Afganistan, in-group (*Potamon ibericum*, *Potamon fluviatile*, *Potamon rhodium*, and *Potamon potamios* from Greece, and *Potamon algeriense* from northern Africa).

	Character								
Species	1	2	3	4	5	6	7	8	9
P. gedrosianum	0	0	0	0	0	0	0	0	0
P. ibericum	1	1	0	1	1	0	1	2	2
P. fluviatile	0	0	1	1	1	0	0	1	1
P. rhodium	0	0	0	1	1	0	1	3	1
P. potamios	0	0	0	1	2	1	1	3	0
P. algeriense	0	0	1	1	1	0	0	1	2

Character 1. Carapace: 0=smooth and concave; 1=smooth and flat.
Character 2. Anteriorlateral carapace margin: 0=well developed; 1=Not well developed, small.
Character 3. 1st gonopod: 0=conical or slender, without swollen mesial part; 1=broad, oval-shaped with swollen mesial part.
Character 4. Serrations on anterior lateral carapace margin: 0=long teeth; 1=short teeth.
Character 5. Teeth on anterior lateral carapace margin: 0=pointed, unequal in length; 1=pointed, equal in length; 2=rounded, unequal in length.
Character 6. Chelipeds: 0=equal in length; 1=unequal in length.
Character 7. Shape and margin of male abdomen: 0=triangular with straight margin; 1=triangular with convex margin.
Character 8. Terminal joint of 1st gonopod: 0=shortly triangular, with variable projecting medial edge; 1=large bulge with lateral margin strongly rounded; 2=spindle shaped; 3=elongatedly conical, mesial part not curved outwards.
Character 9. Flexible zone: 0=slightly bilobed; 1=V-shaped; 2=lobed.

previously based on two juvenile males and one leg reported by Brandis et al. (2000) and Pretzmann (1986), respectively (Fig. 1).

Cladistic analyses resulted in a single parsimonious tree (CI=85, RI=75; Fig. 2). Clade A is a monophyletic group (synapomorphic characters 4, state 1; and 5, state 2) composed of Clade B (*P. fluviatile* and *P. algeriense*) defined by one synapomorphy

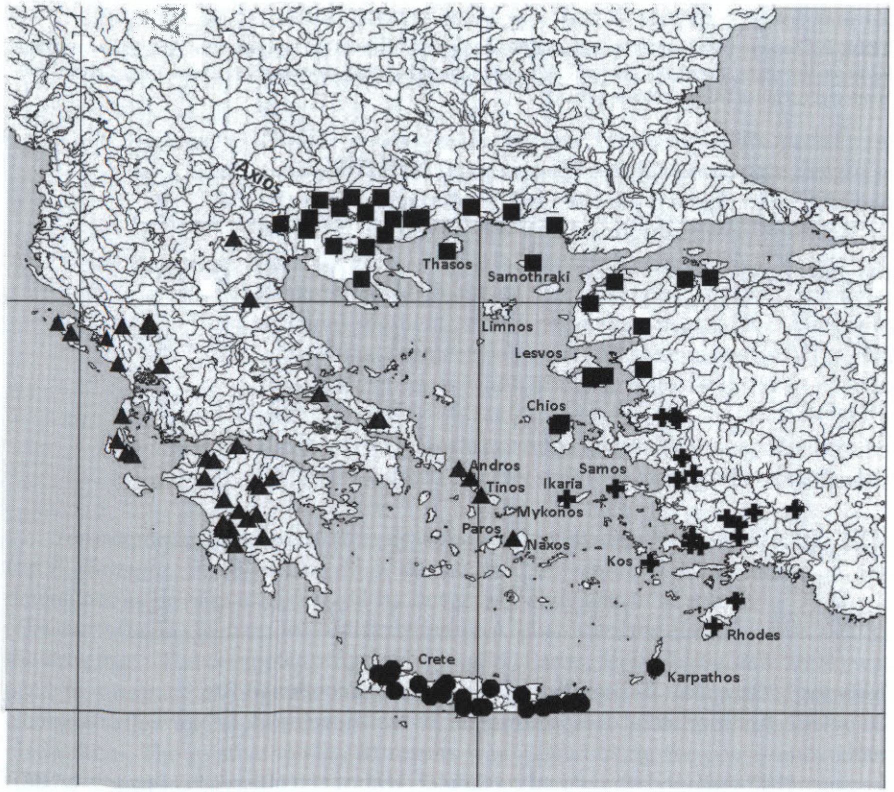

FIGURE 1. Collections sites of collections of *Potamon fluviatile* (▲), *Potamon ibericum* (■), *Potamon potamios* (●) and *Potamon rhodium* (✚).

(character 3, state 1) and Clade C. Clade C, defined by two synapomorphies (character 7, state 1; and character 8, state 2), is a monophyletic group composed of *P. ibericum* and its sister group, Clade D. Clade D, defined by one synapomorphy (character 8, state 3), is a monophyletic group composed of *P. rhodium* and *P. potamios* (Fig. 2).

Vicariant events (e.g. marine transgression and regression and orogeny) are hypothesized as major factors that have shaped relationships among river drainages and islands and current distributions of species of *Potamon* in mainland Greece on the Balkan Peninsula, and on the islands of the North Aegean Sea (e.g. Samothraki, Thassos, Limnos), Eastern Sporades (e.g. Lesbos, Chios, Ikaria, Samos, Rhodes, Kos), the Cyclades (e.g. Andros, Tinos, Naxos, and Paros), and Crete (Figs. 1 and 2). Dispersal of *P. fluviatilis* extended westward from ancestral populations in Anatoli and colonized mainland Greece and its geologically related Cycladic islands (e.g. Andros, Tinos, Naxos, and Paros), and then west to the Italian Peninsula. This is consistent with the geological evolution of the area, where the Cycladic islands are part of the Attica-Cycladic metamorphic belt, which continues north to Attica and southern

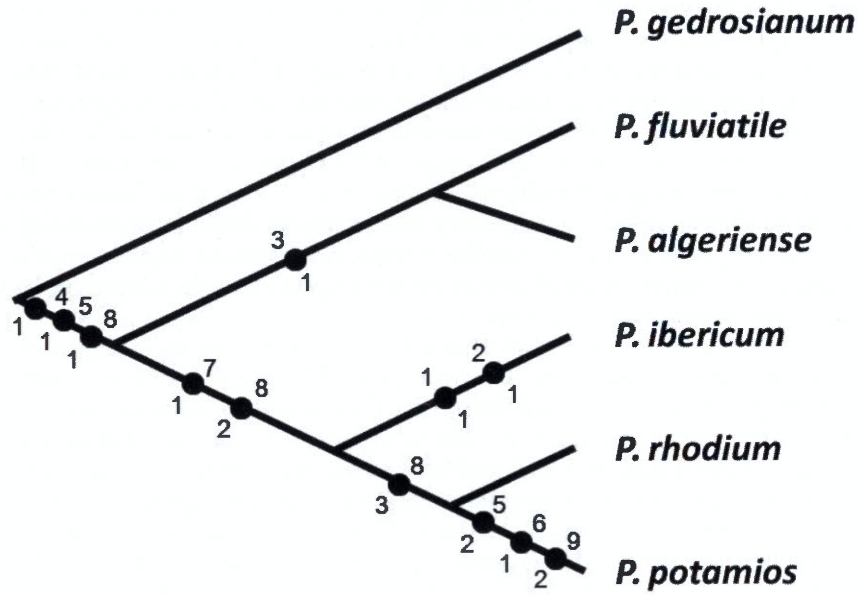

FIGURE 2. Phylogenetic relationships of in-group taxa (*Potamon fluviatile*, *Potamon ibericum*, *Potamon potamios*, and *Potamon rhodium* in Greece, and *Potamon algeriense* from Africa (out-group= *Potamon* (*Orientopotamon*) *gedrosianum*). Numbers over black dots (=synapomorphies) are characters; those below are character states.

Euboea (Higgins and Higgins, 1996). Populations of *P. fluviatilis* probably extended to North Africa prior to the Messinian Salinity Crisis (5.1 mya) during which time (~0.5 my) the region was a steppe landscape which could have supported crab populations in lakes between Sicily and Northern Africa (Stanley and Wenzel, 1985). After the Atlantic Ocean broke through the Straits of Gibraltar, populations in Northern Africa, now recognized as *P. algeriense*, became isolated from those of *P. fluviatilis* in Italy. Our cladistic analysis corroborates the statements of Brandis et al. (2000) who used traditional evolutionary taxonomic methods to hypothesize the relationship between *P. fluviatilis* and *P. algeriense*.

We hypothesize that *P. ibericum* dispersed from Turkey westward to Greece prior to the Mediterranean transgression of the Sea of Marmara and Black Sea, and competitively replaced populations of *P. fluviatilis* east of the Serbo-Macedonian massif, just east of the Axios River (Figs. 1 and 2). Populations of *P. ibericum* on the islands of Thassos, Samothraki, Limnos, Lesvos and Chios are a result of their proximate connections to the mainland prior to marine transgression. Current water depths between all of these islands and their respective mainland areas are 100 m, less than that of the marine transgression of 120 m when the Atlantic Ocean flooded the Mediterranean area after the Messinian Salinity Crisis (Higgins and Higgins, 1996).

The Menderes River and a 1000 m trough in the eastern Aegean Sea south of Chios separate southern populations of *P. ibericum* on Chios and central Anatoli from Clade

D (*P. rhodium* and *P. potamios*), derived from an ancestral population in southern Anatoli (Figs. 1 and 2). Distribution of *P. rhodium* is limited to a small area of southern Anatoli and the islands of Samos, Ikaria, Kos and Rhodes. Water depth between these islands and the mainland vary between 100-400 m, and suggest that *P. rhodium* was probably present on these islands prior to the Messinian Salinity Crisis. Rhodes is separated from Anatoli by a channel 400 m deep, and to the south of the island, the sea-floor drops off rapidly to a depth of over 3000 m in the Rhodes basin (Higgins and Higgins, 1996). We hypothesize the 3000 m deep trench served as a barrier separating populations of *P. rhodium* from the more southern populations of its sister species, *P. potamios*, which occurs on the islands of Crete, Karpathos, and Cyprus, and in the Jordan River system.

A significant number of perennial streams that existed 20 or more years ago in the eastern portion of Crete, and those on islands (e.g. Chios, Mykonos, Naxos, Paros, Tinos) have become completely dry (pers. obs). The desiccation of streams has been directly related to climate change (i.e., reduced precipitation frequency and amount) and increased water withdrawal from springs, streams, and subterranean aquifers for crop irrigation and potable water supplies for an increasing population (particularly in the tourist industry). Unsustainable agricultural policies and common agricultural practices (CAP), and water and soil resource schemes have resulted in loss of 75 % of wetlands in Greece since 1900 (OECD, 2000). As a result, flourishing populations of *Potamon* do not exist in most areas (e.g. central and eastern Crete) that once harbored crabs as large as 18.5 cm in carapace width (Manos Sambobalakis, Ierapetra Taverna, pers. comm., 2007). In interviews of 14 local inhabitants from Kato Zakros on the east coast of Crete west to Archanes in the middle of the island, we determined that *Potamon* crabs had been a significant part of Cretan culture. The freshwater crab was part of the diet of locals and Greeks after 1200 BCE (Joseph Shaw, University of Toronto, pers. comm., 2007), a source of play for children (Stella Ailamaki, Stella Apartments Villa, pers. comm., 2007), in archaeological remains and artwork of Minoans at Kommos and Knossos around 1600 BCE (Evans, 1928; Shaw and Shaw, 2000), and as the basis of at least one song (pers. obs.). As *Potamon* populations are interwoven into the cultural fabric of local Cretan communities, and are one of the largest freshwater macrobenthic organisms whose ecological position is not well understood, we recommend the following: (1) increase environmental education and communication among older and younger generations, agriculturalists, politicians, policy writers, land developers and economists to create an understanding of the need to protect the land and aquatic environments that harbor unique species and the potential benefits for economic activities such as ecotourism; and (2) create an action plan to develop ecotourism around conservation areas (e.g. from the source of existing springs downstream for about 200 m before the installation of water withdrawal equipment for irrigation and potable supplies) to generate revenues for funding protection initiatives and to promote green economic development that is ecologically and socio-culturally sustainable as discussed in Lekakis (1998). The alternative development and biodiversity conservation projects in the Prespa lake system in northwestern Greece and the Dadia-Lefkimi-Soufli forest reserve in northeaster Greece discussed by Valaoras (1998) could serve as models for such a plan.

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APPENDIX I

Locality data (island, prefecture, collection number, locality, data and number of crabs collected or no water in parentheses for species of *Potamon* collected from Greek islands in 2004, 2006, and 2007.

Potamon fluviatile: Mykonos Island, EGM-Mykonos-604, marsh pond at Panomas Beach, 17 July 2006 (0); EGM-Mykonos-605, Lake Maou in NE Mykonos near Fokos Beach, 17 July 2006 (0). Paros Island, EGM-Paros-606, stream in Valley of Butterflies at Biotpoe Petaloudes, about 8 km S of Parikia-Paros, 18 July 2006 (0). Naxos Island, EGM-Naxos-607, unnamed stream discharging into Amiti Bay, 0.4 km NE of Egares, about 7.5 km NE of Naxos Hora, 18 July 2006 (3). Tinos Island, EGM-Tinos-608, Rematia Venia in town of Pyrgos, 20 July 2006 (2); Andros Island, EGM-GR-609, Dionysos Spring at Patouria, about 6 km NW of Andros Hora, 22 July 2006 (1).

Potamon ibericum: Chios Island, EGM-GR-602, Panagia stream (Potamos Velesou), 3.5 km ENE of Volissos, 16 July 2006 (5); EGM-GR-603, Springs of Potamos Velesou, 1.2 km NE of Fyta, about 9 km NE of Volissos, 16 July 2006 (2).

Potamon potamios: Crete, Xania Prefecture: EGM-R-584, Keritas River, 0.5 km E of Alikianos, 10 km SW of Xania, 19 June 2004 (0); EGM-GR-585, SE branch of Keritas River, 1 km E of Forne, 12 km SW of Xania, 19 June 2004 (2); EGM-GR-586, E branch of Tavronidis River at Pappadiana, 4.5 km N of Nea Roumato, 20 km SW of Xania, 19 June 2004 (5); EGM-GR-587, East branch of Tavronidis River at Limni, 20 km SW of Xania, 19 June 2004 (No water); EGM-GR-588, East branch of Tavronidis River at Zounaki, 18 km SW of Xania, 19 June 2004 (No water); EGM-GR-589, Tavronidis River under new main road between Skoutelonas and Vamvakopoulo, 11 km SW of Xania, 20 June 2004 (0); EGM-GR-590, Keritas River, about 14 km SW of Xania, 20 June 2004 (0); EGM-GR-591, unnamed tributary flowing into Stylia, 15 km W of Xania, 20 June 2004 (1); EGM-GR-592, Lake Kourna, about 16 km WSW of Rethymnon, 21 June 2004 (1); Rethymnon Prefecture: EGM-GR-593, unnamed stream in Fangarri Gorge, upstream of Amari Dam being constructed, about 15 km SE of Rethymnon, 21 June 2004 (3); Iraklion Prefecture: EGM-GR-578 and EGM-GR-596, unnamed creek in Kateros Gorge at Agia Irini, about 0.5 km S of Spilia, 10 km S of Iraklion, 15 and 22 June 2004 (2), respectively; EGM-GR-579, Anapodaharis River in Demati, 14 km E of Pirgos, 15 June 2004 (1); EGM-GR-580, Geropotamos River, 0.5 km N of Agia Triada, 5 km SE of Tymbaki and 7 km NE of Matala, 16 June 2004 (0); EGM-GR-581, Geropotamos River at bridge aside military base, 1.5 km SE of Tymbaki, 17 June 2004 (0); EGM-GR-583, unnamed tributary at Schinaria Beach, 1 km SE of Demoni, 18 June 2004 (4); Lasithi Prefecture: EGM-GR-20071, Xaxlakies Gorge, about 9 km E of Sitia, 18 June 2007 (No water); EGM-GR-20072, Springs of Ano Zakros, about 15 air km SE of Sitia, 19 June 2007 (6); EGM-GR-20073, on road between Ano Zakros and Azokeramos, photographed by Elias Ailamaki, 19 June 2007 (1); EGM-GR-20074, crab midden at base of N wall of room 14, Minoan Palace at Kato Zakros, 20 June 2007 (1); EGM-GR-20075, garden in Stavrochori, 18 km NE of Ierapetra, 2003 (1); EGM-GR-20076, sidewalk in Stavrochori, 18 km NE of Ierapetra, 2003 (1); EGM-GR-20077, unnamed spring fed tributary above Stavrochori, 18 km NE of Ierapetra, 22 June 2007 (1); EGM-GR-20078, unnamed spring fed stream at Orino, 16 km NEW of Ierapetra, 22 June 2007 (1); EGM-GR-20079, spring between villages of Kato Chori and Pano Chori, about 5 km NE of Ierapetra (1); EGM-GR-200710, stream at Myrtos, 15 km W of Ierapetra (1); EGM-GR-200711, at spring on road to Thripti between Kato Chori and Pano Chori, 23 June 2007 (1).