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# Fossil and modern sponge fauna of southern Australia and adjacent regions compared: interpretation, evolutionary and biogeographic significance of the late Eocene ‘soft’ sponges

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## Abstract

The late Eocene ‘soft’ sponge fauna of southern Australia is reconstructed based on disassociated spicules and is used to interpret the paleoecology and environmental context of shallow marine communities in this region. The reconstructed sponge association was compared with coeval sponge assemblages from the Oamaru Diatomite, New Zealand, and with the modern ‘soft’ sponge fauna of southern coastal of Australia. Based on the predominance of shallow- and moderately shallow-water species, the late Eocene assemblage is interpreted to have inhabited waters depths of about 100 m. This contrast with the spicule assemblage from New Zealand, which characterized deeper waters based on the presence of numerous strictly deep-water sponge taxa, and the absence of spicules of shallow-water demosponges represented in the Australian material. The southern Australian Eocene sponge assemblages have clear Tethyan affinities evidenced by the occurrence of sponges known today from diverse regions. This distribution suggests much wider geographical ranges of some sponge taxa during the Eocene. Their present distributions may be relictual. The modern sponge fauna inhabiting southern Australian waters shows only moderate differences from these of the late Eocene. Differences are more pronounced at lower taxonomic levels (family and genus).

## Contents

## Introduction

Sponges are among the simplest metazoans and, thus, are crucial for understanding the origin of animals. Their fossil record dates back to the beginning of the Paleozoic Era (e.g. Hamdi *et al*., 1989; Brasier, 1989; Kaesler *et al*., 2004). Some early Vendian fossils have been noted as sponges (Reitner and Mehl, 1995; Hooper and van Soest, 2002), however, these findings were recently questioned (Antcliffe *et al*., 2014). Fossil sponges are cosmopolitan, preserved as both articulated bodies and isolated spicules. The quality of the sponge fossil record varies through geological time, but some exceptionally preserved and rich sponge (or spicule) associations may provide valuable information about the evolution of the group.

Fossil sponges and isolated spicules have been studied extensively since the nineteenth century (e.g. Goldfuss, 1826-33; Zittel, 1877; Roemer, 1860; Quenstedt, 1878; Hinde, 1883, 1893; Hinde and Holmes, 1892; Rauff, 1893-95; and Hall and Clarke, 1899; Mostler, 1972, 1976, 1994; Pisera, 2006 and references therein). The spicules were generally treated from the morphological point of view, as separate disassociated elements, and rarely attributed to particular taxa. Consequently, there are very few papers describing ecological relationships of sponge associations and these deal mostly with those associations from the northern part of the world (e.g., see Koltun, 1959, 1961; Pisera, 1997; Pisera and Busquets, 2002; Pisera and Hladilová,

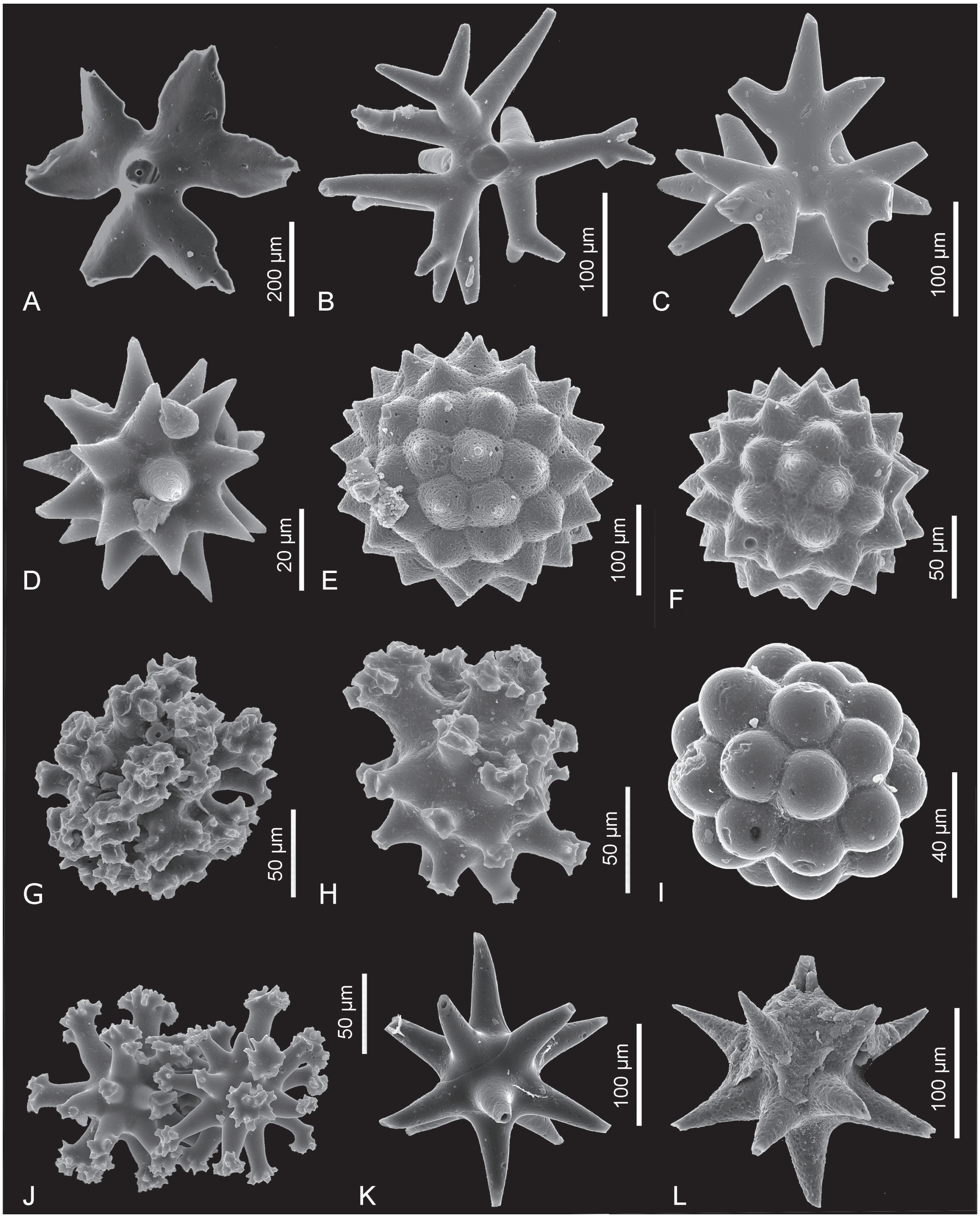

*Fig. 1.* A Triaene of *Penares* cf. *sclerobesa*; B Short-shafted triaene of *Triptolemma cladosum*; C Amphitriaene of *Samus anonymus*; D Spheraster of *Chondrilla nucula*; E-F Spherasters of *Chondrilla secunda*; G, H, J Anthasters of *Diplastrella* cf. *megastellata*; I Micraster of *Tethya* cf. *omanensis*; K, L Oxyasters of *Tethyastra oxyaster* (after Łukowiak, 2015, modified).

2003; Matteucci and Russo, 2005; Pisera *et al*., 2006; Łukowiak *et al*., 2014; Frisone *et al*., 2014). The fossil sponges from the Southern Hemisphere remained understudied. There are a few exceptions such as the detailed study by Hinde and Holmes (1892) on the isolated sponge spicules from the Eocene of Oamaru Diatomite (New Zealand). This study reconstructs the sponge assemblage and infers its bathymetry. Also, Kelly and Buckeridge (2005) interpreted Early Paleogene sponge fauna from the New Zealand Chatham Island in terms of the environmental conditions and water depth.

This approach – the biological interpretation of disassociated sponge spicules – was used to assess upper Eocene spongiolites and spiculites exposed along the southern coast of Australia. The reconstructed assemblage consisted of at least 42 species within 31 genera, 27 families, and 12 orders of ‘soft’ Demospongiae and Homoscleromorpha. Also, some lithistids and rare Hexactinellida were found in the assemblage. The spicules representing demosponge orders Poecilosclerida and Tetractinellida were the most diversified. The rest of the ten orders (Chondrillida, Haplosclerida, Axinellida, Bubarida, Agelasida, Polymastiida, Clionaida, Tethyida, Suberitida, and Homosclerophorida) were less differentiated (for more details see Łukowiak, 2015). The taxonomical assignments in this paper were updated basing on Morrow and Cárdenas (2015) new Demospongiae classification.

In this paper, the reconstructed assemblage is interpreted in a paleoecological and environmental context. Thanks to the comparisons with modern sponge communities of Australia, it was possible to establish the changes in the biota over the past 35 millions of years.

## Material and methods

The samples were collected in April-May 2004 by Andrzej Pisera (with the exception of core samples, donated kindly by Paul Gammon, Canada). About 30 samples of spicule-rich clays, muddy spiculites, and spiculites were processed in the laboratory at the Institute of Paleobiology, Polish Academy of Sciences, Poland. The samples were macerated using Glauber’s salt ($Na_2SO_4$) or hydrogen peroxide ($H_2O_2$ 30%) to remove organic matter, and to clean and separate loose sponge spicules (see Łukowiak, 2015 for additional preparation details). All the investigated material is housed in the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland under the collection number ZPAL Pf.26.

### *Geological context*

Upper Eocene strata with isolated sponge spicules (and bodily preserved sponges) extend over 2000 km along the southern coast of Australia, from Blanche Point in the east (St. Vincent Basin, eastern South Australia), through Norseman and Princess Royal in the north (western Eucla Basin and associated palaeodrainage channels), and Hamersley River and Doyle Road within the Fitzgerald River National Park in the west (Bremer Basin of Western Australia). These sites are characterized by different geological histories and facies development. In the late Eocene, Australia was in its final stages of separation from Antarctica, after which climatic cooling initiated due to inception of the Antarctic Circumpolar Current (for more details see Exton *et al*., 2001; Barker *et al*., 2007; Quaglio *et al*., 2007).

The megathermed to mesothermed climate of Australia, prior to the end of the Eocene was characterized in high climatic seasonality (McLoughlin and McNamara, 2001; Carpenter *et al*., 2014). Deep chemical weathering and the opal pulse that took place in the middle Eocene caused mobilization of silica and increased levels of silica in the oceans (Diekmann *et al*., 2004).

The studied sponge spicules were obtained from various upper Eocene units. Mainly muddy spiculites and spongiolites were sampled from Doyle Road, Princess Royal, and the Hamersley River glauconitic and spiculitic marls and limestones and biosiliceous clays were sampled at Blanche Point (for more details see Łukowiak, 2015).

## Results

### *Short ecological characteristic and biogeographic distribution of the recognized sponge taxa*

The diversity and excellent preservation of the siliceous sponge spicules witness the presence of a very rich sponge fauna in southern Australia waters during the late Eocene. It is estimated that at least nine orders, 27 families, 31 genera, and 42 species of ‘soft’ (including the sponges of the class Homoscleromorpha) demosponges inhabited this area. In addition to these, lithistids were also very common and rare sponges of the class Hexactinellida also appeared. The short tabular combination of the ecological preferences of the reconstructed sponge community and their current biogeographic distribution is shown in the Table 1. Also the most characteristic sponge spicules that were the basis for the taxonomical assignments of most of the sponge taxa are shown in the Figures 1-3. For more details see the chapter ‘Biological interpretation of the morphological types of the

*Table 1.* List of the recognized sponge taxa and the bathymetrical and ecological preferences of their recent counterparts. ALA - Atlas of Living Australia, WPD - World Porifera Database.

| | Bathymetry | Current geographical occurrence/range |
|---|---|---|
| Agelasidae | shallow-water reefs and other clear-water environments in depths less than 150 m (van Soest, 2002e) | |
| *Agelas axifera* | | W and E Australia (e.g. Champion Bay, Hooper and Wiedenmayer, 1994; van Soest et al., 2012) |
| *Agelas wiedenmayeri* | | Cuba (Alcolado, 1984) |
| Pachastrellidae | epibathyal and bathyal habitats; few genera is encrusting or cavity-filling living predominantly in tropical or temperate shallow-waters (Maldonado, 2002) | |
| *Triptolemma cladosum* | ~250 m (van Soest, 2009) | Indonesia (Maldonado, 2002) |
| *Brachiaster simplex* | 200 m (Wilson, 1925; Lévi and Lévi, 1989) | New Zealand, Philippines (WPD, accessed Feb 2014), (fossil *B. claudelevii* is reported from Australia; Pisera and Bitner, 2007) |
| *Alectona millari* | small excavating sponges living cryptically in rather shallow depths (e.g. 54 m, 202 m; Rützler, 2002a) | Azores, Mediterranean Sea, North Sea, Alboran Sea, Australia (WPD, accessed Feb 2014) |
| *Stelletta* | soft, detritic, and hard (rocky) bottoms from shallow waters to bathyal depths (Uriz, 2002c) | all over the world (Uriz, 2002c) including 44 species from (ALA, accessed Feb 2014) |
| Geodiidae | bathyal distribution predominantly on soft bottoms (some representatives occur in caves and overhangs in the littoral and shallow sublittoral zones; Uriz, 2002a) | |
| *Geodia* | | distributed worldwide (Hooper and Wiedenmayer, 1994), including 4 species from Australia (ALA, accessed Feb 2014) |
| Calthropellidae | warm, moderately deep water (~ 600 m) and occasionally from the littoral zone (van Soest and Hooper, 2002b) | N Atlantic, Mediterranean, S and E Africa, Indonesia, New Zealand (van Soest and Hooper, 2002b), and Australia (ALA, accessed Feb 2014) |
| Spirastrellidae | common in shaded subtropical and tropical shallow-waters, including coral reefs (Rützler, 2002c) | |
| *Diplastrella megastellata* | shallow water (few feet; Hechtel, 1965) | Caribbean (Hechtel, 1965) but *Diplastrella* sp. was noted from Australia by McEnulty et al. (2011) |
| *Tethya omanensis* | very shallow waters of not more than 5 m (van Soest and Beglinger, 2008) | Oman and the W Arabian Sea (McEnnulty and Beglinger, 2008) |
| *Tethyastra oxyaster* | coral reefs (Burton, 1934) | E Australia (Burton, 1934; WPD accessed Feb 2013) |
| Placospongiidae | encrusting or branching, massive sponges, mostly occur in shallow tropical and subtropical water habitats, from the intertidal depths to ~ 200 m (Rützler, 2002b; Becking, 2013) | |
| *Placospongia* | | 2 species from Australia (WPD, accessed Feb 2014) |
| *Cliona mucronata* | waters of about 20 m depth (Calcinai et al., 2005; Vacelet et al., 1976) | Mexican Tropical Pacific, Madagascar (Vacelet and Vasseur, 1971; WPD, accessed Feb 2014), Indo-Pacific Ocean (Calcinai et al., 2005), Banada Sea (Topsent, 1897), Australia (ALA, accessed Feb 2014) |
| *Dotona pulchella* | excavating, sampled from water of 70-120 m deep (Carter, 1880) | Mediterranean (Rosell and Uriz 2002) and probably Azores (Topsent, 1904) and the Indian Ocean (Carter, 1880) |
| *Sphaerotylus* | wide bathymetric range, e.g. *S. antracticus* is recorded from 18-385 m (Hentschel, 1914) | 2 species from Australia (ALA, accessed Feb 2014) |
| *Terpios* | growing as thin crusts on and under overhanging and dead corals in rather shallow waters (van Soest, 2002a) | 4 species from Australia (WPD, accessed Feb 2014) |

*Table 1.* Cont.

| | Bathymetry | Current geographical occurrence/range |
|---|---|---|
| *Monocrepidium eruca* | encrusting, surface hispid, deep water (Alvarez and van Soest, 2002) | Indian Ocean (Alvarez and van Soest, 2002; WPD, accessed Feb 2014) |
| *Bubaris* | encrusting sponges with hispid surface that are restricted to rather deep water (Alvarez and van Soest, 2002) | Arctic, Indian Ocean, S Atlantic, Mediterranean Sea, Indonesia, Japan, New Zealand, and Antarctica (Hooper and Wiedenmayer, 1994) |
| *Petrosia* | shallow and deeper warm-temperate to cold waters (Desqueyroux-Faúndez and Valentine, 2002) | widely distributed, including 24 species from Australia (ALA, accessed Feb 2014) |
| *Mycale (Rhaphidotheca) loricata* | waters 845 m deep (Topsent, 1896) | Azores (van Soest and Hajdu, 2002) |
| *Coelodischela massa* | from 70 m depth to relatively deep water (410-505 m) | New Caledonia (Lévi and Lévi, 1983) and Cape Verde Islands (van Soest, 1988) |
| *Trikentrion flabelliforme* | shallow water (3-83 m; Hooper and Wiedenmayer, 1994), 100 m (McEnnulty et al., 2011) | Australia (WPD, ALA, accessed Feb 2014) |
| *Histodermella australis* | waters ~ 130 m deep (van Soest, 2002d; Bergquist and Fromont, 1988) | New Zealand (van Soest, 2002d; Bergquist and Fromont, 1988) |
| *Acarnus* | shallow water of temperate and tropical seas (Hooper, 2002a) | genus known from all over the world including 6 species from Australia (ALA, accessed Feb 2014) |
| *Sceptrintus richardi* | rather deep water of 200-300 m (Topsent, 1898) | Azores, Canaries, and Madeira (WPD, accessed Feb 2014) |
| *Sigmosceptrella quadrilobata* | extremely shallow water of 2-3 m of depth (Vacelet and Vasseur, 1971) | Madagascar and Mauritius (WPD, accessed Feb 2014) |
| *Discorhabdella incrustans* | depth of about 180 m (van Soest, 2002c) | New Zealand (Three Kings Island; van Soest, 2002c) |
| *Crellastrina alecto* | deep waters (600 m depth; van Soest, 2002b) | Azores (van Soest, 2002b) |
| Myxillidae | | all over the world, including Australia (ALA, accessed Feb 2014) |
| *Samus anonymus* | form excavations in coralline algae in shallow water up to 50 m deep (van Soest and Hooper, 2002a) | almost cosmopolitan: Brazil, Caribbean, Indian Ocean, Mediterranean, and Australia (van Soest and Hooper, 2002a; WPD, accessed Feb 2014) |
| *Chondrilla nucula* | tropical and subtropical coastal waters (Boury-Esnault, 2002) | Atlantic, Mediterranean Sea, W and E Pacific, Indo-Malayan region, Indian Ocean, the Red Sea, and Caribbean (WPD, accessed March 2014); New Zealand (*Ch. nucula sensu* Schmidt 1862; for more details see Bergquist, 1968; p. 63), Australia (ALA, accessed Dec 2014) |
| *Chondrilla secunda* | 2-40 m (Fromont et al., 2008) | Australia (WPD, ALA, accessed Feb 2014) |
| *Placinolopha sarai* | | E Philippines (WPD, accessed Feb 2014) |
| *Placinolopha bedoti* | shallow water of 10 m of depth (Topsent, 1897) | Banda Sea and the Indonesian Exclusive Economic Zone (WPD, accessed March 2014) |
| “lithistids” | occur mostly in deep waters but shallow-waters “lithistids” also occur (Pomponi et al., 2001; Pisera and Lévi, 2002; Pisera and Vacelet, 2010) | |
| hexactinellids | deep-water inhabitants; in some cases noted in the extremely shallow-water habitats (Barthel and Tendal, 1994; Leys et al., 2007) | |

spicules-a comparison with living sponges’ (Łukowiak, 2015).

Numerous recognized sponges currently inhabit the waters around Australia [e.g. *Agelas* cf. *axifera* Hentschel, 1911, *Tethyastra oxyaster* (Burton, 1934), *Cliona mucronata* Sollas, 1878, *Chondrilla secunda* Lendenfeld, 1885, *Trikentrion flabelliforme* Hentschel, 1912 as well as *Terpios*, *Stelletta*, *Acarnus*, *Petrosia*,

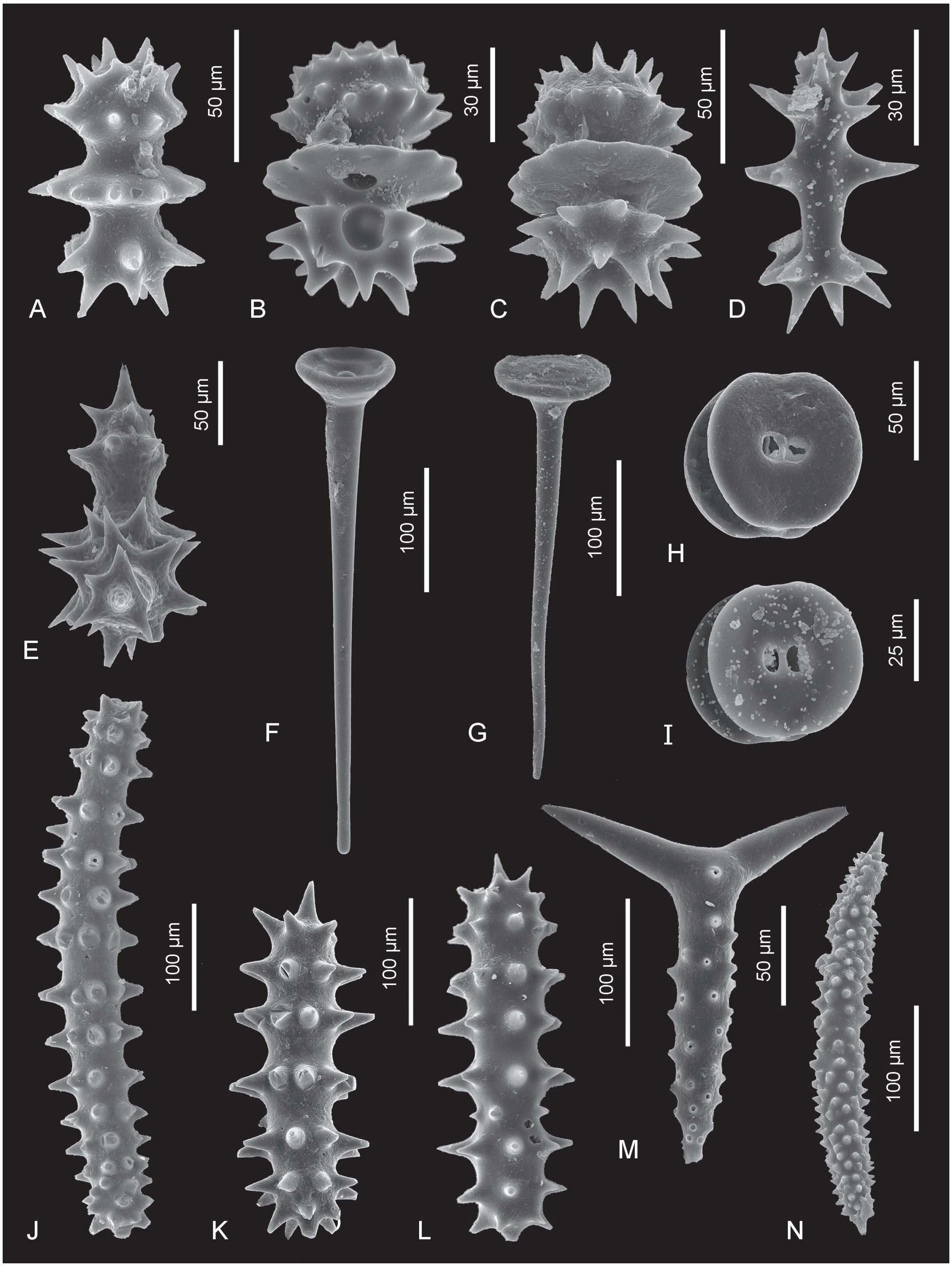

*Fig. 2*. A-D Anisodiscorhabds of *Sigmosceptrella quadrilobata*; E Pseudoastrose acanthotylote of *Discorhabdella* cf. *incrustans*; F Exotyle of *Mycale (Rhaphidotheca)* sp.; G Exotyle of *M. (R.)* cf. *loricata*; H, I Dischelae of *Coelodischela* cf. *massa*; J-L Sanidasters of *Sceptrintus richardi*; M Triod of *Trikentrion flabelliforme*; N Punctated oxea of *Histodermella australis* (after Łukowiak, 2015, modified).

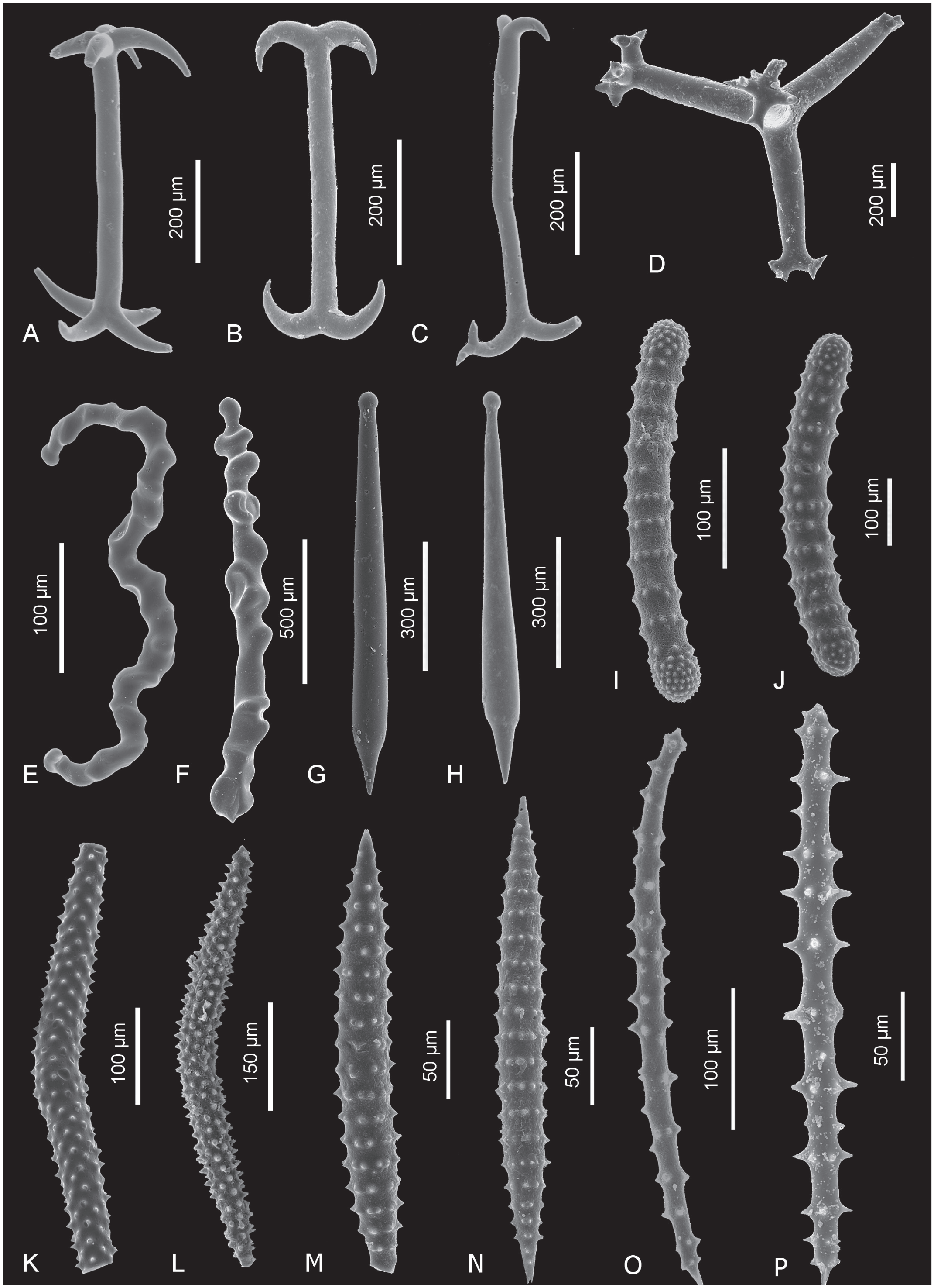

*Fig. 3*. A-C Amphiclads of *Placinolopha* cf. *sarai*; D Lophocalthrop of *Placinolopha* cf. *bedoti*; E Tuberculated diactine of *Monocrepidium* cf. *eruca*; F Tuberculated diactine of *Bubaris* sp.; G, H Mucronate tylostyles of *Cliona* cf. *mucronata*; I, J Verticillate strongyles of *Dotona pulchella*; K, L Acanthoxeas of *Alectona millari*; M, N Verticillate oxeas of *Agelas* cf. *axifera*; O, P Verticillate oxeas of *Agelas* cf. *wiedemayeri* (after Łukowiak, 2015, modified).

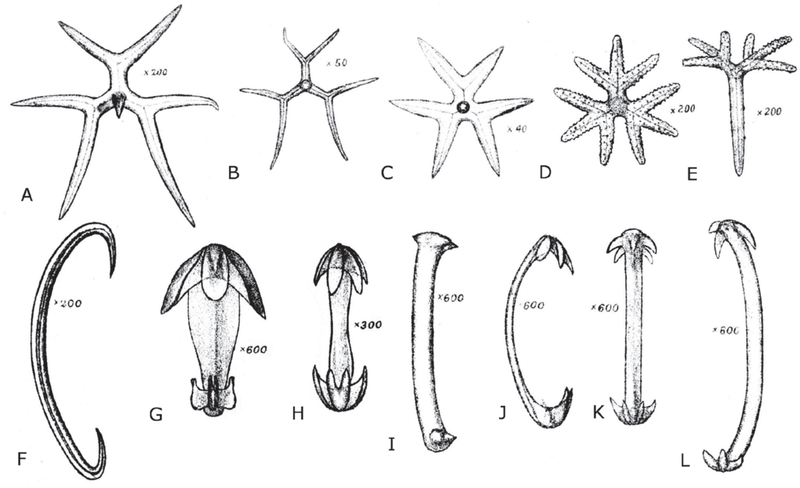

*Fig. 4*. Spicules of deep-water taxa: A-C *Corallistes*; D, E *Thrombus abyssi;* F, G *Cladorhiza;* H-L *Chondrocladia*; after Hinde and Holmes (1892; compiled).

*Sphaerotylus*, placospongiids, myxillids, and geodiids]. In the Eocene assemblage, there were some species that are today considered cosmopolitan morphospecies (e.g. *Samus anonymus* Gray, 1867, *Chondrilla nucula* Schmidt, 1862, and *Alectona millari* Carter, 1879) occurring also around Australia. There are also sponge taxa that are not currently observed in Australian waters but are noted from adjacent and nearby areas, e.g. New Caledonia (*Coelodischela massa* Lévi & Lévi, 1983), New Zealand (*Histodermella australis* Dendy, 1924, *Discorhabdella incrustans* Dendy, 1924, *Brachiaster* sp., and *Bubaris* sp.), the Indian Ocean [*Dotona pulchella* Carter, 1880, *Monocrepidium eruca* (Carter, 1880)], and Indonesia [e.g. *Triptolemma cladosum* (Sollas, 1888), *Placinolopha sarai* Lévi & Lévi, 1989, and *Placinolopha bedoti* Topsent, 1897]. In contrast, there is also a group of sponges that are today known only from geographically distant areas e.g. Arabian Pennisula (*Tethya omanensis* Sarà & Bavestrello, 1995), Madagascar (*Sigmosceptrella quadrilobata* Dendy, 1922), Mediterranean (*Dotona pulchella*), or even the Caribbean (*Agelas wiedenmayeri* Alcolado, 1984, *Diplastrella megastellata* Hechtel, 1965) assuming the morphological characters reflect conspecificity. Other taxa occur today not only in remote parts of the world, e.g. Azores [*Mycale* (*Rhaphidotheca*) *loricata* (Topsent, 1896), *Sceptrintus richardi* Topsent, 1898, and *Crellastrina* sp.], but also are limited only to deep-water habitats (inhabiting waters of about 850 m, 200-300 m, and 600 m, respectively). Their bathymetrical preferences are in opposition to most of the recognized taxa which are shallow water inhabitants living in the continental platform (up to 200 m; e.g. *Samus anonymus*, *Diplastrella megastellata*, *Alectona millari*, *Cliona mucronata*, *Dotona pulchella*, *Discorhabdella incrustans*, *Histodermella* sp., *Brachiaster* sp., *Terpios* sp., *Acarnus* sp., agelasids, geodiids, placospongiids, and petrosiids). Moreover, some of them can be found in extremely shallow-water habitats (e.g. *Tethyastra oxyaster*, *Tethya omanensis*, *Trikentrion flabelliforme*, and chondrillids). From among moderately deep-water taxa (*Sceptrintus*, *Sphaerotylus*, *Coelodischela massa* and representatives of the family Plakinidae, pachastrellids, and bubarids) most are only occasionally found at shallow depths. Despite that, lithistid demosponges today are characteristic of rather deep waters (between 200 and 800 m), some theonellid species occur also in shallow water (see Pomponi *et al.*, 2001; Pisera and Lévi, 2002; Pisera and Vacelet, 2010; and the literature cited therein). Also hexactinellids which are currently deep-water forms in some cases may inhabit extremely shallow-water depths (Conway *et al.*, 2001; Leys *et al.*, 2004).

### *Comparison of Australian Eocene spicule assemblage with reinterpreted Eocene sponge spicules from the Oamaru Diatomite, New Zealand*

The southern Australian late Eocene sponge fauna has never been fully and completely studied. However, the coeval sponge fauna from adjacent New Zealand was already described in the 19th century by Hinde and Holmes (1892). Numerous outcrops of upper Eocene-lower Oligocene strata of Oamaru Diatomite occur on the South Island, Otago, New Zealand.

*Table 2*. Revised taxonomic assignment of the spicules described by Hinde and Holmes (1892) from the late Eocene-early Oligocene Oamaru Diatomite, South Island, New Zealand (with number of species) and sponge list noted from the late Eocene of southern Australia. * identified by Sim-Smith and Kelly (2011).

| **Order** | **Family** | **New Zealand** | **Australia** |
|---|---|---|---|
| Chondrillida | Chondrillidae | | 2 *Chondrilla* |
| Haplosclerida | Chalinidae | ? *Reniera* now *Haliclona* (Reniera) Schmidt, 1862, ? *Chalina* now *Haliclona* (Reniera) Schmidt, 1862 | |
| | Petrosiidae | | *Petrosia* |
| Axinellida | Axinellidae | ? *Axinella* | |
| | Raspailiidae | ? *Hymeraphia* | *Trikentrion* |
| Bubarida | Bubaridae | | *Bubaris, Monocrepidium* |
| Tetractinellida (Astrophorina) | Ancorinidae | 6 *Stelletta* and/or *Geodites* | *Stelletta* |
| | Calthropellidae | | *Calthropella* |
| | Geodiidae | *Geodia*, 2 *Erylus* | 2 *Geodia*, 2 *Penares* |
| | Pachastrellidae | 2 *Pachastrella*, *Triptolemus* now *Triptolemma* de Laubenfels, 1955 | *Triptolemma*, *Brachiaster* |
| | Thoosidae | *Alectona*, 2 *Thoosa* | *Alectona* |
| | Thrombidae | *Thrombus abyssi* | |
| | Astrophorida *incertae sedis* | *Dactylocalycites callodiscus*, 2 undetermined | *Dactylocalycites callodiscus* |
| Tetractinellida (Spirophorina) | Samidae | | *Samus* |
| Agelasida | Agelasidae | | 3 *Agelas* |
| Polymastiida | Polymastiidae | | 2 *Sphaerotylus* |
| Merliida | Hamacanthidae | 3 *Hamacantha* | |
| Poecilosclerida | Acarnidae | *Acarnus*, *Iophon* | *Acarnus* |
| | Cladorhizidae | *Cladorhiza*, 4 *Chondrocladia* | |
| | Crambeidae | *Discorhabdella* | *Discorhabdella* |
| | Crellidae | | *Crellastrina* |
| | Desmacididae | 6 *Myxilla*/6 *Desmacidon* | |
| | Coelosphaeridae | 2 *Forcepia* | 2 *Histodermella* |
| | Esperiopsidae | 4 *Esperiopsis*, *Amphilectus* | |
| | Guitarridae | 2 *Guitarra* | *Coelodischela* |
| | Hymedesmiidae | 4 *Pseudohalichondria*<br>2 *Plocamia* now *Antho* Schmidt, 1870 | |
| | Latrunculiidae | 14 *Latrunculia* | |
| | Mycalidae | 10 *Esperella* now *Mycale* Gray, 1867 | 2 *Mycale* |
| | Myxillidae | *Melonanchora*, 6 *Myxilla*/6 *Desmacidon* | *Myxillidae* |
| | Podospongiidae | 2 *Diacarnus**, *Sigmosceptrella quadrilobata* | 2 *Sceptrintus*, *Sigmosceptrella* |
| Clionaida | Clionaidae | 2 *Cliona* described as *Pronax* | *Cliona*, *Dotona* |
| | Spirastrellidae | 2 *Spirastrella* | 2 *Diplastrella* |
| | Placospongiidae | | *Placospongia* |
| Tethyida | Tethyidae | 2 *Tethya* | *Tethya*, *Tethyastra* |
| Suberitida | Suberitidae | | *Terpios* |
| | ?Halichondriidae | ? *Hymeniacidon* | ? Family *Halichondriidae* |
| Homosclerophorida | Plakinidae | 4 *Corticium*, *Plakina* | 2 *Placinolopha* |
| | Other | ? 2 *Ditriaenella*, 1 undetermined | |
| "lithistids" | Pleromidae | *Lyidium* now *Pleroma* Sollas, 1888 | *Pleroma* |
| | Vetulinidae | *Vetulina* | |
| | Corallistidae | 2 *Corallistes* | Corallistidae |
| | Theonellidae | 2 *Discodermia*<br>undetermined | *Discodermia*, *Theonella*/*Racodiscula* |
| Amphidiscosida | Hyalonematidae | 5 *Hyalonema* | |
| | Pheronematidae | *Pheronema* | |
| Lyssacinosida | Rossellidae | *Caulophacus*, 2 *Crateromorpha* | *Rossella* |
| Hexactinosida | Aphrocallistidae | 2 *Aphrocallistes* | Hexactinosida |

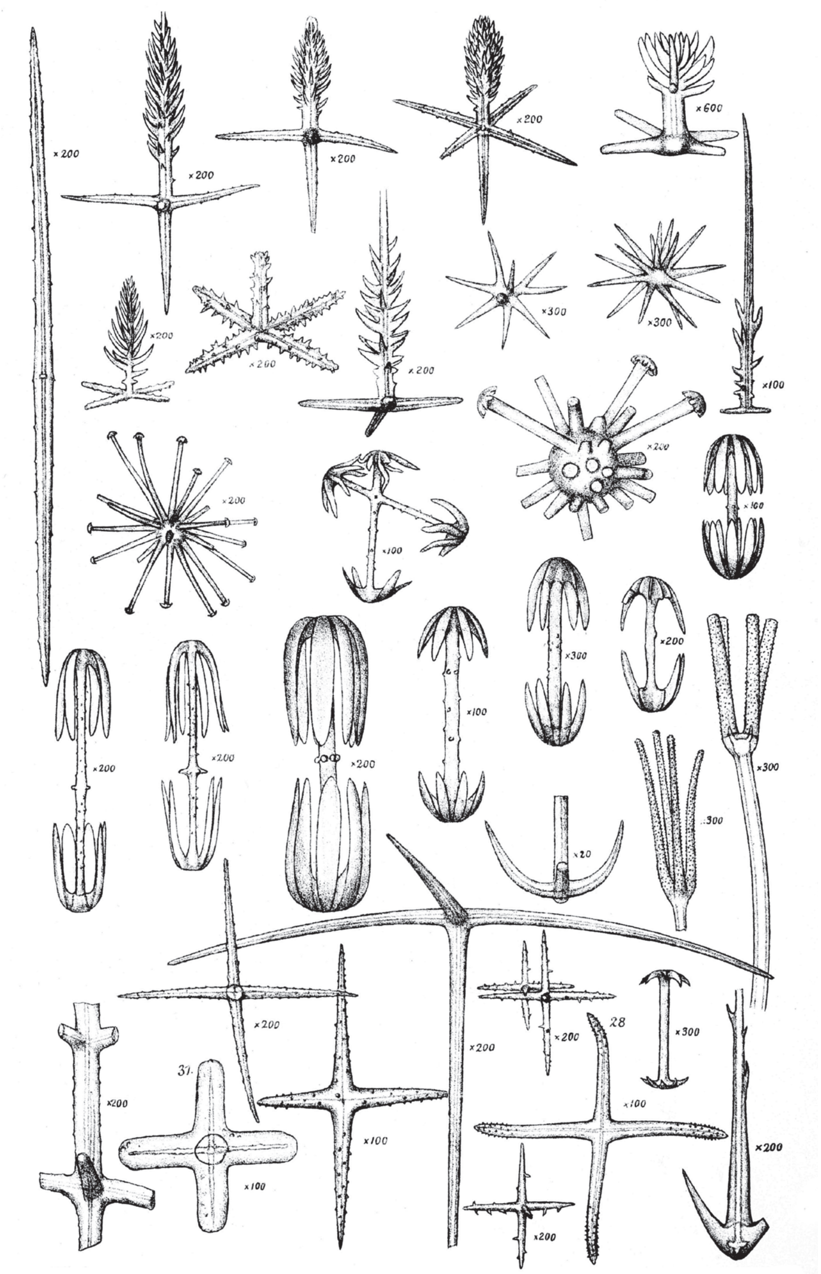

*Fig. 5.* Spicules of deep-water hexactinellids, after Hinde and Holmes (1892).

In these siliceous and siliceo-calcareous sediments the sponge spicules are, next to radiolarians and diatoms, the most common fossils. The great abundance of very well-preserved, abundant, isolated micro- and megascleres (and the lack of bodily preserved specimens) characterize this assemblage. The presented comparison (see Tab. 2) of the sponge spicules is done using modern taxonomy based on the World Porifera Database (accessed on August 2014; and supplemented with taxonomical assignments done by Sim-Smith and Kelly, 2011) reinterpreting attributions by Hinde and Holmes (1892).

The assemblage from the Oamaru region (New Zealand) is, in general, richer in spicule morphotypes. Especially the microscleres are more abundant and diverse than in the Australian association. This fact results in the recognition of higher number of sponge taxa in the assemblage described by Hinde and Holmes (1892). The Oamaru Diatomite sample records about twice as many non-lithistid demosponge species as in the Australian one, and a higher number of both lithistid and hexactinellid spicules as well. Whereas in the upper Eocene sediments of Australia only 42 ‘soft’ sponge species have been recognized (classes Demospongiae and Homoscleromorpha), at least 91 species (and ~11 uncertain or undetermined species) of siliceous ‘soft’ sponges were described in the Oamaru Diatomite. However, when considering the number of genera, the differences between these two sponge assemblages decrease. The Australian assemblage is slightly less diversified regarding the number of genera with 31 taxa described in contrast to 32 genera described from the New Zealand. Most demosponge families known from the Australia occur also in the New Zealand assemblage, but only 17 appear in both these assemblages at the same time (for details see Tab. 2).

The strictly shallow-water sponge taxa that were present in the Australian assemblage (e.g. *Samus anonymus*, *Chondrilla nucula*, *Trikentrion flabelliforme*, and *Cliona mucronata*; see also Figs 4, 5) were not recorded in the Oamaru. On the contrary, deep water astrophorid *Thrombus abyssi* (Carter, 1873) and poecilosclerids *Cladorhiza* and *Chondrocladia* (that are currently limited to deep water) are reported only form New Zealand. Also numerous hexactinellids (11 species) that are accesoric in the Australian assemblage appear in a great number in the New Zealand association. According to the lithistid demosponges, in the Oamaru Diatomite seven species were recognized, including deep-water *Corallistes*, whereas in the Australian assemblage only three families were noted.

It is worth mentioning that entirely preserved lithistids are very common and diversified in Australia, in contrast to Oamaru (Gammon *et al*., 2000a; Pisera personal information). However, the bodily preserved sponges do not deliver many loose spicules to the sediment, due to their complete preservation (non-destruction), and the record of loose lithistid spicules is, thus, sparse in Australian assemblage. But the rarity of hexactinellid spicules is real.

### *Comparison of the Australian late Eocene sponge assemblage with the extant demosponge fauna of southern Australia*

The present-day sponge fauna of the World, its diversity, biogeographic, and bathymetric distribution, as well as its dynamics and interdependence is still poorly understood and studied. But comparing the sponges of Australia with those of other regions it is, next to the Mediterranean and Caribbean, one of the best-known sponge faunas (e.g. van Soest, 1994). However, it is estimated that still at least 60 % of Australian sponges are undescribed (McDonald *et al*., 2005). There are approximately 1,400 species within 313 genera and 83 families of Australian sponges recorded (Hooper and Wiedenmayer, 1994) but about 5,000 species are estimated for the entire regional fauna (Hooper and Lévi, 1994). Recently, sponges of this region have received more attention (e.g. Munro *et al*., 1999) and there are large collections of marine sponges, as well as some independent groups of taxonomic researchers working primarily on the tropical and subtropical Australian sponge faunas (Hooper and Ekins, 2005).

The coasts of Australia are divided into 19 marine demersal bioregions (Hooper and Ekins, 2005). According to this biogeographical classification, the sites analysed in this paper belong to the South Western Region (samples taken from the western part of the southern coasts of Australia) and to the Gulf Province (samples taken from the eastern coasts of South Australia in Gulf St. Vincent, Hooper and Ekins, 2005).

Unfortunately, the studies of the present-day Porifera in Australia are focused mostly on the northern part of the Australian continent (for more details see Hooper and Ekins, 2005, fig. 6). Much less attention has been dedicated to sponges of the southern coast. There are only a few sponge collection sites in the South Western Province and temperate southwestern Western Australia seems to be the most poorly known of all Australian regions (Hooper and Lévi, 1994). There is a high number of endemic species recorded in this area, however, and it is told that the majority of ‘native’ marine fauna resides in the south (Poore, 1995). For example, a biological survey of the major benthic habitats of the south coast in the Fitzgerald Biosphere Reserve identified 102 different sponge taxa (Colman, 1997). The Gulf Province sampling sites seem to be more numerous and are one of the best-recognized and studied areas of southern Australia (for more details see Hooper and Ekins, 2005).

There are some significant differences in taxonomic composition and species richness between the major Australian marine bioregions, however (e.g. Hooper and Lévi, 1994). Also at the smaller ‘intra-regional’ spatial scale frequently the sponges form spatially heterogeneous assemblages with patchy distributions, often with high numbers of species, are not found in adjacent communities (so-called ‘apparent endemics’,

*Table 3.* The list of sponges recorded today from the Spencer Gulf (from Sorokin and Currie, 2009, modified), and sponges recognized in the Eocene Blanche Point Fm., Gulf St. Vincent, eastern part of South Australia.

| **Recent Spencer Gulf sponge list** | | **Late Eocene Blanche Point sponge list** | |
|---|---|---|---|
| Chondrillida | | Chondrillida | |
| | Chondrillidae: *Chondrilla* | | Chondrillidae: *Chondrilla* |
| Haplosclerida | | Haplosclerida | |
| | Chalinidae: *Haliclona* | | |
| | Niphatidae: *Cribrochalina* | | |
| | Petrosiidae: petrosiid | | Petrosiidae: *Petrosia* |
| Axinellida | | Axinellida | |
| | Axinellidae: *Cymbastela*, *Reniochalina* | | |
| | Raspailiidae: *Ceratopsion*, *Echinodictyum*, *Raspailia* | | |
| | Stelligeridae: *Higginsia* | | |
| Biemnida | | Biemnida | |
| | Biemnidae: *Biemna* | | |
| Tetractinellida (Astrophorina) | | Tetractinellida (Astrophorina) | |
| | Ancorinidae: *Ancorina*, *Ecionema*, *Jaspis*, *Stelletta* | | Ancorinidae: *Stelletta* |
| | | | Calthropellidae: *Calthropella* |
| | Geodiidae: geodiid | | Geodiidae: *Geodia, Penares* |
| | | | Pachastrellidae: pachstrellid |
| | | | Thoosidae: *Alectona* |
| | | | *Dactylocallodiscus* Astrophorina *incertae sedis* |
| Tetractinellida (Spirophorina) | | Tetractinellida (Spirophorina) | |
| | | | Samidae: *Samus* |
| Polymastiida | | Polymastiida | |
| | | | Polymastiidae: *Sphaerotylus* |
| Poecilosclerida | | Poecilosclerida | |
| | Acarnidae: *Acarnus* | | Acarnidae: *Acarnus* |
| | Chondropsidae: *Chondropsis* | | |
| | Crellidae: *Crella* | | Crellidae: *Crellastrina* |
| | | | Coelosphaeridae: *Histodermella* |
| | Desmacididae: *Desmacidon* | | |
| | | | Guitarridae: *Coelodischela* |
| | Microcionidae: microcioinid, *Clathria*, *Echinoclathrina*, *Holopsamma* | | |
| | Mycalidae: *Mycale* | | Mycalidae: *Mycale* |
| | Myxillidae: myxillid | | Myxillidae |
| | | | Podospongiidae: *Sceptrintus* |
| | Tedaniidae: *Hemitedania* | | |
| Clionaida | | Clionaida | |
| | Clionaidae: *Cliona*, *Spheciospongia* | | Clionaidae: *Dotona* |
| | | | Spirastrellidae: *Diplastrella* |
| | | | Placospongiidae: *Placospongia* |
| Tethyida | | Tethyida | |
| | Tethyidae: *Tethya* | | Tethyidae: *Tethyastra* |
| Suberitida | | Suberitida | |
| | Suberitidae: *Caulospongia* | | |
| | Halichondriidae: *Halichondria* | | |

Hooper and Kennedy, 2002). This is the reason why these two provinces (South Western Province and Gulf Province) must be here treated separately.

In both the cases, orders Dictyoceratida, Dendroceratida, Verongiida, and haplosclerid family Callyspongiidae will be excluded from the analysis because sponges of these taxa do not produce a mineral skeleton and thus do not preserve in the fossil record. Additionally, in the

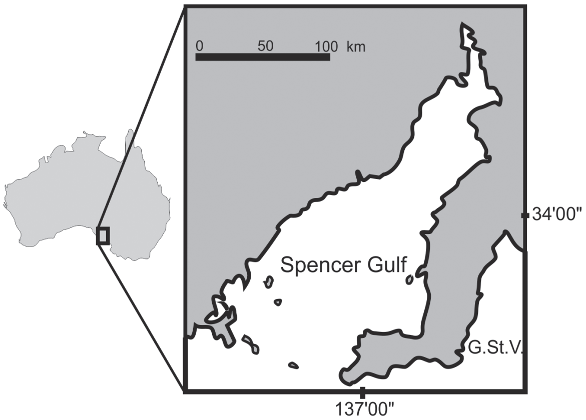

*Fig. 6*. Location of Spencer Gulf, South Australia; G. St. V.-Gulf St. Vincent.

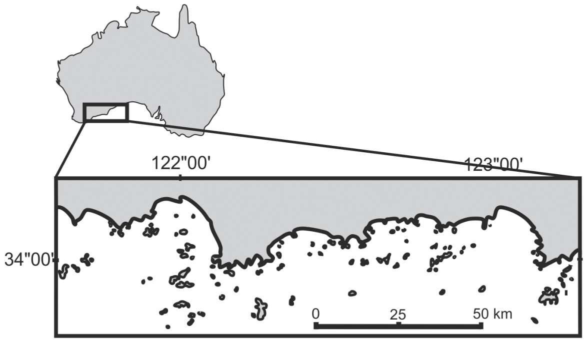

*Fig. 7*. Map of the Recherche Archipelago study sites, southern part of W Australia (after McDonald *et al*., 2005, modified).

case of the South Western Province, also the family Halisarcidae as one with a non-mineral skeleton will be excluded as well.

### *Gulf Province (Spencer Gulf) vs. Blanche Point Formation sponge fauna*

As there are no complex elaborations of demosponge fauna from the Gulf St. Vincent (which could be the equivalent of the late Eocene Blanche Point sponge assemblage), the comparison of studied assemblage will be performed using the Spencer Gulf sponge list – the nearest, well-described area within the Gulf Province (Sorokin and Currie, 2009; Fig. 6).

In the Spencer Gulf, in the shallow-water depths ranging from 12 to 55 m, there are ten orders, 22 families, and 28 genera of the class Demospongiae recognized. Among the 65 demosponge species present only 14 taxa could be given full species names (Sorokin and Currie, 2009; see also Tab. 3).

### *South Western Province vs. Western part of southern Australia Eocene sponge fauna*

As there are no comprehensive elaborations of the Recent sponge fauna from the South Western Province (Fig. 7), the comparison of the late Eocene sponge assemblage of western part of south Australia will be done with the sponge list investigated in the Recherche Archipelago (Southwestern Region of Western Australia) – the closest geographically well-investigated area. The sponges of this region were reported from the depths of 0-25 m by McDonald, Kendrick, and Fromont (2005, SRFME Interim Final Report), and kindly supplied by Jane Fromont (WAM, Perth). Additionally, this sponge list will be completed with the deeper-water sponge list (sampled in depths between 100-1100 m), reported from the Albany and Bald Island coasts which are also situated in the South Western Province (McEnnulty *et al*., 2011; see also Tab. 4). In the South Western Province there are 14 orders, 35 families, and 75 genera of the class Demospongiae recognized.

Whereas in the Recent assemblages of S Australia 37 families had been recognized, only 26 were recognized in the fossil one. From among these 37 families only 18 have their fossil representatives. On the other hand, nine other families were recognized in the fossil assemblage that are not recorded in this area in Recent. Regarding genera, today there are 77 recognized, whereas only 30 have been found in the fossil state. Among these, only 13 occur also in the fossil assemblage (e.g. *Stelletta*, *Cliona*, *Geodia*, *Chondrilla*, *Terpios*, *Diplastrella*, *Tethya*, *Tethyastra*, *Petrosia*, *Mycale*, *Acarnus*, *Latrunculia* and *Agelas*), which corresponds to about 16 % of all the genera known in this area today.

Generally, considering the number of orders represented in the fossil and Recent assemblages, these two seem to be very similar (14 and 11 respectively). The only exceptions are the orders Biemnida, Desmacellida, and Trachycladida which were not recorded in Eocene of western part of southern Australia. The diversity at the family level, however, shows significant difference. In both discussed provinces only about half of families recognized have their representatives in the Eocene assemblage. On the other hand, some families (nine for Spencer Gulf Province and for South Western

*Table 4*. List of extant sponges recorded from the Recherche Archipelago, South Western Australia (taken from McEnnulty *et al*., 2011 and McDonald *et al*., 2005, modified), and fossil sponges recognized in the southern part of W Australia.

| **Recent South Western Province sponge list** | | **Late Eocene W Australia sponge list** | |
|---|---|---|---|
| Chondrillida | | Chondrillida | |
| | Chondrillidae: *Chondrilla* | | Chondrillidae: *Chondrilla* |
| Haplosclerida | | | Haplosclerida |
| | Chalinidae: *Haliclona* | | |
| | Niphatidae: *Cribochalina, Gelliodes, Amphimedon* | | |
| | Petrosiidae: *Neopetrosia, Petrosia, Xestospongia* | | Petrosiidae: *Petrosia* |
| | Phloeodictyidae: *Aka, Oceanapia, Tabulocalyx* | | |
| Axinellida | | | Axinellida |
| | Axinellidae: *Axinella, Cymbastela, Dragmacidon, Phakellia, Ptilocaulus, Reniochalina* | | |
| | Raspailiidae: *Ceratopsion, Raspailia, Echinodictyum* | | Raspailiidae: *Trikentrion* |
| Bubarida | | Bubarida | |
| | | | Bubaridae: *Bubaris, Monocrepidium* |
| | Dictyonellidae: *Dictyonella, Rhaphoxya, Acanthella* | | |
| Biemnida | | Biemnida | |
| | Biemnidae: *Sigmaxinella, Biemna* | | |
| Tetractinellida (Astrophorina) | | Tetractinellida (Astrophorina) | |
| | Ancorinidae: *Jaspis, Rhabdastrella, Stelletta, Asteropus, Ecionema, Ancorina, Psammastra* | | Ancorinidae: *Stelletta* |
| | | | Calthropellidae: calthropellid |
| | Geodiidae: *Erylus, Geodia* | | Geodiidae: *Geodia, Penares* |
| | | | Pachastrellidae: *Triptolemma, Brachiaster* |
| | | | Thoosidae: *Alectona* |
| Tetractinellida (Spirophorina) | | Tetractinellida (Spirophorina) | |
| | | | Samidae: *Samus* |
| | Tetillidae: tetillid | | |
| Agelasida | | | Agelasida |
| | Agelasidae: *Agelas* | | Agelasidae: *Agelas* |
| Polymastiida | | | Polymastiida |
| | Polymastiidae: *Polymastia* | | Polymastiidae: *Sphaerotylus* |
| Desmacellida | | | Desmacellida |
| | Desmacellidae: *Desmacella* | | |
| Poecilosclerida | | | Poecilosclerida |
| | Acarnidae: *Acarnus* | | Acarnidae: *Acarnus* |
| | Chondropsidae: *Chondropsis, Phoriospongia, Psammoclema* | | |
| | Crambeidae: *Monanchora* | | Crambeidae: *Discorhabdella* |
| | Crellidae: *Crella, Anisocrella* | | Crellidae: *Crellastrina* |
| | Coelosphaeridae: *Coelosphaera* | | Coelosphaeridae: *Histodermella* |
| | Dendoricellidae: *Pyloderma, Fibulia* | | |
| | | | Guitarridae: *Coelodischela* |
| | Hymedesmiidae: *Phorbas, Hymedesmia* | | |
| | Iotrochotidae: *Iotrochopsamma, Iotrochota* | | |
| | Latrunculiidae: *Latrunculia* | | Latrunculiidae: *Latrunculia, Sigmosceptrella* |
| | Microcionidae: *Antho, Clathria, Echinoclathria, Holopsamma, Echinochalina* | | |
| | Mycalidae: *Mycale* | | Mycalidae: *Mycale* |
| | | | Myxillidae: myxillid |
| | | | Podospongiidae: *Sceptrintus* |
| | Tedaniidae: *Hemitedania, Tedania, Strongylamma* | | |
| Clionaida | | Clionaida | |
| | Clionaidae: *Cliona, Spheciospongia* | | Clionaidae: *Cliona, Dotona* |
| | Spirastrellidae: *Diplastrella* | | Spirastrellidae: *Diplastrella* |
| | | | Placospongiidae: *Placospongia* |

*Table 4.* Cont.

| **Recent South Western Province sponge list** | | **Late Eocene W Australia sponge list** | |
|---|---|---|---|
| Tethyida | | Tethyida | |
| | Tethyidae: *Tethya, Xestospongia, Tethyastra* | | Tethyidae: *Tethyastra, Tethya* |
| | Hemiasterellidae: *Hemiasterella* | | |
| Trachycladida | | Trachycladida | |
| | Trachycladidae: *Trachycladus* | | |
| Suberitida | | Suberitida | |
| | Suberitidae: *Protosuberites, Rhizaxinella, Caulospongia* | | Suberitidae: suberitid |
| | Halichondriidae: *Halichondria, Hymeniacidon* | | |
| | Styolocordylidae: *Stylocordyla* | | |
| Homoscleromorpha | | Homoscleromorpha | |
| | homosclerophorid | | Plakinidae: *Placinolopha* |
| lithistids (undifferentiated) | | lithistids | |

Province) do not currently occur in this area and are present only in the fossil assemblage. On the genus level, this disproportion seems to be even more significant because only ~15% of genera in the Gulf Province and ~14% of genera in the South Western Province have their fossil representatives.

## Discussion

### *Paleoecology and biogeography*

The inconsistence in bathymetric preferences among recognized sponge taxa – the dominance of shallow-water sponges with co-occurrence of lithistids, some hexactinellids, and two strictly deep-water demosponge taxa – has already been discussed by Gammon *et al*. (2000a, b) who studied and interpreted the geology of the Paleogene of southern Australia. They proposed special environmental conditions e.g., the increased amount of nutrients, low light, calm hydrodynamics, and a high level of dissolved silica. These extraordinary conditions were caused by a specific paleogeographical setting and a high runoff from the thick regolith developed on the Australian continent which allowed the migration of deep-water lithistids as well as some hexactinellids into neritic depths during the Eocene.

The hypothesis of the shallow-water setting is also supported by the co-occurrence of rare other organisms, e.g. the diatom *Arachnodiscus erhenbergii*, which is currently known from temperate and tropical waters of mangrove-seagrass-algal communities (Round *et al*., 1990; Clarke, 1994). In the most western samples, the presence of rare zooxanthellate corals, which live in the photic zone, and ostracods indicating water depths of 50-100 m, also suggest moderately shallow water (James and Bone, 2000). Moreover, other abundant fossils, the coccoliths, gastropods, and ascidian sclerites, suggest the deposition of these sediments occurred in a relatively shallow and quiet sea floor environment below the wave base (Daily *et al*., 1976; James and Bone, 2000). This hypothesis is also supported by sedimentological data e.g. presence of an authigenic verdine mineral (odinite) which occurs in modern shallow tropical waters (of not more than 60 m) and wave ripples that are characteristic for shallow water (for more details see e.g. James and Bone, 2000; Gammon *et al*., 2000a, b; McGowran and Alley, 2008).

The geographic range of some sponges has not changed since the late Eocene. But in some cases sponge taxa recognized in a fossil material were not found in the south Australian waters today. In the case of cryptic or excavating sponges there are two possible explanations of their current absence in Australia: 1) either these sponges have changed their geographical range since the late Eocene, or 2) their cryptic/excavating nature resulted in them being overlooked, and in fact, they occur today around Australia. This second possibility, in my opinion, seems to be more plausible as it is postulated in the latest studies (see e.g. Łukowiak *et al*., 2013). Currently, some among the recognized sponge taxa inhabit deep waters of geographically distant regions, during the late Eocene, however, they seem to have lived in shallow-water habitats. This suggests a shift in their bathymetrical preferences since the Eocene. Also, the present occurrence of some of the recognized taxa in the zone ranging from the North

Atlantic to Indian Ocean and their absence in Australian waters is intriguing. It may be caused by different paleogeography in the Eocene. At that time, i.e., about 34 mya, the ancient equatorial sea called the Tethyan Ocean still existed. Tethys separated the southern continent (Gondwana) from the northern one (Laurasia). This sea, which formed during the Early Cretaceous (Wiedenmayer, 1994), was the dominating marine seaway extending far north-east. In terms of its extent, it is an equivalent of the major Recent oceans (NW and N Indian Ocean, Mediterranean, and the N Atlantic) with the Gibraltar Passage being opened. When the closure of the connection with the Indo-Pacific Ocean took place during the Early Miocene period, some of the Tethyan sponge taxa (the ones with wide longitudinal distribution in the Eocene) may have survived only in some refuges, i.e., the E Atlantic, Mediterranean, and the Arabian Sea. This part of the Tethys was closed (along the Zagos Crush Zone in the Middle East) only during the Oligocene, leaving a shallow seaway between the Eastern Mediterranean and the Gulf of Oman (Wiedenmayer, 1994). In the Miocene the Mediterranean was closed in the east (during the Tortonian) and in the west (during the Messinian). The closure provoked a Messinian salinity crisis which devastated marine faunas (Cita, 1984; Braga *et al*., 2006). In a result of such paleogeographic changes, the once continuous populations of the Tethyan sponges became separated and either went extinct, or differentiated/changed their habitats surviving as relict forms. Examples of such taxa that were widespread during the Eocene (even if not reported from other parts of the world, although it likely results from nonpreservation/lack of studies) seem to be *Mycale* (*Rhaphidotheca*) *loricata*, *Sceptrintus richardi*, and *Crellastrina* sp. These taxa currently only inhabit the deep waters around the Azores. *Tethya* cf. *omanensis* is known only from the Arabian Sea. Another example of a sponge with wider Cenozoic distribution is the crambeid *Discorhabdella hindei* Boury-Esnault, Pansini and Uriz, 1992. It occurs in the Mediterranean Sea (Alboran Sea) and reveals more similarities to the distant New Zealand species *Discorhabdella incrustans* than to other species of this genus known from the Azores (*D. tuberosocapitatum*; Boury-Esnault *et al*., 1992). In some cases, the recent distribution pattern of some sponge taxa (e.g. *Alectona millari*, *Samus anonymus*, and *Dotona pulchella*) overlaps (at least to some degree) with the former range of the Tethys. The Tethyan relicts have also been discovered among other animal taxa, e.g. gastropods and brachiopods (Zezina, 2009), echinoderms (Ozawa *et al*., 2009), and ostracods and foraminifers (Benson, 1976). On the other hand, it is worth noting that the molecular studies of such widely-distributed Recent sponge taxa show that they are often molecularly distinct evolutionary lineages (i.e., *Chondrilla caribensis* vs. *Chondrilla nucula*; Rützler *et al*., 2007), although very similar morphologically. Thus, they are lumped together into one cosmopolitan morphospecies (Klautau *et al*., 1999; Wörheide *et al*., 2002). Such morphospecies may consist, in fact, of several cryptic sibling species with high genetic diversity (that is not clearly manifested at the morphological level across their wide geographic ranges; e.g. Wörheide *et al*., 2002; Xavier *et al*., 2010 and the literature cited therein). This problem, however, is impossible to solve with the fossil material.

### *Comparison with Oamaru Diatomite sponge fauna*

The diatomites of Oamaru, New Zealand, described by Hinde and Holmes (1892) are considered to have been deposited at considerable depths. Although Hinde and Holmes (1892) interpreted this sponge assemblage as indicative of water depth not less than *ca* 1000-1500 fathoms (1800-2700 m), it is more likely that these sponge communities inhabited waters of lesser depth. On the other hand, Edwards (1991) suggests these sediments to be deposited rather between 75 and 150 m. The presence of a high number of strictly deep-water sponge taxa, as well as the lack of typically shallow-water sponges in these upper Eocene sediments, place the factual bathymetry of these sediments somewhere in-between these two hypotheses as postulated by Kelly and Buckeridge (2005). They established the water depth as being 500 to 800 m, similar to that of Chatham Rise (east of New Zealand), which is characterised by a similar combination of demosponges, lithistids, and hexactinellids.

In the Oamaru, there are numerous hexactinellids (e.g. *Hyalonema*, *Monorhaphis*, *Caulophacus*) that belong to Amphidiscophora and are typical for very deep environments. Likewise, the occurrence of deep-water poecilosclerids (e.g. *Cladorhiza*, *Esperiopsis*, and *Chondrocladia*), which are reported currently from the bathyal zone, as well as the presence of the deep-water astrophorid *Thrombus abyssi*, support this supposition. However, it must be remembered that the Oamaru Diatomite assemblage also consists of some extremely shallow-water sponges (e.g. *Myxilla*). This admixture of shallow-water forms may be explained by their transport from surrounding areas.

The studied Australian community is characteristic of a shallower depth. Such an interpretation is supported by the fact that hexactinellid spicules are rare in Australia, in contrast to New Zealand. Moreover, there are numerous shallow-water non-lithistid demosponge taxa (e.g. *Sceptrintus richardi*, *Samus anonymus*, *Diplastrella megastellata*, *Cliona mucronata*, *Placospongia*, and the chondrillids) that are absent in the New Zealand association.

In contrast to Oamaru, Australian lithistids (families Pleromidae, Corallistidae, and Theonellidae), are mostly known from entirely preserved individuals. They are extremely common and diversified but they delivered only sparse loose spicules. Worldwide, theonellids occur both in shallow and deep waters, while pleromids are found in considerable depths of about 600 m. The same is true for Corallistidae (Pisera and Lévi, 2002). On the other hand, the lithistid family Vetulinidae, which is known from the Caribbean (Barbados) from the depth of 126-600 m, was recorded only in the New Zealand assemblage (Pisera and Lévi, 2002).

### *Differences and similarities between Recent and fossil sponge faunas of Australia*

The lack of some sponge families in the fossil record can be explained by data loss during the process of fossilization, as well as the difficulties with the systematic assignment of the studied spicules (because of their simple, non-characteristic morphology). However, the presence of a higher number of sponge taxa in the Eocene assemblage is difficult to explain. It can result from 1) the poor study of the area (the sampling bias), and overlooking, especially small, cryptic, excavating or encrusting taxa, 2) the real changes in the taxonomic diversity of demosponges since the late Eocene. Indeed, some of the studied taxa that have no Recent representatives in the waters surrounding the south of Australia, such as thoosids and spirophorids, are excavating and cryptic, respectively. Placospongiids, on the other hand, are sometimes encrusting, while the spirastrellids are noted to be limestone-excavating and encrusting. Most probably, the mode of life of the above-mentioned taxa caused that they are not reported (overlooked) from Australia and actually may live in this area. Their presence may be confirmed after more careful studies. On the other hand, the lack of the representatives of the families Pachastrellidae, Guitarridae, and Coelosphaeridae (that are present in the fossil assemblage) in these waters today is difficult to understand. It seems that the only reasonable explanation is that these sponge taxa have changed their geographic range due to post-Eocene climate changes.

The current absence of the families Polymastiidae and Spirastrellidae in the Spencer Gulf may be only a matter of sampling bias because representatives of these families are today reported from adjacent area, e.g., the coasts of Coorong National Park, about 150 km north of Adelaide [Atlas of living Australia (ALA), accessed on August 2013]. This may be the case as the patchy sponge distribution at the 'intra-regional' spatial scale occurs with sometimes as little as 15% similarity in the species composition between geographically adjacent reef sites (Hooper, 1998).

On the other side, the apparent lack of the Axinellidae and Dendoricellidae in the fossil material may be explained by the fact that the sponges belonging to these families possess rather morphologically simple spicules which are difficult to assign to a particular family. The same is true for the order Haplosclerida whose members also usually produce such simple spicules. The absence of the poecilosclerid families Microcionidae, Desmacididae, Chondropsidae, and Tedaniidae is more questionable. These sponges usually bear very characteristic spicule morphotypes that are easy to distinguish. Most likely, their absence in the fossil material is factual rather than an effect of misinterpretation, overlooking or removal.

The lack of representatives of some demosponge families in the South Western Province, e.g. thoosids, and their presence in the fossil assemblage, may be explained by their ecology. Thoosidae are usually small limestone-excavating sponges that live in burrows made in calcareous algae, scleractinian corals, or octocorals. Thus, it is very easy to overlook them. Similarly, the sponges from the poecilosclerid family Crambeidae (e.g. *Discorhabdella*) are thinly encrusting animals (van Soest, 2002c). For this reason, their overlooking in general faunistic studies, which are often performed by dredging, would not be surprising as well. This applies for placospongiid and samid sponges, too. On the contrary, the apparent absence of families Axinellidae, Halichondriidae, Dictyonellidae Chalinidae, Niphatidae, and Phloeodictyidae in the fossil material is likely an artefact of 'nondetermination' due to the uncharacteristic spicule morphotypes (mainly simple styles and oxeas, rarely some microscleres). These types of spicules occur in a wide range of demosponge families and thus are useless for distinguishing various taxa. For this reason, it is important to remember that their absence in the Eocene samples is most probably artificial.

Nowadays, the poecilosclerids *Sigmosceptrella quadrilobata* and *Sceptrintus richardi* may really be absent in Australian waters as none of these species are recorded from this area (ALA, accessed on Aug 2014). Also, the families Tedaniidae, Hymedesmiidae, and Dendoricellidae recognized currently in the southern Australia are absent in fossil material. They have rather characteristic, and easy to recognize and distinguish spicules, (e.g. onychaetes, subtylostyles, acanthostyles, toxas, and isochelae) which really suggest a change in their biogeographic distribution since the late Eocene. The apparent absence of the family Hemiasterellidae in the fossil material, which also has rather characteristic astrose spicules, may not be real because the spicules of hemiasterellids are similar to the oxyasters of Astrophorina. Therefore, they might have been misassigned.

It seems that the only real difference between the Eocene and Recent sponge fauna is the absence of families Microcionidae, Dendoricellidae, Desmacididae, Chondropsidae, Tedaniidae, Hymedesmiidae, Iotrochotidae, Stylocordylidae, and Trachycladidae in the fossil assemblage. Also, it appears to be probable that some astrophorines (families Calthropellidae and Pachastrellidae), poecilosclerids (families Guitarridae and Coelosphaeridae), and family Bubaridae in today's waters are absent, contrary to the Eocene fauna. The rest of the changes (the lack of taxa that are excavating or boring in habitus in Recent southern Australian waters, as well as taxa with simple spicule morphology in the fossil assemblage) do not seem to be factual. Rather, it was caused by various biasing factors that could have influenced the estimations of diversity.

The absence of rather deep-water inhabitants, lithistids, and hexactinellids in the Recent fauna, that occur in the fossil assemblage, may also be explained by the fact that most of them could have had different (shallower) bathymetrical ranges during the Eocene. These might be due to the conditions that allowed them to inhabit shallow water, i.e., high silica level. Also more favourable water temperatures in that time might have made shallow water more attractive habitat to live (Exton *et al*., 2001; Quaglio *et al*., 2007) as the temperature may be one of the factors that drives faunal changes (Carballo *et al*., 2008 and the literature cited therein).

On the other hand, the current presence of various poecilosclerids and hadromerids around Australia, that are absent in the Eocene fauna, suggests the actual changes in the taxonomical composition.

## Conclusions

Based on sponge composition, the rare non-sponge micro- and macrofauna, as well as published geological data, the 'soft' sponge assemblage of the late Eocene of southern Australian is interpreted as inhabiting silica-rich, shallow coastal water of about 100 meters of depth.

This interpretation is also supported by the comparison of the Australian fossil assemblage with similar but deeper-water Eocene spicule material from the Oamaru Diatomite, New Zealand. This assumption is based on the presence in Oamaru site of numerous sponge taxa (both, amphidiscophoran hexactinellids and non-lithistid demosponges) that are typical for deep waters of at least few hundreds of meters. The absence of shallow-water demosponges (that are present in Australia) support it as well.

As it shows the distribution pattern of the recognized sponge taxa, the studied assemblage has a clear Tethyan affinity. Some studied sponge taxa today inhabit the areas that are congruent with the range of the Tethys in the past. Also, the recent occurrence of some other fossil sponge taxa only in distant geographic regions and oceans is interpreted as a relic of such Tethyan distribution. It also proves that in geological past some sponge taxa had a wider geographic distribution and that they have survived to the present only in refugia.

The comparison of the studied late Eocene sponge fauna with the sponge communities inhabiting southern Australian waters today demonstrates a great similarity at the order level. The differences between both assemblages are more pronounced at lower levels (family, genus), with only about half of the Recent sponge families from Australia present in the Eocene assemblage. However, considering all difficulties that have played a role in the process of recognition, assignment, and comparison of fossil sponges with their Recent counterparts, there is no dramatic change in 'soft' sponge fauna composition in this area since the Eocene.

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