Discovery of the freshwater sponge genus *Corvospongilla* Annandale (Porifera: Spongillida) in Australia with the description of a new species and phylogeographic implications

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Abstract

A recent discovery of freshwater sponges in an unexplored hydrographic basin in north-western Australia provided the opportunity to investigate the genus *Corvospongilla* Annandale (Spongillida: Spongillidae) using integrative systematics. Emendation of the genus diagnosis is provided. A comparative analysis of a *Corvospongilla* global dataset of morphological traits together with biogeographic patterns disclosed a new Australasian *Corvospongilla* species and along with molecular analyses provided the basis for a phylogenetic and phylogeographic tree for some Asian, Afrotropical and Australasian lineages.

Keywords Evolutionary novelty · Freshwater biogeography · Gondwanian tracks · Morphological and molecular analysis · SEM

Introduction

The Australian freshwater sponge fauna (Demospongiae: Spongillida) is poorly studied. Species richness and endemism values are comparatively high, i.e., Australia has 26 recorded species, 23 of which are Australian endemics,

while the Australasian Bioregion has 36 recorded species (Racek 1969; Stanisc 1978–1979; Manconi et al. 2016; Pronzato and Manconi 2019, 2021). To shed more light on Australian freshwater sponge diversity, the collection of the Western Australian Museum is currently being studied from both a morphological and molecular standpoint.

The present focus is on *Corvospongilla* Annandale, 1911 one of the most species rich genera ($n = 19$ species until now) of the order Spongillida. This genus is characterized by ‘pseudobiotules as skeletal microscleres’, ‘three gemmular morphs with variable architecture of theca’ and ‘strongyles to oxeas as megascleres’ all traits supporting the need for deep integrative analyses (Manconi and Pronzato 2002, 2019; Pronzato et al. 2017). We report on the integrative analysis of congeneric species assigned to *Corvospongilla* in a biogeographic context. This has allowed us to report on (1) the first record of the genus in the Australasian Region; (2) the discovery of a new species from North Western Australia on the basis of a comparative morphological analysis with the other species of the genus; (3) assessment of morphological and molecular traits to delineate a species group from Australia, Africa and Asia; (4) determination of the phylogeographic pattern of the genus *Corvospongilla* confirming Gondwanian tracks in its evolutionary history.

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Methods

Study area

Species of *Corvospongilla* from all biogeographic realms in which the genus occurs have been considered for morphological analyses. Collections of sponges in North Western Australia were carried out during technical surveys of the Moochalabra Dam (Fig. 1). Staff of the Water Corporation of Western Australia discovered sponge growth on off-take structures at site 1 (15°36'54.83"S 128°06'13.19"E) and site 2 (15°36'56.85"S 128°06'12.83"E) within the dam and collected specimens for identification (Table 1). This reservoir is fed by the Moochalabra Creek which starts at an elevation of 205 m and ends at 5.24 m when it flows into the King River (tributary of Cambridge Gulf, Timor Sea), dropping ~200 m over its 21.7 km length (<http://bonzle.com/c/a?a=p&cmd=sp&zix=r&p=162783&st=&s=Moochalabra%20Dam&pg=1&m=0&c=1&x=128%2E12429&y=%2D15%2E4869&w=40000&mpsec=0>, accessed 29/8/2019). The Dam supplies the town of Wyndham with drinking water (<https://www.watercorporation.com.au/about-us/news/media-statements/media-release/swimming-prohibited-in-moochalabra-dam>, accessed 29/8/2019). The Wyndham area is characterised by a hot semiarid climate (*BSh*) by Köppen climate classification (Geiger 1954, 1961; Peel et al. 2007).

Studied museum collections

Representative samples of Australian *Corvospongilla* were compared to type material and specimens from historical collections and to the original descriptions of congeneric species (see Table 1). Holotype and paratypes of the new species were registered at the Western Australian Museum (WAM) and schizotypes in the FW-POR collection (Italy).

Institutional acronyms: NMHUK(BMNH), The Natural History Museum, London, United Kingdom; FW-POR, R. Manconi and R. Pronzato collection, Italy; IM, Indian Museum [including ZEV, Zoological Survey of India], Calcutta, India; MCN, Museu de Ciências Naturais, Fundação Zoobotânica, Puerto Alegre, Brazil; MRAC, Musée Royal de l'Afrique Centrale de Tervuren (KMMA), Belgium; MSNG, Museo civico di Storia Naturale 'G. Doria', Genova, Italy; QM, Queensland Museum, Australia; SNSB-BSPG, Bavarian State Collection for Palaeontology and Geology; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; WAM, Western Australian Museum, Perth, Western Australia; ZMB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany.

Morphological analysis

In vivo images were not available. Although the WAM ethanol preserved samples were in a poor status of preservation a set of macro- and micro-morphotraits (architecture of skeleton, traits of skeletal megascleres and microscleres,

Fig. 1 *Corvospongilla moochalabrensis* sp. n. (Order Spongillida). Type locality (black dot) at Moochalabra Dam off-take site 2 (15°36'56.85"S 128°06'12.83" E) in the King River Hydrographic Basin of North Western Australia

Table 1 Genus *Corvospongilla*. Materials morphologically and molecularly examined for the phylogenetic analysis, with notes on collections and geographic coordinates

Species	Specimens/collection details	Sites	Morphological analysis	Molecular analysis
<i>Corvospongilla moochalabrensis</i>	WAM Z29235 holotype 75% Ethanol coll. L. Zappia & I. Read 22.II.2012	Moochalabra Dam off-take site 2, NW Australia 15°36'56.85"S 128°06'12.83"E	FW-POR 853 Schizotype	No data
<i>Corvospongilla moochalabrensis</i>	WAM Z98322 paratype 75% Ethanol coll. Dalcon Environmental 18.VI.2003	Moochalabra Dam, NW Australia 15°37'15.66"S 128°06'06.09"E	FW-POR 863 Schizotype	FW-POR 863 Schizotype
<i>Corvospongilla moochalabrensis</i>	WAM Z29234 paratype 75% Ethanol coll. L. Zappia & I. Read 22.II.2012	Moochalabra Dam off-take site 1, NW Australia 15°36'54.83"S 128°06'13.19"E	FW-POR 854 Schizotype	No data
<i>Corvospongilla moochalabrensis</i>	WAM Z29245 paratype 75% Ethanol coll. L. Zappia & I. Read 6.XII.2012	Moochalabra Dam off-take site 1, NW Australia 15°36'54.83"S 128°06'13.19"E	Fw-Por 860 Schizotype	FW-POR860 Schizotype
<i>Corvospongilla moochalabrensis</i>	WAM Z29246 paratype 75% Ethanol coll. L. Zappia & I. Read 6.XII.2012	Moochalabra Dam off-take site 1, NW Australia 15°36'54.83"S 128°06'13.19"E	FW-POR 862 Schizotype	FW-PO R862 Schizotype
<i>Corvospongilla moochalabrensis</i>	WAM Z29247 paratype 100% Ethanol coll. L. Zappia & I. Read 6.XII.2012	Moochalabra Dam off-take site 1, NW Australia 15°36'54.83"S 128°06'13.19"E	FW-POR 861 Schizotype	FW-POR 861 Schizotype
<i>Corvospongilla becki</i>	USNM topotypes dry coll. M.A. Poirrier IX.1976	Duck Lake, Atchafalaya basin, St. Martin Parish, Louisiana, USA 30°08'N 91°37'W	FW-POR 919 FW-POR 920 FW-POR 921 Schizotopotypes	No data
<i>Corvospongilla burmanica</i>	NMHUK(BMNH) 82.3.22.1–3 box 6 type dry	Pimpili village, Vashishti River, Ranagiri District, India 17°31'56"N 73°31'4"E	FW-POR 420 Schizotype	FW-POR 420 Schizotype
<i>Corvospongilla caunteri</i>	NMHUK(BMNH) 14.11.24.27 ex-ZEV 4776/7, cotype	Hazratgunj, Lucknow, Uttar Pradesh, India	FW-POR 637 Schizotype	FW-POR 637 Schizotype
<i>Corvospongilla lapidosa</i>	NMHUK(BMNH) 08.2.11.1 cotype, dry	River Godavery Nasik, Maharashtra, India	FW-POR 638 Schizotype	FW-POR 638 Schizotype
<i>Corvospongilla lemuriensis</i>	MSNG 60893a topotype, dry coll. R. Manconi 9.IX.2016	Farihy Amboromalandi Reservoir, Betsiboka River basin, Madagascar 16°7'22.26"S 46°44'53.974"E	FW-POR 804 Schizotype FW-POR 807 Schizotype	FW-POR 804 Schizotype
<i>Corvospongilla mesopotamica</i>	MSNG 51766 holotype coll. H.A.A. Saadalla VIII.1997	Himreen Reservoir, Diyala River, Kurdistan, Iraq 34°7'N 44°58'E	FW-POR 574 Schizotype	FW-POR 574 Schizotype
<i>Corvospongilla siamensis</i>	MSNG 56533 holotype coll. N. Ruengsawang 12.II.2008	Ban Huai Sai, Pong River, Mekong Basin, Thailand 16°46'20.40"N 102°42'48.22"E	FW-POR 733 Schizotype	FW-POR 733 Schizotype
<i>Corvospongilla thysi</i>	MRAC 1311 type	Lake Barombi-ma-Mbu, Cameroun, Africa	FW-POR 472 Schizotype	FW-POR 472 Schizotype No data
<i>Corvospongilla ultima</i>	NMHUK(BMNH) 14.11.24.29 ex-ZEV 4906/7 fragment	Tanjore, Tamil Nadu, India	FW-POR 639 Fragment	FW-POR 639 Fragment

Table 1 (continued)

Species	Specimens/collection details	Sites	Morphological analysis	Molecular analysis
<i>Corvospongilla ultima</i> var. <i>spinosa</i>	NMHUK(BMNH) 14.11.24.30 ex-ZEV 5106/7 fragment	Taloshi, Koyna Valley, Satara District, Maharash- tra, India	FW-POR 640 Fragment	FW-POR 640 Fragment
<i>Corvospongilla seckti</i> (as <i>C. volkmeri</i>)	NMHUK(BMNH) 89.9.25.10 ex-MCN 86 schizoparatype coll. J.C. Mello de Carvalho 30.XII.1961	Lagoa Redonda, Sousa, Par- aíba State, Brazil, South America 06°47'58"S 038°19'43"W	FW-POR 642 Schizotype	FW-POR 642 schizotype No data
<i>Corvospongilla</i> <i>zambesiana</i>	NMHUK(BMNH) 1906.2.28.2 13IIC, frag- ment	River Zambezi, Africa	FW-POR 623 Fragment	No data
<i>Corvospongilla</i> sp. 1	100% Ethanol	Lake Itamba, Tanzania, Africa	SNSB-BSPG.GW2358	SNSB-BSPG.GW2358
<i>Corvospongilla</i> sp. 1	100% Ethanol	Lake Itamba, Tanzania, Africa	SNSB-BSPG.GW2354	SNSB-BSPG.GW2354

gemmular architecture and gemmuloscleres morphology) was considered diagnostic at the family, genus and species levels (Manconi and Pronzato 2002, 2019). Representative fragments of sponges were dissected by hand for light microscopy (LM) and scanning electron microscopy (SEM, Vega3Tescan, Czech Republic). Spicules processed by dissolution of organic matter in boiling 65% nitric acid, were rinsed in water, suspended in ethanol and dropped onto slides and/or stubs (Manconi and Pronzato 2000, 2015). Dry body fragments, dissociated spicules, entire gemmules and their cross-sections were sputter-coated with gold and observed under SEM. Measurements of spicules of each diagnostic spicular type and gemmules, were performed by LM and by SEM. The terminology of diagnostic morpho-traits follows Manconi and Pronzato (2002). Taxonomic status was checked in the World Porifera Database (Van Soest et al. 2020).

Molecular analyses

Total genomic DNA was extracted from tissue fragments of the adult specimens, or in case of *C. lemuriensis*, from the juveniles freshly hatched from gemmules in petri dishes using the NucleoSpin®. Tissue DNA extraction Kit (Macherey–Nagel) following the manufacturer's protocol. Primarily, amplification of the entire ITS region was attempted for all specimens using the primers ITS-RA2-fwd (5'-GTC CCT GCC CTT TGT ACA CA-3') in combination with ITS2.2-rvse (5'-CCT GGT TAG TTT CTT TTC CTC CGC-3') (Wörheide 1998). Alternatively, two minimalist ITS2 barcoding regions were amplified ("5.8S-ITS2" and "ITS2-28S" cf. Erpenbeck et al. 2019) [Primers: 5.8_Freshies_1180_9f: 5'-GCA CGT CTG TCT GAG CGT CCG-3' / ITS2_Freshies_1174_3r: 5'-GCT TCG CAC TTS AAG GGA CGC-3' (5.8S-ITS2) and ITS2_Freshies_1176_5f: 5'-TTG

CGC GTC GGG AAC TCG AC-3' / 28S_Freshies_1178_7r: 5'-GCT TAT TGA TAT GCT TAA ATT CAG C-3' (ITS2-28S)]. The 25 µL PCR mix comprised 5 µL 5 × green GoTaq® PCR Buffer (Promega Corp, Madison, WI), 4 µL 25 mM MgCl₂ (Promega Corp, Madison, WI), 2 µL 10 mM dNTPs, 2 µL BSA (100 µg/ml), 1 µL each primer (5 µM), 7.8 µL water, 0.2 µL GoTaq® DNA polymerase (5 µ/µL) (Promega Corp, Madison, WI) and 2 µL DNA template. The PCR regime comprised an initial denaturation phase of 94 °C for 3 min followed by 35 cycles of 30 s denaturation at 94 °C, 20 s annealing (45 °C for ITS-RA2-fwd / ITS2.2-rvse; 52 °C for 5.8_Freshies_1180_9f / ITS2_Freshies_1174_3r; 55 °C for ITS2_Freshies_1176_5f / 28S_Freshies_1178_7r). Elongation time was 60 s (for ITS-RA2-fwd / ITS2.2-rvse), respectively, 45 s (for 5.8_Freshies_1180_9f / ITS2_Freshies_1174_3r and ITS2_Freshies_1176_5f / 28S_Freshies_1178_7r) at 72 °C each followed by a final elongation at 72 °C for 5 min after the 35th cycle. PCR products were purified with a Freeze-Squeeze Method (Thuring et al. 1975) before cycle sequencing using the BigDye-Terminator Mix v3.1 (Applied Biosystems) following the manufacturer's protocol. Both strands of the template were sequenced on an ABI 3730 automated sequencer. PCR products were cleaned with the Freeze-Squeeze methods following Thuring et al. (1975), cycle sequenced with BigDye-Terminator Mix v3.1 (Applied Biosystems) and sequenced on an ABI 3730 automated sequencer. Sequences were basecalled, trimmed, assembled and checked in CodonCode Aligner v 3.7.1.1 (www.codoncode.com). Origin of the sequences was verified with BLAST against NCBI GenBank (www.ncbi.nlm.nih.gov/genbank). Sequences of this project are deposited in the European Nucleotide Archive (ENA, www.ebi.ac.uk/ena) under study accession number PRJEB41019 and in the Sponge Barcoding Database (SBD, www.spongebarcoding.org, Wörheide and Erpenbeck 2007). Sequences were

concatenated and aligned using MAFFT (Katoh and Standley 2013) prior to maximum likelihood reconstructions using PhyML (which regards gaps as missing data, Guindon et al. 2010), as implemented in Geneious 2019.2.1 (Kearse et al. 2012) under the F81 model as suggested by jModeltest2 (Darriba et al. 2012). Sequences of *Ephydatia muelleri* were chosen as outgroup as they provided comparatively short distances to the *Corvospongilla* ingroup. Median Joining network (Bandelt et al. 1999) reconstructions on *Corvospongilla* were performed with PopART (<http://popart.otago.ac.nz>) under an epsilon parameter of zero.

Systematic accounts

Class Demospongiae Sollas, 1888

Order Spongillida Manconi and Pronzato 2002

Family Spongillidae Gray, 1867

Genus *Corvospongilla* Annandale 1911

[Type species *Corvospongilla loricata* (Weltner 1895)]

Diagnosis (revised after Manconi and Pronzato 2019; emended parts in italics). Encrusting, flat to massive, lobate growth form. Consistency extremely hard to fragile. Spongin scanty except for the well-developed basal spongin plate and the gemmular theca. Skeletal network *irregularly* alveolar to isotropic with *sometimes vague* ascending pauci- to multi-spicular tracts toward surface supporting conules and ridges *if present*. *Skeletal* megascleres strongyles to oxeas smooth, tubercled-granulated or spiny. *Skeletal* microscleres as pseudobiotules frequently rare, straight to slightly curve with smooth shaft of variable length and *pseudorotules* at tips. *Pseudorotules* with hooks (*corvus*) *variably long and curve*. Gemmules of *various* morphs, sometimes coexistent, single or grouped, in the skeletal network (free gemmules) or adhering to the basal spongin plate (sessile gemmules) with

or without a variably stout spicular cage around the theca. Foramen from apical to lateral with a short porous tube. *Three gemmular morphs according to the architecture of the trilayered to mono- or bi-layered theca*. Gemmular theca with variably thick pneumatic layer of rounded chambers with *compact laminae*. Gemmuloscleres variably embedded and tangentially arranged in the theca, from elongated, spiny to smooth, stout strongyles to oxeas to strongylox-eas, straight or variably curved to *boomerang-shaped*, ring-shaped or oval. Spicules of larvae slender, smooth to spiny oxeas.

Etymology The genus name *Corvospongilla* refers to the *corvus* as the typical diagnostic morphotrait ‘pseudobiotule as skeletal microscleres with ornamentation at tips a few long, curved, smooth hooks’. The suffix *corvo* refers to the particular shape of these hooked tips on the basis of the Latin term *corvus* meaning harpoon, hook and rising from a Roman naval boarding device (mobile catwalk with an hook at the tip) used in naval battles.

Corvospongilla moochalabrensis sp. n. Manconi and Erpenbeck

Figures 1, 2, 3, 4, 5, 6, 7, 8, Table 1.

Examined material Holotype: WAM Z29235/FW-POR853 schizotype, type locality Moochalabra Dam off-take site 2 (15°36′56.85″S 128°06′12.83″E), Moochalabra Creek, King River Hydrographic Basin, North Kimberley Region, east North Western Australia, coll. L. Zappia & I. Read, 22 February 2012, 75% Ethanol.

Paratypes WAM Z29234/FW-POR854 schizotype, Moochalabra Dam off-take site 1 (15°36′54.83″S 128°06′13.19″E), *ibid.*, coll. L. Zappia & I. Read, 22 February 2012, 75% Ethanol; WAM Z29245/FW-POR

Fig. 2 *Corvospongilla moochalabrensis* sp. n. (Order Spongillida) from North Western Australia. Holotype WAM Z29234/schizoholotype FW-POR 853. SEM micrographs. **A** Basal skeleton of tangential

smooth oxeas as megascleres (bottom view). **B** Skeleton fragment of smooth oxeas with a few ascending large tracts (cross section)

Fig. 3 *Corvospongilla moochalabrensis* sp. n. (Order Spongillida) from North Western Australia. Holotype WAM Z29234/schizoholotype FW-POR 853. SEM micrographs. **A** Gemmules sessile in a carpet (top view) partly sharing the spicular cage of smooth oxoas (megascleres) at the basal spongin plate armed by tangential smooth oxoas (megascleres); **B** Gemmular theca surface armed by the cage of smooth oxoas (megascleres); **C** Gemmular theca with outer layer of compact spongin and some pseudobirotules (skeletal hooked microsceres) present at the surface; **D** Foramen closed by a membrane at

the top of gemmular theca and surrounded by spicular cage of skeletal oxoas and few hooked microsceres (pseudobirotules); **E** Gemmule with spicular cage, thick pneumatic theca, and staminal cells (thesocytes) in the gemmular cavity (cross section); **F** Gemmular theca trilayered with thin outer layer of compact spongin, well-developed chambered pneumatic layer with a single layer of tangentially embedded gemmuloscleres and multilayered compact inner layer (cross section)

Fig. 4 *Corvospongilla moochalabrensis* sp. n. (Order Spongillida) from North Western Australia. Holotype WAM Z29234/schizoholotype FW-POR 853. SEM micrographs. **A** Basal skeleton armed by tangential smooth oxoas (megascleres) and rare pseudobiotules (microscleres); **B–D** Different views and magnification of pseudobi-

rotule (microscleres) sparsely distributed in the skeleton of mesohyl; **E** Entire gemmular theca with tangential gemmuloscleres and cross section of the spicular cage (megascleres); **F** Gemmular theca trilayered with a single layer of gemmuloscleres tangentially embedded in the chambered pneumatic layer (cross section)

860, *ibid.*, coll. I. Read, 6 December 2012, 75% Ethanol; WAM Z29247/FW-POR 861, *ibid.*, 100% Ethanol; WAM Z29246/FW-POR 862, *ibid.*, 75% Ethanol; WAM

Z98322/FW-POR863, Moochalabra Dam (15°37'15.66"S 128°06'06.09"E), coll. Dalcon Environmental, 18 June 2003, 75% Ethanol.

Fig. 5 Spicular complement of *Corvospongilla moochalabrensis* sp. n. (Order Spongillida) from North Western Australia. Holotype WAM Z29234/schizoholotype FW-POR 853. SEM micrographs. **A** Pseudobiotrutes (microscleres) with long hooks at tips; **B** Smooth oxeas as megascleres; **C** Spiny strongyles and oxeas to strongyloxeas as gemmuloscleres

Comparative materials *Corvospongilla becki* Poirrier 1978 USNM topotypes/FW-POR 919, 920, 921 schizotypes, dry, Duck Lake, 25 Sept. 1975, leg. det. Poirrier, Louisiana, USA; *Corvospongilla burmanica* subsp. *bombayensis* Kirkpatrick, 1908 BMNH 82.3.22.1-3 box 6 type/FW-POR 420 schizotype, dry, Pimpli, Vashisthi Valley, Ranagiri District, India; *C. burmanica* (?) BMNH 86.10.29.1/FW-POR 636, River Kuano, Uttar Pradesh, India; *Corvospongilla caunteri* Annandale 1911 BMNH 14.11.24.27 ex-ZEV 4776/7 paratype/FW-POR 637 schizotype, Hazratgunj, Lucknow, Uttar Pradesh, India; *Corvospongilla lapidosa* (Annandale 1908) BMNH 08.2.11.1 paratype/FW-POR 638 schizotype, River Godavery Nasik, Maharashtra, India; *C. lapidosa* BMNH/FW-POR 149, River Kuano, Uttar Pradesh, India; *Corvospongilla lemuriensis* Manconi and Pronzato 2019

MSNG 60893a holotype/FW-POR 807 schizoholotype, FW-POR 804 topotype, Farihy Amboromalandi Reservoir, Madagascar; *Corvospongilla loricata* (Weltner 1895) ZMB 2093 SE325-SE37-41 type/fragment FW-POR 511, locality unknown, Africa; *Corvospongilla mesopotamica* Manconi and Pronzato 2004 MSNG 51766 holotype/ FW-POR 574 schizotype, River Diyala, Kurdistan, Iraq; *Corvospongilla siamensis* Manconi and Ruengsawang, 2012 MSNG 56533 holotype/FW-POR 733, MSNG 56533a paratype, Pong River, Lower Mekong Basin, Thailand; *Corvospongilla thysi* (Brien, 1968) MRAC 1311 type/FW-POR 472 schizotype, Lake Barombi-ma-Mbu, Cameroon, W-Africa; *Corvospongilla ultima* (Annandale 1910) BMNH 14.11.24.29 ex-ZEV 4906/7 fragment/FW-POR 639, Tanjore, Irinchinopoli District, India; *C. ultima* var. *spinosa* Annandale, 1912

Fig. 6 *Corvospongilla moochalabrensis* sp. n. (Order Spongillida) from North Western Australia. Pseudobirotules with hooks as microscleres. Paratype WAM Z29235/schizoparatype FW-POR 854. Drawings from LM micrographs

BMNH 14.11.24.30 ex-ZEV 5106/7/FW-POR 640, Taloshi, Koyna Valley, Satara District, Maharashtra, India; *Corvospongilla volkmeri* de Rosa Barbosa, 1988 BMNH 89.9.25.10 (ex-MCN 86) schizoparatype /FW-POR 642, Lagoa Redonda, Sousa, Paraíba State, Brazil; *Corvospongilla zambesiana* (Kirkpatrick, 1906) BMNH 1906.2.28.2, 13IIC/FW-POR 623 R. Zambezi, Zimbabwe; *Corvospongilla* sp. 1 SNSB-BSPG.GW 2354/2358-FW-POR 950/951/954, Lake Massoko/Lake Kingiri/Lake Itamba, 11 Nov. 2011, coll. M. Genner, Lake Itamba, Tanzania, Africa.

Diagnosis *Corvospongilla moochalabrensis* is characterized by a combination of unique traits of the spicular complement as ‘smooth slender oxeas as megascleres with tips ranging from abruptly pointed to fusiform and rare oxeas thin, straight, fusiform’ and ‘pseudobirotules as microscleres with curved shaft and pseudorotules with long hooks’ and gemmular architecture as ‘gemmules of a single morph, i.e., sessile with spicular cage of smooth oxeas (megascleres)’, ‘sessile gemmular theca trilayered with well-developed chambered pneumatic layer’, ‘spiny strongyles to oxeas and strongyloxeas as spiny gemmuloscleres’.

Etymology The specific epithet *moochalabrensis* refers to the Moochalabra Dam (type locality).

Life cycle Sponges growing on the dam were in the active vegetative phase and always bearing gemmules both in the wet season (summer; December and February) and in the arid season (winter; June) when they were collected.

Habitat Dense sponge populations occurred in shallow water of Moochalabra Dam on grids of in-take and off-take structures within the dam and were collected during dam maintenance (grid cleaning). Water in the dam, after filtration, chlorination and disinfection meets strict Australian Drinking Water Guidelines. During the wet season, the dam inflow may contain sediment, depending on levels of rainfall in the catchment, and in winter a temperature gradient may occur in the dam, which can lead to sediments being resuspended, causing seasonal turbidity (<https://www.watercorporation.com.au>, accessed 29/8/2019). Sponge associated organisms were abundant bryozoans (with statoblasts) strictly growing with sponges, together with diatoms, nematodes, water mites, and chironomid larvae.

Geographic range Currently known only from the type locality of Moochalabra Dam, in the North Kimberley Region, north Western Australia (Fig. 1).

Description. Growth form encrusting. Colour light brown to brown in ethanol in the same specimen. Consistency

Fig. 7 Left: Maximum-likelihood phylogram of *Corvospongilla* species based on ITS2 fragments. The new species, *C. moochalabrensis* is depicted in bold. Numbers on branches are bootstrap probabilities. The scale bar indicates substitutions per site. Right: Median-joining network of the *Corvospongilla* ITS2-genotypes: Open circles represent

sent genotypes (I–IV) with the respective states of the nine variable characters to their right. Their pairwise p-distances are given in the table at the bottom right. Black circles denote unsampled intermediate genotypes

hard, fragile in alcohol. Spongin scanty in the skeleton, conspicuous in the gemmular theca and basal spongin plate. Basal spongin plate notably developed around sessile gemmules. Surface slightly hispid from tips of irregularly arranged oxeas. Oscules inconspicuous. Ectosomal skeleton irregularly arranged oxeas (no special architecture). Choanosomal skeleton (on the basis of few basal fragments) as network of megascleres with multi-spicular (up to 10–15 spicules) meshes. Megascleres oxeas smooth, slender, abruptly pointed to fusiform, straight to slightly bent ($167\text{--}205 \times 8\text{--}14\text{ }\mu\text{m}$, WAM Z29235/FW-POR 853; $195\text{--}233 \times 9\text{--}13\text{ }\mu\text{m}$, WAM Z98322/FW-POR 863; $n = 25$ spicules measured per sample). Oxeas smooth, thin, straight, fusiform ($112\text{--}158 \times 2\text{--}5\text{ }\mu\text{m}$, WAM Z29235/FW-POR 853; $n = 25$ spicules measured per sample) also present. Microscleres pseudobiotules abundant, scattered in the skeleton and near gemmular carpets; pseudobiotules entirely smooth, with thin shaft evidently bent to straight, notably variable in length ($28\text{--}56 \times 1.5\text{--}2\text{ }\mu\text{m}$, WAM Z29235/FW-POR 853;

$21\text{--}37 \times 1.5\text{--}2\text{ }\mu\text{m}$, WAM Z98322/FW-POR 863; $n = 25$ spicules measured per sample). Pseudorotules smooth ($8.7\text{--}23\text{ }\mu\text{m}$ in diameter) armed with long, acute hooks ($n = 4\text{--}5$). Gemmules subspherical, light brown (alcohol), exclusively sessile at the sponge basal portion, strictly adhering to the basal spongin plate in groups, sharing in part the gemmular cage of smooth oxeas. No free gemmules in the skeletal meshwork. Gemmular cage of abundant, smooth, stout oxeas (megascleres) tangentially arranged at the theca surface. Gemmular theca subspherical ($\sim 530\text{ }\mu\text{m}$ in diameter with cage, $\sim 340\text{ }\mu\text{m}$ without cage) of a single morph, trilayered, armed by a single layer of gemmuloscleres and enclosed by the spicular cage (cage and theca easily detachable from each other). Outer layer of spongin with small concavities to bubbles (resembling pneumatic chambers). Pneumatic layer ($23\text{--}26\text{ }\mu\text{m}$ in thickness) as chambered laminar spongin to form rounded small chambers and armed by scattered gemmuloscleres tangentially embedded. Inner layer with sublayers of laminar compact spongin. Foramen

Fig. 8 Biogeographic pattern of the genus *Corvospongilla* (20 recent species) in the Neotropical, Afrotropical and Oriental bioregions with enclaves in the Nearctic, Palearctic and Australasian bioregions. *Corvospongilla moochalabrensis* sp. n. from NW Australia (red) is

the first Australasian record of the genus. One Miocene fossil species (blue) is recorded from the north-western Nearctic. Emended after Manconi and Pronzato (2019)

single, apical with a short simple collar and aperture oriented upward in gemmular carpets. Gemmuloscleres spiny from strongyles to oxeas and strongyloxeas ($33\text{--}66 \times 3.5\text{--}9\text{ }\mu\text{m}$, WAM Z29235/FW-POR 853; $33\text{--}93 \times 9.3\text{ }\mu\text{m}$, WAM Z98322/FW-POR 863; $n=25$ spicules per each sample) straight to slightly bent with spines and tubercles of various sizes, more dense at tips; spines simple with acute tips, to large and ornate with apical microspines.

Molecular results

Full-length ITS sequences of 790–808 bp (incl. 5.8S and the flanking regions of 18S and 28S) were obtainable from *C. mesopotamica*, *C. lemuriensis* and *Corvospongilla* sp. 1 (Tanzania). For the remaining material only the minimalist barcodes (“5.8S-ITS2” and “ITS2-28S” cf. Erpenbeck et al. 2019) were successfully amplified. Here, the more than a century-old type material of *C. burmanica*, *C. caunteri*, *C. ultima*, *C. ultima* var. *spinosa*, and *C. lapidosa* could be amplified. These minimalist barcodes comprise lengths of 77 bp (5.8S-ITS2) and 99–101 bp (ITS2-28S), respectively. Amplification and sequencing of *C. thysi*, *C. zambesiana* and *C. seckti* (as *C. volkmeri*) was attempted,

but did not lead to sequences unambiguously identifiable as *Corvospongilla*. From the remaining comparative specimens (Table 1) no sequences could be obtained. The concatenated data set, restricted to both minimalist barcoding regions only, comprised 15 taxa and 207 characters of ITS2. Nine character positions were variable among the *Corvospongilla* spp. (four transitions, four transversions, one indel, see Fig. 7, also for genetic distances). In the phylogenetic reconstructions (Fig. 7) the sequences of *Corvospongilla* fall in three distinct clades with an unsupported relationship to each other. Inclusion/exclusion or choice of outgroup did not affect internal relationships of the *Corvospongilla* ingroup. *C. moochalabrensis* sp. n. displays a distinct ITS2 barcode and forms a clade with *C. ultima*. The molecular difference between *C. moochalabrensis* and *C. ultima* is a G–C transversion. The remaining (Asian) *Corvospongilla* species, i.e., *C. burmanica*, *C. caunteri*, *C. mesopotamica*, *C. lapidosa* and *C. siamensis* share a barcode and form a supported clade, likewise *C. lemuriensis* and the Tanzanian *Corvospongilla* sp. 1 are supported and distinctive (Fig. 7). The Median Joining network reconstruction of the 177 ingroup characters resulted in a linear, unbranched arrangement of the *Corvospongilla*

genotypes with the Australian and African/Madagascan species at either ends showing 1, respectively, 3 steps to the closest genotype from Asia (see Fig. 7).

Discussion

Corvospongilla moochalabrensis sp. n. from Australia is ascribed to the genus *Corvospongilla* on the basis of the comparative analysis of skeleton and gemmular morphology, and differs at a global level from all other known species of the genus in its unique combination of morphotraits. The new species is characterised by the traits ‘megascleres slender entirely smooth oxeas’, ‘microscleres abundant pseudobiotules with long hooks and curved shaft’, ‘sessile gemmules with well-developed chambered pneumatic layer armed by a single tangential layer of variably embedded gemmuloscleres’, and ‘spicular cage of slender smooth oxeas’.

It diverges from lineages of most bioregions (Fig. 8) due to its ‘megascleres smooth oxeas’ vs ‘megascleres stout strongyles variably ornate to smooth’ viz. Oriental (*C. bhavnagarensis*, *C. burmanica*, *C. lapidosa*, and *C. siamensis*), Afrotropical (*C. boehmii*, *C. lemuriensis*, *C. micramphidiscoides*, *C. scabriscipulis*, *C. sodenia*, *C. thysi*, *C. victoria*, and *C. zambesiana*), Palaearctic (*C. loricata* and *C. mesopotamica*), Nearctic (*C. becki*) and Neotropical (*C. seckti*) (Penney and Racek 1968; Manconi and Pronzato 2004, 2019; Ruengsawang et al. 2012).

Most species of the genus display a notably diverse morphological range and combinations of megascleres as ‘spiny oxeas, smooth oxeas, smooth strongyles, spiny strongyles, or a mix of these spicule types’ except for *C. moochalabrensis* (Penney and Racek 1968). However, the variable types of megascleres could be related to their morphofunctional roles and topographic distribution in the sponge body as (a) main skeletal spicules, (b) spicules belonging to the cage of gemmular theca, or (c) larval spicules. Moreover, in some cases details of morphotraits are unknown, e.g., gemmules are unknown in the Afrotropical *C. sodenia* and *C. zambesiana*, and gemmular cage of megascleres and larvae with their spicules are unknown for several *Corvospongilla* species.

In contrast the trait ‘pseudobiotules as skeletal microscleres’ is morphologically stable in all species, although these spicules are variable in abundance up to notably rare, and their morphometries and microtraits have a relatively narrow range. The trait ‘long curved hooks of pseudobiotules (microscleres)’ (Figs. 4B–D, 5A) rare in the genus is shared by the new species with three African species, i.e., *C. zambesiana* (Manconi and Pronzato 2009), *C. micramphidiscoides* (Manconi and Pronzato 2009) and *C. boehmii* (Penney and Racek 1968; Manconi and Pronzato 2009).

The most closely allied species are *C. ultima* and *C. caunteri* (India) sharing with *C. moochalabrensis* ‘megascleres entirely smooth oxeas’. However, megascleres of *C. ultima* and *C. caunteri* are ‘stout oxeas (15–20 µm thick) abruptly pointed’ (Penney and Racek 1968; Soota et al 1983) while in *C. moochalabrensis* they are ‘slender oxeas (2–14 µm thick) from abruptly pointed to fusiform’. As for other diagnostic traits, *C. moochalabrensis* with ‘abundant pseudobiotules (microscleres) with long curved hooks’, ‘gemmules sessile, armed by cage and with well-developed chambered pneumatic layer’, ‘single layer of tangential gemmuloscleres’ diverges from *C. ultima* and *C. caunteri* that are characterised by ‘rare pseudobiotules (microscleres) with short feebly curved hooks’, ‘free and/or sessile gemmules’, ‘absence of gemmular cage’ and ‘gemmular theca with feebly developed pneumatic layer armed by double layer of rare gemmuloscleres as stout spiny strongyles tangential on inner layer of theca’ (Penney and Racek 1968).

At the level of gemmular architecture the new species trait ‘sessile with trilayered theca and well-developed chambered pneumatic layer’ is exclusively shared with *C. lemuriensis* from Madagascar. The present record of ‘unusual gemmular architecture as a third gemmular morph’ confirms a new trait as an evolutionary novelty for the genus, i.e., ‘sessile with a well-developed pneumatic layer and spicular cage’.

In support of the morphological results, molecular distinction is given to all other *Corvospongilla* species analysed in this study, although only by one transition to *C. ultima*. The minimalist barcodes resulted in a short discriminating sequence and in turn enabled the comparison with century-old type material. The lack of molecular distinction between *C. burmanica*, *C. caunteri*, *C. mesopotamica*, *C. lapidosa* and *C. siamensis* with ITS2 may indicate a faster evolution of morphological traits among those Asian species than is accessible with this molecular marker (Erpenbeck et al. 2019, 2020 for similar findings among other freshwater sponge species).

The genus *Corvospongilla* was considered absent from Australia until now (Manconi and Pronzato 2008, 2019). The discovery of the new species enlarges the range of extant *Corvospongilla* species to include the Australasian Bioregion and indicates a wider biogeographic pattern of the genus in the southern hemisphere. However, spicular remains from the stomach contents of a freshwater turtle *Emydura subglobosa* (Kreff, 1876) were identified as *Corvospongilla caunteri* (QM G317009, unpublished record) from Policeman’s Crossing (13°35’11” S 130°38’28” E), Daly River Mission, Daly River in the Northern Territory, Welsh, M. (field coll.), Kennedy, J. (id.). New samples from the Daly River area and verification of this QM specimen will be fundamental to determining the geographic range of *Corvospongilla* in Australia.

The present record from Australia of the new species *C. moochalabrensis* increases the species number to 20 for the genus *Corvospongilla* (Manconi and Pronzato 2007, 2008, 2009, 2015, 2019; Van Soest et al. 2020). The genus is widespread with the exception of Antarctica and the Pacific (Oceanian) (Fig. 8), and is present in Palearctic ($n = 1$), Nearctic ($n = 2$), Neotropical ($n = 1$ widely spread), Oriental ($n = 6$), and Australasian ($n = 1$ present paper) bioregions, with the highest species richness in the Afrotropical Bioregion ($n = 9$) (Manconi and Pronzato 2019). Most species are extremely rare and have limited ranges i.e., endemic sensu stricto to a single hydrographic basin or a restricted area, e.g., type locality (Manconi and Pronzato 2004, 2019). At the global scale *Corvospongilla* shows a notably wide disjunct range. This biogeographic pattern better matches the vicariance versus the dispersal model and indicates a wide radiation, particularly in Afrotropical and Oriental bioregions. The morphological novelty of diverging gemmular architectures seems not to favour the species spreading widely (Manconi and Pronzato 2004, 2007, 2019).

The evolutionary success of *Corvospongilla*, in terms of radiation and geographic range, could be related to cryptobiosis and to the morphofunctional performance of asexual propagules, e.g., resistance to desiccation and hatchability for persistence and dispersal viz. ‘sessile gemmules without pneuma’, ‘sessile gemmules with pneuma’ and ‘free gemmules with pneuma’ (Manconi and Pronzato 2004, 2019; Manconi et al. 2004). These different functional morphs appear to fully perform their asexual reproductive and survival role in continental water with a wide range of climates and environmental conditions (Manconi and Pronzato 2016b). Unfortunately data on fossils are almost lacking (Pronzato et al. 2017).

In synthesis, the comparative study of significant representatives of *Corvospongilla* by molecular and morphological analysis, together with assessment of biogeographic patterns, yielded results on which to build a phylogenetic and phylogeographic tree. With the exception of *C. ultima*, all analysed *Corvospongilla* species fall into molecular clades resembling their distinct bioregions (Afrotropical, Oriental, Australasian), a pattern previously unexplored for freshwater sponges.

This new integrated assessment enlarges the geographic pattern of the genus *Corvospongilla* to Australia, and increases the number of species in the genus to 20. The spicular complement of strongyles and oxeas (in a variety of combinations) together with three gemmular morphs suggest that *Corvospongilla* is an ancient taxon. This appears to be supported by the notably disjunct biogeographic pattern of the genus, confirming it could be related to Gondwanan separation, although the enclave in the Nearctic Region

suggests that the spreading of this lineage in inland waters could be more ancient.

The current data highlight the problem of *Corvospongilla* systematics, biogeography and phylogenetic relationships in the evolutionary history of Spongillida (Manconi and Pronzato 2019) and supports the need for further in depth analyses.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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