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The Mediterranean-southern African disjunct distribution pattern

The genus *Ephydatia* (Spongillina: Spongillidae) in Africa: a case of Mediterranean vs. southern Africa disjunct distribution

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SUMMARY

A synthesis on the taxonomy, geographic distribution and ecology of the genus *Ephydatia* in Africa is reported and discussed. This genus is characterised, in the context of the present biogeographic patterns of African freshwater sponges, by a peculiar disjunct distribution in the Palaearctic Africa and Southern Africa with a large gap from Sahara to Namibia, South Africa and southern Mozambique. The bipolar pattern is consistent with a model of Mediterranean-southern African disjunction with intermediate isolated enclaves in highlands of eastern Africa.

SPONGE DIVERSITY IN AFRICAN INLAND WATER

The highest taxonomic richness of Spongillina (Porifera: Demospongiae: Haplosclerida) at the biogeographic scale is recorded from the Neotropical (63 species), Palaearctic (59 species) and Afrotropical (49 species) regions, while lower values are known in the Oriental (37 species), Australasian (33 species), Nearctic (32 species) and Oceanic Pacific Islands (5 species) (Manconi and Pronzato, 2002, 2005, 2008ab; Pronzato and Manconi, 2002).

At the continental scale the African Spongillina comprises 17 genera and 57 species belonging to 4 families, namely Malawispongiidae (2 genera, 2 species), Metaniidae (1 genus, 1 species), Potamolepidae (4 genera, 17 species), Spongillidae (9 genera, 10 species) and 1 *incertae sedis* genus (1 species) (Weltner, 1913; Arndt, 1936; Penney and Racek, 1968; Bănărescu, 1995; de Silva and Volkmer-Ribeiro, 1998, 2001; Manconi et al., 1999, 2008; Manconi and Pronzato, 2002, 2004, 2008ab, 2009). Most species (75.8 %) are exclusive to this continent and a notable value of endemicity *s.s.* at the species (39.6 %) and genus level (35 %) characterises the Afrotropical region, even though

several species have been recorded only once (*i.e.* 23 species are known only for the holotype) and only a few species are reported more than ten times (*e.g. Eunapius nitens, Metania pottsi*). Species richness seems to be underestimated mainly for the unexplored Madagascan subregion with only two records (*i.e.* Nosy Be and Mascarenas Islands). Although an endemic Afrotropical sponge fauna exists, the present-day distribution pattern is characterised by recurring disjunct ranges reflecting the history of the continent with Afro-Oriental, Afro-Australian and Afro-Neotropical lineages related to the Gondwanaland geological, climatic and hydrological vicissitudes (Manconi and Pronzato, 2002, 2008ab, 2009).

Palaearctic Africa harbours cosmopolitan, Holarctic and Afro-Palaeo-Oriental elements exclusively belonging to the family Spongillidae (*Ephydatia fluviatilis, Trochospongilla horrida, Eunapius carteri*) (Manconi and Pronzato, 2008c; Manconi et al., 2008). A few relic populations of *Eunapius carteri saharensis* inhabit isolated extremely harsh freshwater bodies of the Tassili 'n Ajjer in the Algerian Sahara (Tuzet, 1953; Manconi et al., 2008). The southern margins of these geographic ranges, in the Saharan Nile, overlap the northernmost occurrence of tropical elements (genera *Corvospongilla, Dosilia, Eunapius* and *Spongilla*) (Manconi and Pronzato, 2009).

The tropical zone of Sub-Saharan Africa is characterised by the richest sponge fauna in large rivers, lakes and swamps with a frequent syntopy of species belonging to different families (Manconi and Pronzato, 2008c).

Taxonomic richness strongly decreases to 7 genera belonging to 2 families in southern Africa. The rare occurrence of the circum-tropical families Metaniidae (*Metania* sp.) in the Okavango and Potamolepidae (*Potamolepis* sp., *Potamophloios* sp.) in the Okavango, Chobe River and Lake Nhlabane matches the southernmost margin of their range in Africa (Curtis, 1998; Heeg, 2002; Manconi and Pronzato, 2002, 2009). Spongillidae are represented by four genera south of the Cunene-Limpopo basins. The Afro-Oriental-Australasian genus *Stratospongilla* seems to be restricted to KwaZulu-Natal whereas the widespread genus *Trochospongilla* is recorded only from Namibia (Etosha Pan) (Annandale, 1909; Arndt, 1936; Brien and Govaert-Mallebrancke, 1958). The circumtropical-temperate genus *Eunapius*, one of the most speciose in Africa, is known in the western part of southern Africa exclusively for the Panafrican *E. nitens* in the Namibian River Kuvelai (Etosha Pan), while the eastern coastal area of KwaZulu-Natal harbours *E. ambiguus* and *Eunapius* sp. apparently endemic to the River Umhloti and Lake Cubhu, respectively (Heeg, 2002; Manconi et al., 2008).

This paper aims to report on the cosmopolitan genus *Ephydatia* in the context of the present knowledge of African freshwater sponges biogeography.

TAXONOMY OF THE GENUS *EPHYDATIA* LAMOREAUX, 1816

The taxonomy of the genus *Ephydatia* is based on the morphology of one class of skeletal megascleres and on the gemmular traits such as the architecture of the theca, and the spatial arrangement and morphology of gemmuloscleres (Penney and Racek, 1968; Poirrier, 1974; Ezcurra De Drago, 1975; Manconi and Pronzato, 2002; Pronzato and Manconi, 2002). These conspicuous but limited diagnostic micro-traits render it extremely difficult to discriminate among strictly allied species within the genus, also because a wide variation of morphological and morphometric characters is displayed at both the individual (*e.g.* during the annual cycle) and intra-population level (Burton, 1958; Poirrier, 1974; Ezcurra de Drago, 1975, 1976; Manconi, unpubl.). The phenotypical plasticity of these micro-traits supported in the past the description of several varieties/subspecies subsequently synonymised to incorporate a few widespread species (Penney and Racek, 1968) such as *E. fluviatilis* (cosmopolitan), *E. muelleri* (Holoarctic), *E. robusta* (United States, Mexico, California), *E. japonica* (United States, Manchuria, Japan), *E. facunda* (Brazil, Argentina), *E. ramsayi* (Australia, New Zealand, New Guinea), *E. meyeni* (India, China), and *E. fortis* (Indonesia, Philippines, Vanuatu, Japan) each possibly representing a species complex. A more restricted distribution characterises other species *i.e. E. millsii* in Florida and *E. syriaca* in the Near East (Penney and Racek, 1968; Manconi and Pronzato, 2002, 2008b).

In southern Africa, Kirkpatrick (1907) described *E. fluviatilis* var. *capensis* from a *vleis* of the Cape although focusing on considerable morphometric differences with respect to the typical European forms. As a consequence the South African variety was considered until now junior synonym of *E. fluviatilis* (Annandale, 1909, 1914; Weltner, 1913; Topsent, 1932; Arndt, 1938; Burton, 1958; Penney and Racek, 1968; Ezcurra de Drago, 1975; Manconi and Pronzato, 2002, 2008b, 2009; Pronzato and Manconi, 2002). The revision of the genus *Ephydatia* with a detailed morphometric study of gemmulosclere traits by Ezcurra De Drago (1975) resulted in the assignment of *E. fluviatilis* var. *capensis* to the subspecies *E. fluviatilis ramsayi* characterised by a tropical-southern austral range. In summary at present ten species are considered valid.

The recent analysis of a collection held in the National Collection of Freshwater Invertebrates at the Albany Museum (AMSG, Grahamstown, South Africa) has provided support to carry out a wider investigation on the southern African spongillinofauna. Results indicate that sponges belong exclusively to the genus *Ephydatia* in a few but representative southern Africa hydrographic basins (Manconi, in prep.). Although preliminary, the comparative analysis of diagnostic traits of *Ephydatia* from the AMGS collection *vs.* the holotype of *E. fluviatilis capensis vs. E. fluviatilis* from the southern margin of

the western Palaearctic range (*i.e.* Algeria, Mediterranean islands) *vs. E. syriaca* from the Near East indicates significant morphological divergences (Manconi, in prep.).

DISTRIBUTION AND ECOLOGY OF THE GENUS *EPHYDATIA* IN AFRICA

The genus *Ephydatia* (*i.e. E. fluviatilis*) has been recorded from the Algerian Maghreb (Oued Smar, Oued Kerma, Oued Lekral, Lakes of Halloula, and canal of Lake Tonga near El Kala) and Saharan Africa along the Egyptian River Nile (Mallawi, Dayr Mawas, Luxor, Isna, Aswan, and Kitchener's island) (Gauthier, 1928; Seurat, 1930; Topsent, 1932; Gugel, 1993; Manconi and Pronzato, 2009) (Fig. 1).

Only two records are hitherto reported for the tropical Sub-Saharan area in Lake Mohasi (*i.e. E. fluviatilis*) in the Kagera system (upper Nile basin, Rwanda) (Arndt, 1938) and in the Mwenie River (*i.e. E. muelleri*) near Harare in Zimbabwe (Ezcurra De Drago, 1976).

In southern Africa the genus *Ephydatia* is known from Namibia (Nama Pan at Otjiozondjupa)(Curtis, 1998), Valkenberg Vlei at Cape Town (Kirkpatrick, 1907), Cape Flats east of Zeekoe Vlei (Brink, 1958; Burton, 1958), and River Kammenassie in the Little Carroo (Annandale, 1909).

The new data (AMGS collection) on the occurrence in the Eastern Cape, Free State, NW Province, Gauteng, KwaZulu-Natal and southern Mozambique (Fig. 1) enlarge the geographic range to northeast into a more tropical-subtropical region and matches the presence of the genus *Ephydatia* in the eastern and northern Africa (Zimbabwe, Rwanda and Saharan Nile). Surveys in Madagascar could help to more clearly define this geographic pattern in the southeast.

Southern Africa forms of the genus *Ephydatia* inhabit both highlands and floodplains in a wide range of habitats from permanent riverine and standing water to ephemeral water (pans, *vleis*, streams) in widely fluctuating water level conditions related to the cyclic rainy and dry seasons. Under unstable conditions (*e.g.* temporary or intermittent water) most freshwater sponges show a cryptobiosis strategy of gemmules to survive extreme environmental stress (*i.e.* long-term dry or cold period, exposure to hot air and direct sunlight).

The new data also greatly expanded the knowledge on the environmental-climatic requirements of the genus *Ephydatia* in the sub-Saharan Africa. The occurrence in coastal water bodies and in pans agrees with the record of the genus in brackish waters such as in the Meere Kiel (Lentz, 1882), coastal lakes of Louisiana (Poirrier, 1974), and estuaries in the Mediterranean area (Manconi, unpubl.). This is evidence for the African representatives of the genus *Ephydatia* of brackish conditions tolerance supporting their potential to survive fluctuations in salt

concentration during water level changes (*e.g.* in pans) and to spread in neighbouring coastal hydrographic basins during marine transgressions.

The altitudinal distribution ranges from coastal hydrographic basins at sea level or a few metres of elevation along the Cape provinces, KwaZulu-Natal and southern Mozambique, to highland areas in Gauteng, NW Province and Free State. As for the climate, these sponges occur in arid and semi-arid zones (Namibia, Kalahari, South African highland), in cooler more temperate climate (south-western South Africa) but also in moist conditions with high rainfall as in tropical southeastern coasts (north-eastern South Africa and south-eastern Mozambique), in Zimbabwe and in the equatorial area (Rwanda). The temperature/rainfall ranges indicate an eurythermal element.

The geographic distribution together with the wide range of habitat and environmental conditions could indicate that the African forms of the genus *Ephydatia* may be separate but strictly allied species.

DISPERSAL POTENTIAL

Since the dispersal potential represents a constraint to define disjunct distributions it is necessary also to consider that reproductive strategies of freshwater sponges involve both sexual and asexual modes with propagules represented by planktonic larvae and gemmules (resting stages), respectively. The larva parenchymella of *Ephydatia* is able to perform short distance drift downstream, being constrained by the discontinuity of fragmented habitats and its dispersal potential is related uniquely to changes in drainage pattern of the hydrographic net (*e.g.* river capture).

On the other hand gemmules, extremely conservative structures since the Cretaceous (Ott and Volkheimer, 1972), seem to have played a key role in the colonization of inland water with a double functional role both to persist *in situ* and to perform dispersal in a wide variety of extremely fragmented habitats (Pronzato and Manconi, 1994, 1995, 2002; Manconi et al. 2004; Manconi and Pronzato, 2002, 2004, 2008ab).

The cryptobiotic behaviour of gemmular totipotent cells together with a complex architecture of the gemmular theca in the genus *Ephydatia* seems to represent a preadaptation to facilitate a hypothetical passive dispersal by floods, wind, ungulates, and birds (Racek, 1969; Bănărescu, 1990; Manconi and Pronzato, 1994, 1996; Pronzato and Manconi, 1994; Manconi et al., 1996). From a morpho-functional point of view the pneumatic layer favours floating downstream, spicules are radially arranged to strengthen the gemmular theca, and spiny gemmuloscleres could hook efficiently onto a potential carrier (Manconi and Pronzato, 1994, 1996, 2008b; Pronzato and Manconi, 1994, 1995, 2002). Freshwater sponges appear however to be not highly successful

colonizers in fragmented habitats as highlighted by their absence in the Canary Archipelago (Tenerife, Gran Canaria, Gomera) in contrast with the common presence of different species of bryozoans producing resting stages (*i.e.* statoblasts) (Manconi, unpubl.). Overall, a biogeographical analysis on the hypothetical relationships between the evolutionary success of freshwater sponges (*i.e.* geographic range extent, species richness and abundance) and the efficiency of gemmules as potential dispersal devices highlighted that genera/species with complex cryptobiotic gemmules do not match a wider geographic range (Manconi and Pronzato, 2008b).

All gemmular traits of species belonging to the genus *Ephydatia* strongly support also a defensive role of gemmules to persist *in situ* (cfr. Manconi et al., 2004; Manconi and Pronzato, 2004) and the life cycle appears to be synchronised with the local long-term seasonal rhythm (Racek, 1969; Pronzato and Manconi, 1991, 1994, 1995, 2002; Pronzato et al., 1993).

In addition, fossil remains indicate the persistence of the genus *Ephydatia* in Namibia (*E. kaiseri*) since the Eocene (53 myr) (Rauff, 1926) while more recent subfossil spicules are known from the dunes area of the Cape (Blankenbergs dam) (Ehrenbergs, 1854 in Arndt, 1936).

CONCLUSIONS

The present attempt of biogeographical analysis shows that the genus *Ephydatia* is characterised by a disjunct distribution in Palaearctic Africa and southern Africa with a large gap from Sahara to Namibia, South Africa and southern Mozambique with two enclaves in the tropical-equatorial area. This pattern is consistent with a model of disjunction with intermediate isolates (Fig. 1).

The causes of this disjunct pattern in Africa are uncertain but clearly related to the geological history of the continent together with its long-term climatic dynamics and the natural history of the taxon. Possibly it could be due to i) the fragmentation of earlier distribution patterns due to the effect shifts in elevation and slope of hydrographic basins and remodelling in the coastline, or ii) spreading favoured by suitable climatic-hydrological conditions, or iii) vicariance events in different hydrographic basins along latitudinal-climatic clines of the geographic range or iv) poor sampling and consequent knowledge gaps in species distribution and taxonomy.

At present it is not possible to know the age of the taxon *Ephydatia*, what we surely know is that palaeontological data proved that the genus was present in both southern Africa and central Europe since the Eocene (Rauff, 1926; Pisera and Saez, 2003; Pisera, 2006).

The environmental-climatic requirements and the life style of the genus in Africa seem favourable to dispersal in fragmented-discontinuous habitats with

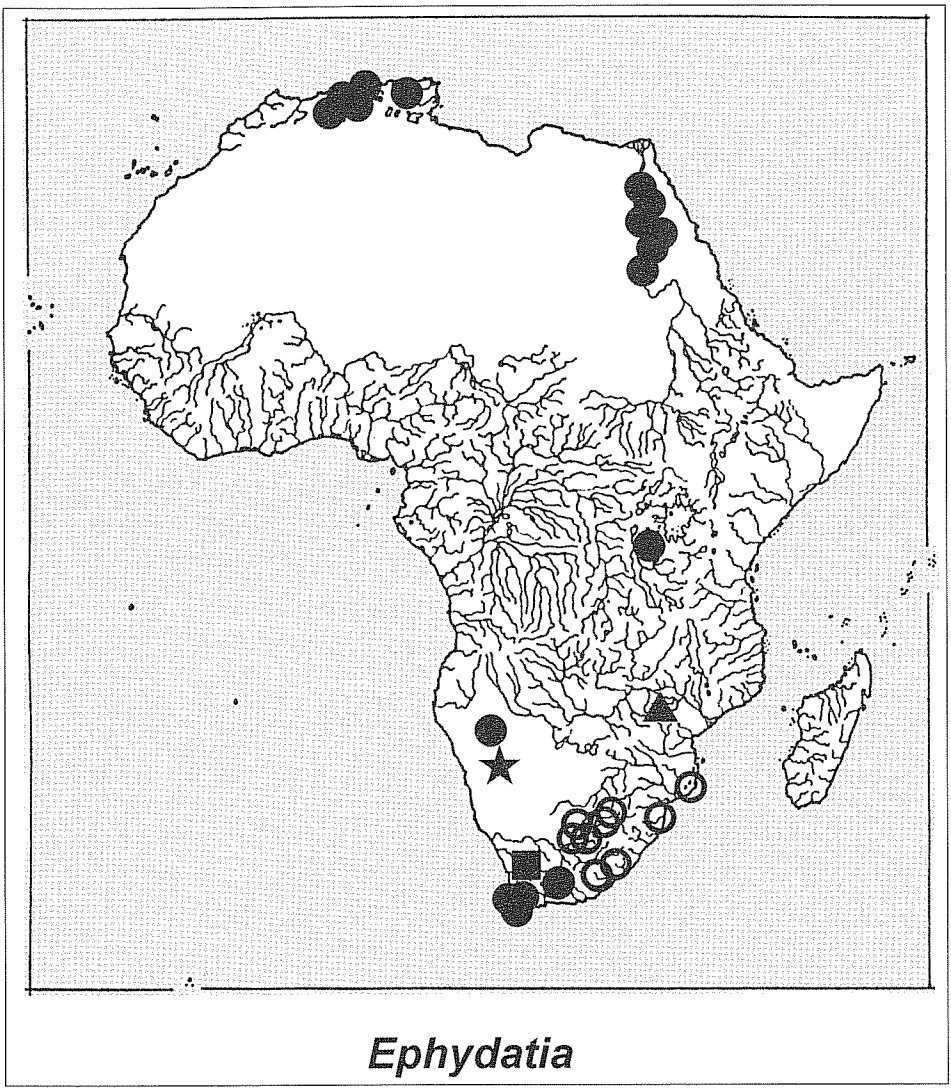

Fig. 1 - Geographic distribution of the genus *Ephydatia* in Africa. *E. muelleri* (black triangle), *E. fluviatilis* (black circles: previous records; empty circles: present records), *E. kaiseri* (star: Eocenic fossil), *Ephydatia* sp. (black square).

unpredictable rainfall and high water level fluctuations. Recent surveys in Eritrea (10 sites), Tunisia (22 sites), and South Africa (20 sites) did not however find any specimens in these sub-arid and arid areas (Manconi, unpubl.). The geographic range of the genus *Ephydatia* in Africa matches the wide gap focused on by De Winter (1971) and Quézel (1978) on the range of many arid area species occurring in the northern as well as in the southern arid areas of Africa. This distribu-

tion diverges however from the pattern of the south-western/north-eastern "drought corridor" suggested by Balinsky (1962) because of the presence of sponge enclaves in highly moist habitat in the equatorial Africa and Zimbabwe.

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