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Taxonomy of freshwater sponges of Maharashtra, India, with illustrated descriptions and notes on ecology and habitats (Porifera: Spongillida: Spongillidae)

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Abstract

We present additional taxonomic descriptions, with Scanning Electron Microscopy (SEM) illustrations, field observations documented by colour photographs, and notes on habitats and ecology of *Corvospongilla ultima* (Annandale), *Eunapius crassissimus* (Annandale), *Stratospongilla bombayensis* (Carter), *S. gravelyi* (Annandale) and *S. indica* (Annandale) from recent sponge collections made in western Maharashtra, India. *Stratospongilla gravelyi* is rediscovered after a century, and along with it, *C. ultima* and *S. indica* are illustrated with SEM images for the first time, unequivocally differentiating these two species. Additional taxonomic, ecological data and illustrations of *Corvospongilla lapidosa* (Annandale), *Dosilia plumosa* (Carter), *Ephydatia meyeni* (Carter), *Eunapius carteri* (Bowerbank) and *Radiospongilla cerebellata* (Bowerbank) are also provided to supplement the previously published SEM illustrations. All ten spongillid species treated here were originally described from India and three of them are known to be endemic to the Indian region. Present study is the first re-examination of these Indian spongillid species using SEM, providing greater resolution of their important taxonomic characters and careful documentation of their habitats.

Key words: Porifera, Spongillidae, India, taxonomic descriptions, scanning electron microscopy, habitats, ecological notes

Introduction

Taxonomic studies on Indian freshwater sponges have a long history. These sponges were initially studied by Carter (1849; 1881; 1882) and Bowerbank (1863), but it was Annandale (1911) who first presented a comprehensive account of taxonomy and biology of all the freshwater sponges from this region. Penney & Racek (1968) later provided additional data for all freshwater sponges of the world during their revision. But both these works do not incorporate either SEM observations on spicules / gemmules or habitus images. Studies on freshwater sponges of India after Annandale are sparse and have been summarised previously (Jakhalekar & Ghate 2013). According to Soota (1991), the Indian region possesses 30 species of freshwater sponges in 10 genera of the family Spongillidae Gray. However, Manconi et al. (2013) recognise 28 species in 10 genera for this region. Spongilla lacustris Linnaeus and Trochospongilla pennsylvanica (Potts) were reported earlier from the Indian region (Annandale 1911) but were not considered by Manconi et al. (2013), probably due to the temperate range of the former and the disjunct distributional record of the latter species. Lack of subsequent records of these species from the Indian region after Annandale, obviously due to paucity of freshwater sponge workers in India, has only made this situation more problematic. This issue needs re-examination of the material of these two species studied by Annandale, collected respectively from Himalayan region and Travancore (now, Thiruvananthapuram, Kerala). We therefore presently consider the species number of freshwater sponges for the Indian region to be 28. Out of these, 10 species are endemic to India (Manconi et al. 2013).

We previously reported on the taxonomy of five freshwater sponges from Maharashtra State, India, including the descriptions based on scanning electron microscopy, field observations documented with colour photographs, and notes on the habitats and ecology of five species (see Jakhalekar & Ghate 2013). Here we provide similar information about five more species, and also additional data on the previously reported species.

Methods

A total of 176 sponge specimens were collected and studied, and observations from additional 100+ specimens were made in the field, from 51 localities in the western region of Maharashtra State of India (see Fig. 1 and Table 1). Geographic co-ordinates for localities were recorded using Google-Earth and the map of localities was prepared using DIVA-GIS version 7.5.0. Western Maharashtra primarily comprises the northern region of the Western Ghats of India, with a narrow coastal strip of Konkan region to the west and the Deccan plateau to the east. Western Ghats are considered to be one of the biodiversity hotspots of the world (Myers *et al.* 2000). This area receives most rainfall between June and September due to the south-west monsoon (Mani 1974).



FIGURE 1. Map of freshwater sponge localities from western Maharashtra, India. Symbol denotes the type of habitat and colour-code represents the number of freshwater sponge species found in that particular habitat. For example, reservoir type of habitat with one species is shown as circle marked with 'X' and filled with red colour.

Fifty-one localities with freshwater sponges from western Maharashtra were classified into five types of habitats, definitions of which broadly follow Williams *et al.* (2003). (i) Temporary Pools (Fig. 2A): mainly rainwater pools, strictly short-lived with distinct wet and dry phases, area not more than 25 m². (ii) Ponds (Fig. 2B): seasonal or permanent, natural or man-made lentic water-bodies with area between 25 m² and 2 ha. (iii) Fort Tanks (Fig. 2C): type of ponds located at an average altitude of about 1000 m a.s.l., with an average water temperature of 1-2 °C less than the low altitude ponds, low human disturbance, carved into basaltic rocks of hill forts, thus rich in substrata suitable for settlement and growth of sponges. Also, some physical and chemical properties of the water and relative abundance in micro-invertebrate fauna are different from that of the low altitude ponds (S. Padhye and M. Kulkarni, pers. comm.). (iv) Reservoirs (Fig. 2E): permanent lentic water-bodies with areas greater than 2 ha, natural or man-made. (v) Rivers (Fig. 2D): natural, large lotic water-bodies.



FIGURE 2. Types of Habitats. A—Temporary Pool. B—Pond. C—Fort Tank. D—River. E—Reservoir.

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ıavla, Pune	18.7766306, 73.4268611	RS							+				1
thane, Raigad	18.52088, 73.18314	RV									+		1
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nar, Pune	19.119995, 74.095429	RV					+						1
hoj, Ahmadnagar	18.93073, 74.2626	RV							+				1
het, Pune	18.386176, 73.618027	RV		+							+	+	e
et, Pune	18.642, 73.751	RV					+						1
1a, Satara	17.7972667, 73.8217028	RV					+		+	+	+		4
LITIES PER SPECIES			6	3	3	4	24	7	18	11	4	4	

TABLE 1. (Continued)

The majority of the sponge collections were made between 2011 and 2015 from the shallow peripheral areas of the water-bodies. Dry seasons (summers) were mostly preferred for collections, as it was easier to collect the sponges from deeper zones of the water-beds by wading and the presence of mature gemmules in good number was also ensured. Sponges were photographed in the field with a Canon PowerShot A2100 IS camera and then removed carefully along with gemmules from the substrata using a scalpel. Sponges were fixed in 4% formaldehyde and later stored in 70% ethanol; some specimens were preserved dry.

Skeletons of dry sponges were examined and photographed by Light Microscopy (LM) under a stereo-zoom trinocular microscope (Leica MZ6), assembled with a Canon PowerShot S50 camera. Images taken at different focal planes were later stacked using CombineZM freeware. Spicules and gemmules were studied as described earlier (Jakhalekar & Ghate 2013). Mature spicules (n = 25, of each type) and gemmules (n = 10) were measured under LM, using a calibrated ocular micrometer (Erma and Ernst Leitz Wetzlar); in addition, spicules and gemmules were also measured from Scanning Electron Micrographs. The measurements are given as (minimum-average-maximum).

Diagnostic characters such as the skeletal architecture, shape and measurement of spicules and gemmular structure were noted, as these are critical in identification of freshwater sponges (Manconi & Pronzato 2002, 2008). Identification was mainly based on comparison with the original descriptions of species and the comprehensive works by Annandale (1911) and Penney & Racek (1968). Synonymies for all species studied here have been given in detail by Annandale (1911), Penney & Racek (1968) and Manconi & Pronzato (2002), and hence are not repeated here. Terminology follows Boury-Esnault & Rützler (1997) and Manconi & Pronzato (2002).

Taxonomic Descriptions

Additional taxonomic descriptions with colour photographs and SEM illustrations, geographic distribution at global scale, Indian records, and taxonomic remarks about five species, *Corvospongilla ultima* (Annandale, 1910), *Eunapius crassissimus* (Annandale, 1907), *Stratospongilla bombayensis* (Carter, 1882), *S. gravelyi* (Annandale, 1912) and *S. indica* (Annandale, 1908) are presented below.

Phylum Porifera Grant, 1836

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Perez & Boury-Esnault, 2012

Order Spongillida Manconi & Pronzato, 2002

Family Spongillidae Gray, 1867

Genus Corvospongilla Annandale, 1911

[Type Species: Spongilla loricata Weltner, 1895]

The genus *Corvospongilla* is distributed in Africa, Asia (Iraq, Indian sub-region, Thailand), north and south America (Manconi & Pronzato 2002, 2004, 2015; Ruengsawang *et al.* 2012; Pinheiro *et al.* 2013). Manconi & Pronzato (2004) have recently given a synopsis of this genus. *Corvospongilla* is one of the species-rich genera of Spongillidae currently including 18 species (Ruengsawang *et al.* 2012; van Soest *et al.* 2016), five of which are known from the Indian freshwaters. Four species of *Corvospongilla*, namely *C. bhavnagarensis* Soota, Pattanayak & Saxena, 1983, *C. caunteri* Annandale, 1911, *C. lapidosa* (Annandale, 1908) and *C. ultima* (Annandale, 1910), are reported to be endemic to India (Annandale 1911; Penney & Racek 1968; Soota *et al.* 1983; Soota 1991; Manconi & Pronzato 2002; Jakhalekar & Ghate 2013; Manconi *et al.* 2013).

Corvospongilla ultima (Annandale, 1910)

Fig. 3, Table 1.

Material. Five specimens were studied. For localities see Table 1.

Description. Encrusting sponge growing to a medium diameter of about 10 cm, but never greater than 1 cm in thickness. Colour in life deep green to brown; dry specimens appear light grey to beige. Surface somewhat rough but never bearing any spicular projections (Fig. 3A). Oscula few, small but conspicuous, not raised above the surface, there may however appear a small collar-like structure surrounding them. Sometimes radiating furrows are also seen starting near the oscula (Fig. 3B), but these are not prominent. Skeleton formed by large number of megascleres and considerable amount of spongin, thus the consistency is quite dense and hard. Sponge often forming a membrane-like structure at the base (Fig. 3C).

Megascleres stout, near straight to gently curved, smooth oxeas $(228-\underline{263}-306 \times 17-\underline{18}-21 \mu m)$ (Figs 3D,E), some have a sparsely roughened surface, as seen under SEM (Fig. 3F). Spicules, for most of their length, cylindrical but tapering at the tips. Microscleres micropseudobirotules $(21-\underline{26}-35 \times 2-\underline{2.2}-2.6 \mu m)$ (Figs 3K,L), with completely smooth slender shaft and pseudorotules (diameter: $13-\underline{14}-16 \mu m$) bearing 6–8 curved spines. The pseudorotules are completely smooth, umbonate with shaft not projecting beyond them. Gemmuloscleres nearly straight to curved, regularly spined strongyles of variable sizes $(25-\underline{41}-54 \times 5-\underline{7.5}-11 \mu m)$ (Figs 3I,J).

Gemmules moderate in number, found singly, attached to substratum as well as free in the sponge, usually concentrated from the centre to the base, never present on surface. Attached gemmules at the base of sponge enclosed in cage made of spicules similar to megascleres ($120-124 \times 15-18 \mu m$) (Figs 3G,H), often forming a continuous mat of dark brown to black colour, whereas free gemmules appear off-white (Fig. 3A inset). Spicular cage not attached to gemmular theca. Gemmules spherical or sub-spherical ($361-390-443 \mu m$) (Fig. 3M) with theca composed of outer layer, moderately developed pneumatic layer, and inner layer (Fig. 3N). Gemmuloscleres found embedded at the base of granular pneumatic layer, parallel to inner layer of gemmular theca, some also seen at the surface of gemmule. A single foramen and short cylindrical foraminal tube present, which appears to be protruding slightly due to presence of crater-like depression surrounding the foramen (Fig. 3O).

Distribution. Endemic to India (Penney & Racek 1968; Manconi & Pronzato 2002; Ruengsawang *et al.* 2012; Manconi *et al.* 2013).

Remarks. This species was originally described as *Spongilla (Stratospongilla) ultima* from Cape Comorin (now, Kanyakumari), Tamilnadu, India, by Annandale (1910). Later, when revising *Corvospongilla*, Annandale (1912) included the species *ultima* under it (genus transfer), and additionally described a variety from Koyna valley, Maharashtra, namely *C. ultima* var. *spinosa*. This variety, however, after examining the type slides, was synonymised with its parent species by Penney & Racek (1968). Soota (1991) subsequently recorded Rajasthan as an additional locality for the species.

Characters of our material of *C. ultima* collected from western Maharashtra match well those described earlier (Annandale 1910; Annandale 1911; Annandale 1912; Penney & Racek 1968). *Corvospongilla ultima* can be clearly distinguished from its Indian endemic congener, *C. lapidosa* (Annandale), as the megascleres of the former species are stout oxeas while those of the latter species are stout strongyles. Megascleres of this species have been known previously to be entirely smooth oxeas, but in our study using higher resolution SEM examination it is clear that the surface of megascleres is sparsely and very minutely roughened (Fig. 3F). This minor character might have been overlooked in the past as it cannot be observed using light microscopy. Type material of *C. ultima* needs to be studied using SEM to test the validity of this character.

Genus *Eunapius* Gray, 1867

[Type Species: Spongilla carteri Bowerbank, 1863]

The Genus *Eunapius* is cosmopolitan in distribution (Manconi & Pronzato 2002) and presently 17 species are assigned to it (van Soest *et al.* 2016). Penney & Racek (1968) redefined this genus and Manconi *et al.* (2008) provided a comprehensive study of species of *Eunapius* from the continent of Africa. Four species of *Eunapius* are known from India, of which *E. calcuttanus* (Annandale, 1911) (with an unconfirmed report from Myanmar) and *E.*

geminus (Annandale, 1911) are considered restricted to the India (Annandale 1911; Penney & Racek 1968; Soota 1991; Manconi & Pronzato 2002; Manconi *et al.* 2008; Jakhalekar & Ghate 2013; Manconi *et al.* 2013).

Eunapius crassissimus (Annandale, 1907)

Fig. 4, Table 1.

Material. Three specimens were collected and field observations of several additional dried specimens were also noted; live sponge not seen. For localities see Table 1.

Description. Sponge forming encrustations of moderate to large size with a thickness of about 1–2 cm. Colour of dried specimens ranges from light grey to beige. Surface overall even, not forming conspicuous projections. Oscula round, small but conspicuous, numerous and not elevated; obscure and not well defined furrows are sometimes seen on surface, usually near oscula (Fig. 4A). Skeleton dense and of considerable strength, composed of multispicular tracts with appreciable amount of spongin, bundles of spicules make skeletal meshes at the surface with large roughly circular cavities in it (Fig. 4B); skeleton near base mainly isotropic meshwork of unispicular tracts, cavities of which hold the grouped gemmules (Fig. 4C).

Megascleres stout, cylindrical, almost straight to slightly curved and entirely smooth strongyles $(230-\underline{261}-311 \times 19-\underline{20.5}-23 \ \mu\text{m})$ (Fig. 4E). Very rarely immature megascleres are also found as slender oxea. Microscleres absent. Gemmuloscleres moderately spined, cylindrical, straight to slightly curved strongyles, sometimes terminating in broad but pointed end, spines near ends curved towards centre (66-<u>86</u>-104 X 4-<u>4.9</u>-6.2 μ m) (Figs 4F,G).

Gemmules moderate in number, concentrated near base of sponge but never attached to substratum, groups of 4–6 gemmules bound together by a continuous pneumatic layer are found singly in the cavities of skeletal network ($665-\underline{795}-974 \times 541-\underline{578}-623 \mu m$) (Figs 4C,D). Gemmules roughly spherical (Figs 4H,I) with a well developed tri-layered theca, inner layer distinct for every gemmule in group (diameter measured at inner layer: $191-\underline{235}-282 \mu m$); whereas thick, cellular pneumatic layer and outer layer are continuous and thus hold individual gemmules together (Figs 4J–L). Outer layer shows ornamentation due to presence of large polygonal air spaces of underlying pneumatic layer, with gemmuloscleres arranged sparsely and tangentially. Each gemmule in the group has a single foramen that opens out by means of a foraminal tube, which is characteristically bent (Fig. 4J).

Distribution. India, tropical SE Asia and Australia (Penney & Racek 1968; Racek 1969; Masuda 2004; Manconi *et al.* 2008; Manconi *et al.* 2013).

Remarks. *Eunapius crassissimus* can be easily diagnosed by its smooth strongyle megascleres and regularly spined strongyle gemmuloscleres. These characters differentiate *E. crassissimus* from its commonly occurring congener, *E. carteri* (Bowerbank), as the latter species possesses large smooth oxeas as megascleres and short smooth oxeas as gemmuloscleres. In the field, *E. crassissimus* can be recognised by its grouped gemmules and peculiar form of skeleton which is strikingly different from *E. carteri*.

Annandale (1907a) described *E. crassissimus* from Museum tank, Calcutta (now, Kolkata), India, and also noted some interesting observations on the biology of this species (Annandale 1907b). Soota (1991) further reported it from Orissa (now, Odisha) and Assam. As per the latest checklist by Ghate (2012), *E. crassissimus* has never been reported from Maharashtra State. Therefore this becomes an addition to the freshwater sponge fauna of this region and the first report of this sponge from western India. It is interesting to note that Annandale, who extensively surveyed the Igatpuri region and reported several freshwater sponge species, more than 100 years ago, did not document *E. crassissimus* from this area. All our specimens and observations of this species happen to be from the freshwater-bodies of Igatpuri. It is likely that *E. crassissimus* may have dispersed to this region sometime during the last century.

Masuda (2004) provided SEM images of Cambodian material of E. crassissimus. Our material from India, when studied under SEM, shows similar structures, however the spines on gemmuloscleres of our material appear more prominent and curved. This variation might also be due to the difference in maturity of spicules and the environment in which the sponge grows.



FIGURE 3. *Corvospongilla ultima*. A—Habitus; inset shows free (off-white) and sessile (black) gemmules. B—Surface of the sponge, note the radiating furrows. C—Base of the sponge. D, E—Megascleres (SEM). F—Finely roughened surface of megasclere (SEM). G, H—Spicules of the gemmular cage (SEM). I, J—Gemmuloscleres (SEM). K, L—Microscleres (SEM). M—Gemmule (SEM). N—Cut gemmule (SEM). O—Close-up of cut gemmule showing gemmuloscleres embedded at the base of granular pneumatic layer with foraminal tube (SEM). Scale: A—2 cm; B, C—5 mm; D, E—50 µm; F—5 µm; G, H—20 µm; I—5 µm; J—10 µm; K, L—10 µm; M, N—100 µm; O—20 µm.



FIGURE 4. *Eunapius crassissimus*. A—Habitus. B—Surface of the sponge. C—Base of the sponge. D—Vertical section through the skeleton, with grouped gemmules near base. E—Megasclere (SEM). F, G—Gemmuloscleres (SEM). H, I—Grouped gemmules (SEM). J—Cellular pneumatic layer and foraminal tube (SEM). K, L—Cut gemmules (SEM). Scale: A—2 cm; B-D—5 mm; E—50 µm; F, G—10 µm; H, I—100 µm; J—20 µm; K, L—100 µm.

Genus Stratospongilla Annandale, 1909

[Type Species: Spongilla bombayensis Carter, 1882]

The genus *Stratospongilla* was proposed as a subgenus of *Spongilla* Lamarck by Annandale (1909). Later, in their comprehensive work, Penney & Racek (1968) redefined and elevated it to full generic rank. Manconi & Pronzato (2002) have further redefined this genus. *Stratospongilla* is known from Africa, Asia and Australia (Penney & Racek 1968; Racek 1969; Manconi & Pronzato 2002). Bonetto & Ezcurra de Drago (1967; 1968; 1973, as cited in Muricy *et al.* 2011) and Ezcurra de Drago (1978) described a few species and also included some under *Stratospongilla* from the Neotropic, but all these have now been transferred to other genera in the family Potamolepidae Brien (Volkmer-Ribeiro 1970; Manconi & Pronzato 2002; Muricy *et al.* 2011; Manconi *et al.* 2012). *Stratospongilla penneyi* Harrison, 1979 was described from North America (Harrison 1979) but the validity and taxonomic status of this species needs further study (Manconi & Pronzato 2016a). Twelve species are currently recognised under this genus (van Soest *et al.* 2016), of which four are found in Indian freshwaters: *S. bombayensis* (Carter, 1882), *S. gravelyi* (Annandale, 1912), *S. indica* (Annandale, 1908) and *S. sumatrana* (Weber, 1890). *Stratospongilla gravelyi* is considered endemic to India (Annandale 1911; Penney & Racek 1968; Soota 1991; Manconi & Pronzato 2002; Manconi & Pronzato 2016a). Twelve species are currently recognised under this genus (van Soest *et al.* 2016), of which four are found in Indian freshwaters: *S. bombayensis* (Carter, 1882), *S. gravelyi* (Annandale, 1912), *S. indica* (Annandale, 1908) and *S. sumatrana* (Weber, 1890). *Stratospongilla gravelyi* is considered endemic to India (Annandale 1911; Penney & Racek 1968; Soota 1991; Manconi & Pronzato 2002; Manconi *et al.* 2013).

Stratospongilla bombayensis (Carter, 1882)

Fig. 5, Table 1.

Material. Seventeen specimens were collected and studied. Observations were also noted on numerous live examples in the field. For localities see Table 1.

Description. Encrusting sponge covering large area of substratum, thickness never greater than 4–5 mm. Colour in life ranges from light to dark green; dry sponges appear white, grey, pale yellow to beige and even black. Surface fairly even, not forming conspicuous structures; however, when examined closely, shows spicules projecting singly, thus may appear velvety; conspicuous radiating furrows often seen on surface of large sponges in the vicinity of minute oscula (Figs 5A,B). Skeleton moderate in strength and brittle, ectosome consisting of uniform but vague network of megascleres; choanosomal region shows anisotropic reticulation with distinct paucito multi-spicular vertical tracts connected by horizontal secondary tracts of megascleres; skeleton at base formed of uniform unispicular reticulation, cavities of which hold gemmules (Figs 5D–F). Spongin not prominent.

Megascleres slender, almost straight or very slightly curved, spined except at their ends or sometimes entirely smooth oxeas with extremely pointed tips (289–<u>325</u>–433 X 10.4–<u>12.5</u>–14.5 μ m) (Figs 5G–J). Spines on megascleres minute with broad base and sharp tips often curved towards middle of spicule (Fig. 5J). Microscleres absent. Gemmuloscleres of two types: stout, short, entirely spined, straight to moderately curved (sausage shaped) strongyles (42.6–<u>42.8</u>–43 X 11.5–<u>11.6</u>–11.7 μ m) (Figs 5K,L), spines stubby with broad base and blunt ends; and slender, longer, entirely spined, straight to curved oxeas (46–<u>49</u>–54 X 3.1–<u>3.3</u>–3.5 μ m) (Figs 5M,N), spines long, slender and erect.

Gemmules abundant in number, found singly, fixed to substratum as well as free in the skeleton, mostly confined to the basal region (Figs 5C,E,F), spherical to hemi-spherical with tri-layered theca. Outer layer off-white in colour, about spherical, flattened at the base to facilitate firm adhesion to the substratum, with spined strongyle gemmuloscleres embedded horizontally as well as placed tangentially at the surface; a few megascleres may also be found in association with it (Figs 5O,Q). Pneumatic layer not well defined, air spaces not evident, formed of ill-organised spongin (Figs 5T,U) with spined oxea gemmuloscleres embedded mostly radially, some at an angle and a few even horizontally at the surface (Figs 5P,R). Inner layer distinct. Sometimes a carpet of fixed gemmules (641–661 μ m) can be found on substratum if the skeleton of dried sponge has fallen off (Fig. 5C). Free gemmules (254–310 μ m) found in the skeleton lack outer layer and are thus deficient in spined strongyle gemmuloscleres. Gemmular foramen single with a well-developed, long, cylindrical, almost straight foraminal tube (Figs 5S,T).

Distribution. India and South Africa (Penney & Racek 1968; Manconi & Pronzato 2002; Manconi et al. 2013).



FIGURE 5. *Stratospongilla bombayensis*. A, B—Habitus. C—Carpet of gemmules. D—Surface of the sponge. E—Base of the sponge. F—Vertical section through the skeleton showing vertical spicular tracts and gemmules near the base. G, H—Megascleres (SEM). I—Smooth tip of megasclere (SEM). J—Spiny shaft of megasclere (SEM). K, L—Gemmuloscleres, spined strongyles (SEM). M, N—Gemmuloscleres, spined oxeas (SEM). O—Outer membrane of gemmule with tangential spined strongyle gemmuloscleres (SEM). P—Pneumatic layer with spined oxeas gemmuloscleres (SEM). Q—Sessile gemmule, with outer later (SEM). R—Free gemmule, without outer layer (SEM). S—Gemmular foramen (SEM). T—Foraminal tube and pneumatic layer without discernible air-spaces (SEM). U—Cut gemmule, without outer layer (SEM). Scale: B—2 cm; D-F—5 mm; G, H—50 µm; I, J—10 µm; K—5 µm; L—10 µm; M, N—10 µm; O—20 µm; P—10 µm; Q—100 µm; R—50 µm; S—10 µm; T—20 µm; U—100 µm.

Remarks. Carter (1882) originally described this sponge as *Spongilla bombayensis* from the Islands of Bombay, India. Later records from India include Igatpuri, Khed (Pune) (both from Maharashtra), Bangalore (Karnataka), Naukuchia (Uttar Pradesh) and Rajkot (Gujarat) (Annandale 1911; Soota 1991). Annandale (1911) also mentions having received specimens of this species from Natal (South Africa). The type locality of *S. bombayensis* species, i.e. Mumbai, has now grown into an extremely populated metropolis and many freshwater habitats have deteriorated. Our material from different localities (see Table 1), of which Lohgad Fort and Igatpuri are the closest to the type locality at distances of 75 and 100 km respectively, represent the typical form of the species as described by Carter (1882), Annandale (1911), Penney & Racek (1968) and Manconi & Pronzato (2002).

Manconi & Pronzato (2002) redescribed *S. bombayensis* and provided SEM images of the holotype. Our material shows similar ultra-structure of spicules and gemmules, and also confirms the presence of spined oxeas in the gemmular theca as true gemmuloscleres and not as microscleres as contemplated earlier (Manconi & Pronzato 2002).

Morphological similarities between *S. bombayensis* and *S. sumatrana* (Weber, 1890) are intriguing and have been discussed in detail by Penney & Racek (1968). These authors have pointed out the possibility that further detailed work on this issue may even necessitate the synonymy between these two species of *Stratospongilla*. To address the variation found in *S. sumatrana*, Annandale (1919) had named some varieties but later Penney & Racek (1968) resurrected var. *indica* and var. *gravelyi* back to full species rank and suggested the inclusion of var. *centralis* under *S. indica* and retention of var. *rivularis* under *S. sumatrana*. Manconi *et al.* (2013) also reported the presence of several ecomorphs in *S. sumatrana*. In spite of the study of holotype of *S. bombayensis* (Manconi & Pronzato 2002) its distinctness from *S. sumatrana* needs to be examined; molecular work might resolve this issue.

Stratospongilla gravelyi (Annandale, 1912)

Fig. 6, Table 1.

Material. Six specimens were studied, which includes material collected near the type locality of this species. Many small encrustations were also observed near the type locality but were not collected. For localities see Table 1.

Description. Sponge forming small to medium encrustations with thickness of about 2–3 mm. Colour in life bright green; dry sponges yellow to beige. Surface even, not showing any obvious spicular projections, with branched radiating furrows. Oscula inconspicuous (Figs 6A–C). Skeleton not very dense, brittle and formed of uniform reticulation of uni- to pauci-spicular tracts (Figs 6D,E). Spongin not prominent.

Megascleres slender to near-robust, straight to gently curved, moderately but conspicuously spined oxeas with sharp tips $(201-\underline{222}-245 \times 11.4-\underline{13.2}-15.6 \ \mu\text{m})$ (Figs 6G,H). Spicules cylindrical for most of their length but tapering at the ends. Spines on megascleres short, with broad base and sharp tips, sparse in the middle but denser near the ends of the spicule, those in middle erect whereas those near ends curve towards tip of spicule; incipient spines seen in immature spicules. Microscleres absent. Gemmuloscleres of two types: Strongyles (29.2-<u>29.5</u>-29.9 X 10.2-<u>10.5</u>-10.8 μ m) stout, short, straight, curved to sometimes forming a wide C-shaped arc, densely spined on convex surface and tips, spines adpressed to the surface, never erect, smooth on concave surface (Figs 6I,J). Oxeas (50-<u>56</u>-65 X 3.9-<u>4.3</u>-4.9 μ m) slender, longer, near-straight to gently curved, entirely spined, spines broad and somewhat stubby, also showing roughened surface due to extremely minute spines (Figs 6K,L).

Gemmules moderate in number, found singly, fixed to substratum (sessile) as well as free in skeleton, mostly at the base, spherical to sub-spherical with a well-developed tri-layered theca. Outer layer of gemmules mostly dark brown or black, (Fig. 6F), about spherical with flat base attached firmly to the substratum, with spined strongyle gemmuloscleres embedded horizontally in multilayer in compact spongin (Figs 6N–Q). Pneumatic layer considerably developed, with irregular air spaces with spined oxea gemmuloscleres embedded mostly radially, some at an angle and some horizontally at the surface (Figs 6R–T). Inner layer well recognisable. Sessile gemmules (783–<u>786</u>–790 μ m) were rare but free gemmules (376–<u>393</u>–409 μ m) were relatively abundant. Free gemmules in the skeleton are without outer layer and spined strongyle gemmuloscleres. Single gemmular foramen present with a straight, moderately long, cylindrical foraminal tube (Fig. 6U). Foramen of fixed gemmule opens laterally (Fig. 6Q).

Distribution. Endemic to the Western Ghats of Maharashtra, India (Penney & Racek 1968; Manconi *et al.* 2013; present study)

FIGURE 6. *Stratospongilla gravelyi*. A-C—Habitus. D—Surface of the sponge. E—Base of the sponge. F—Sessile gemmule under light microscope, with outer layer. G, H—Megascleres (SEM). I, J—Gemmuloscleres, spined strongyles (SEM). K, L—Gemmuloscleres, spined oxeas (SEM). M—Gemmuloscleres (LM). N—Outer membrane of gemmule with tangentially embedded spined strongyle gemmuloscleres (SEM). O—Section through outer membrane of gemmule, with outer layer and part of substratum (SEM). Q—Section through outer membrane of sessile gemmule, with outer layer and part of substratum (SEM). Q—Section through outer membrane of sessile gemmule (SEM). R—Free gemmule, without outer layer (SEM). S—Cut gemmule, without outer layer (SEM). T—Details of pneumatic layer (SEM). U—Foraminal tube (SEM). Scale: A—2 cm; D, E—5 mm; F—500 µm; G—20 µm; H—50 µm; I, J—5 µm; K, L—10 µm; M—20 µm; N—50 µm; O—20 µm; P-S—100 µm; T—20 µm; U—50 µm.

Remarks. This species was originally described as *Spongilla (Stratospongilla) gravelyi* Annandale, 1912 from R. Koyna at Taloshi, Satara, and Maharashtra, India. Our material of *S. gravelyi* from localities in the Western Ghats of Maharashtra (see Table 1), the closest one—R. Venna at Medha, Satara located at less than 15 km distance from the present day Taloshi village, represents typical morphological characters described by Annandale (1912) and Penney & Racek (1968). Since the original description of *S. gravelyi* (Annandale 1912) there have been no further published records of this species and it appears that no one has seen this rare sponge in more than 100 years. Present study can therefore be considered as the rediscovery of *S. gravelyi*. With the new locality data, it extends the known range of this species in the Western Ghats of Maharashtra.

Photographs of sponges and SEM images of spicules and gemmules of S. gravelyi are presented here for the first time. Some fine morphological characters like the spiny nature of megascleres and gemmuloscleres, the ultrastructure of outer and pneumatic layer of gemmular theca and the arrangement of two different kinds of gemmuloscleres therein, are better revealed with SEM. Better resolution of these morphological characters is essential in differentiating S. gravelyi from its commonly occurring congener S. bombayensis and the other Indian species of Stratospongilla. Megascleres of S. gravelvi are spined oxeas but are overall more robust than those of S. bombayensis. Spines on megascleres of S. gravelvi are relatively sparse in the middle, denser near the ends, curve towards the tips of the spicule, whereas those in S. bombayensis are relatively denser in the middle, curved towards the middle of the spicule; the tips of the spicule are smooth. Spines on the convex surface of the strongyle gemmuloscleres of S. gravelyi, though faint, can be observed using LM (Fig. 6M), and have been documented previously (Annandale 1912). These adpressed spines are found on the convex surface and at the tips of the spicule, whereas the concave surface is completely smooth. This character in the strongyle gemmulosclere distinguishes S. gravelyi from its Indian congeners, S. bombayensis and S. indica, which have strongyle gemmuloscleres entirely covered with stubby and erect spines. The multi-layered horizontal arrangement of strongyle gemmuloscleres in the compact spongin of outer layer of gemmular theca is also an interesting character in S. gravelvi. The other type of gemmulosclere of S. gravelyi, i.e. spined oxea, shows micro-spined surface in addition to the regular blunt spines. The oxea gemmuloscleres of S. bombayensis are with longer, erect and relatively sharp spines but smooth surface. The radial arrangement of spined oxea gemmuloscleres in the pneumatic layer is similar to that of S. bombayensis. There are differences in the structure of the pneumatic layer. Stratospongilla gravelyi shows a better organised pneumatic layer with irregular but recognisable air spaces therein, whereas that of S. bombayensis is rather ill-organised and composed of spongin without discernible air spaces.

Stratospongilla indica (Annandale, 1908)

Fig. 7, Table 1.

Material. Six specimens were collected and studied, which includes material collected near the type locality of this species. Large and numerous encrustations were also observed and studied in the field. For localities see Table 1.

Description. Sponge forming large encrustations with thickness not greater than 2–3 mm. Colour in life bright to deep green, dry encrustations whitish or pale green (Figs 7A,B). Surface grossly even, but sometimes appears velvety due to the skeletal spicules projecting perpendicularly and singly. Oscula not very conspicuous but found in the centre of the branched radiating furrows which are prolific (Fig. 7C). Skeleton moderately strong but brittle, with uniform network of uni- to pauci-spicular tracts of megascleres joined together by very sparse spongin (Figs 7D–F).

Megascleres slender, almost straight to gently curved, entirely spined, cylindrical strongyles ($193-\underline{207}-254 \times 11.4-\underline{12.7}-14.5 \mu m$) (Fig. 7G). Spines in median region of megascleres relatively sparse, strong, erect and comparatively long, whereas those near ends denser, short and inclined towards tips of the spicule (Fig. 7H). Microscleres absent. Two kinds of gemmuloscleres present. Strongyles ($37-\underline{42}-47.5 \times 8.2-\underline{10.4}-11.6 \mu m$) stout, short, straight to gently curved, sometimes forming knob-like structure at the ends, entirely spined with spines little denser at tips, spines erect and stubby (Figs 7I–K). Oxeas ($50-\underline{54}-56 \times 3.6-\underline{4.1}-4.7 \mu m$) slender, longer, almost straight to curved, entirely spined, spines erect and considerably sharp, surface roughened because of sparse, extremely minute spines (Figs 7L,M).

Gemmules moderate in number, found singly, adhering to substratum (sessile) (diameter: about 570 μ m) as well as free (359–<u>411</u>–430 μ m) in skeleton, mostly found near base, spherical, with tri-layered theca. Outer layer of

FIGURE 7. *Stratospongilla indica*. A, B—Habitus. C—Radiating furrows with pores. D—Close-up of the surface of the sponge. E—Base of the sponge. F—Section through the skeleton. G—Megasclere (SEM). H—Tip and shaft of megasclere (SEM). I-K—Gemmuloscleres, spined strongyles (SEM). L, M—Gemmuloscleres, spined oxeas (SEM). N—Sessile gemmule, with outer layer (SEM). O—Free gemmule, without outer layer (SEM). P—Cut gemmule, without outer layer (SEM). Q—Details of pneumatic layer (SEM). R—Gemmular foramen (SEM). Scale: B—2 cm; D-F—5 mm; G—20 µm; H—10 µm; I—5 µm; J-M—10 µm; N–P—100 µm; Q, R—20 µm.

gemmule dark brown to black, near-spherical with flattish base in contact with the substratum, with spined strongyle gemmuloscleres embedded horizontally (Fig. 7N); pneumatic layer moderately developed, with obscure irregular air spaces with spined oxea gemmuloscleres embedded mostly radially, a few found horizontally at the surface (Figs 7O–Q); inner layer thin but recognisable. Free gemmules often without the outer layer and thus do not possess spined strongyle gemmuloscleres. Single gemmular foramen present, with a short and straight foraminal tube (Figs 7P,R).

Distribution. Thailand, India, Africa (Penney & Racek 1968; Manconi & Pronzato 2002; Manconi *et al.* 2013) **Remarks.** Originally described as *Spongilla indica* Annandale, 1908 from R. Godavari at Nasik (now, Nashik), Maharashtra, India, this species is also known from Chakradharpur, Chota Nagpur and Igatpuri (Annandale 1919; Soota 1991). Our material of this species from Igatpuri (located at about 40 km distance from R. Godavari at Nashik), and Pune exhibit typical characters as described earlier by Annandale (1908; 1911) and Penney & Racek (1968).

Megascleres of *S. indica* are very distinct, spined strongyles, based on which the species can be easily differentiated from its Indian congeners *S. bombayensis* and *S. gravelyi*, which possess spined oxeas. This first SEM study of *S. indica* also reveals some minute characters, like shape and pattern of spines on megascleres and gemmuloscleres, nature and ultra-structure of pneumatic layer and foraminal tube of the gemmules, etc. Gemmuloscleres of *S. indica*, when studied under SEM, appear morphologically closer to those of *S. bombayensis* and differ from *S. gravelyi* as discussed before (see remarks for *S. gravelyi*). Gemmules of *S. indica* show similarity at ultra-structural level to that of *S. bombayensis* and *S. gravelyi*, but the pneumatic layer in *S. indica* appears somewhat intermediately developed when compared with that of the other two species; also shape of the foraminal tube of *S. indica* is barely different from that of the other two species.

Additional information on following five freshwater sponge species previously described in Jakhalekar & Ghate (2013) is provided here.

Corvospongilla lapidosa (Annandale, 1908)

Figs 8A-C, Table 1.

Material. Twenty-two specimens were collected and studied, which include material from the type locality of this species. In addition, several encrustations were also observed in the field. For localities see Table 1.

Description. Sponge forming large and numerous encrustations with surface invariably and conspicuously hispid and mostly conulose in larger specimens. Conules formed of large number of megascleres and measure up to 2–3 mm in height. Colour in life off-white, grey, brown, reddish-brown, very rarely green but restricted near the surface. Few noticeable oscula (diameter 4–6 mm) along with innumerable small pores observed at the surface of large sponges. Shallow and ill-defined furrows also seen sometimes at the surface. Skeleton thick, strong and of almost stony consistency. Spongin very sparse. Basal membrane evident.

Megascleres smooth strongyles $(271-\underline{295}-319 \times 23-\underline{27}-30 \ \mu\text{m})$. Microscleres micropseudobirotules (about 37 X 1.8 μm ; diameter of pseudorotules: 9.4–9.6–9.8 μm). Gemmuloscleres spined strongyles (about 48 X 6 μm). (For illustrations see Figs 14 & 15 in Jakhalekar & Ghate 2013.)

Gemmules attached to substratum as well as free in the skeleton but always concentrated near the base. Fixed gemmules appear dark brown to black, free gemmules off-white to pale yellow (diameter: about $360-412 \mu m$).

Distribution. Endemic to India (Penney & Racek 1968; Manconi & Pronzato 2002; Ruengsawang *et al.* 2012; Manconi *et al.* 2013).

Remarks. *Corvospongilla lapidosa* was originally described from Igatpuri, Nasik (now, Nashik), Maharashtra, India with an additional record from R. Godavari at Nashik (Annandale 1908 & 1911). Later Indian reports are from Pulta (W Bengal), Azi Dam, Rajkot (Gujarat), Pune (Maharashtra) and Manjira reservoir, Sangareddy (Adhra Pradesh) (Rao & Khan 1982; Soota 1991).

Megascleres of *C. lapidosa* have been regarded to be of only one type, i.e. stout and completely smooth strongyles (Annandale 1908 & 1911; Penney & Racek 1968; Soota 1991; Jakhalekar & Ghate 2013). Manconi & Pronzato (2004), in their synopsis of this genus, however give an identification key that includes the species *C. lapidosa* in the 'presence of two kinds of megascleres' group. There might have been a possible confusion as

Annandale (1911) also mentions and illustrates another kind of megasclere (i.e., slender smooth oxea) in addition to the usual stout smooth strongyle (see Fig. 26 p. 124 in Annandale 1911), but at the same time also speculates that it may be an immature form of the latter. Almost all of the megascleres of *C. lapidosa* in our material (including material from the type locality) were found to be entirely smooth strongyles. Although some slender oxeas could be found, these were present in only few samples; and whenever present, these were always in low number (<10%). Therefore, it is clear that *C. lapidosa* possesses only one type of megasclere, i.e. stout, smooth strongyles.

Earlier studies by Annandale (1908, 1911), Penney & Racek (1968), Soota (1991), Manconi & Pronzato (2004), and Ruengsawang *et al.* (2012) report *C. lapidosa* to produce only fixed or sessile gemmules. We, however, observed sessile as well as free gemmules in this species; the free gemmules were confined to the basal region of the skeleton.

Additional field photographs of *C. lapidosa* are provided here (Figs 8A–C). Larger specimens of *C. lapidosa*, especially on flat, rocky substrata, seem to grow with radiating extensions at the periphery (Fig. 8B). The external surface of *C. lapidosa* is quite distinctly conulose and, hence, to some degree the species can be differentiated from another Indian endemic *C. ultima* in the field, which shows rough but largely even surface. This however may not be considered as a very firm character since Annandale (1912) has reported spiny surface in *C. ultima* and we have also observed rough, but not conulose, surface once in *C. lapidosa* (Fig. 8C) (discussed below).

Dosilia plumosa (Carter, 1849)

Fig. 8D, Table 1.

Material. Ten specimens were studied. Additional live sponges were observed but not collected. For localities see Table 1.

Description. Sponge forming distinctly lobed masses, often small to medium, never seen of large size. Surface grossly even but shows spicular projections, thus minutely hispid. Colour in life emerald green, in alcohol it discolours to off-white; dry sponges appear pale yellowish-brown. Skeleton anisotropic reticulation of megascleres joined by copious spongin.

Megascleres smooth oxea $(353-\underline{456}-533 \times 15-\underline{20}-25 \ \mu\text{m})$. Microscleres euasters (diameter: $24-\underline{30}-37 \ \mu\text{m}$) and spined oxeas with few central rays ($52-\underline{64}-75 \times 17-\underline{30}-38 \ \mu\text{m}$). Gemmuloscleres birotules ($68-\underline{79}-89 \times 4.4-\underline{5.7}-7.2 \ \mu\text{m}$; diameter of rotules: $20.6-\underline{24.2}-27.8 \ \mu\text{m}$). (For illustrations see Fig. 4 in Jakhalekar & Ghate 2013.)

Gemmules (diameter: about 853-871 µm) distinctly ovoid, off-white to pale yellow.

Distribution. India, Pakistan, Philippines (Penney & Racek 1968; Manconi & Pronzato 2002; Cândido *et al.* 2010; Manconi *et al.* 2013).

Remarks. Carter (1849) described this species as *Spongilla plumosa* from the Islands of Bombay, India. Gray (1867) erected the genus *Dosilia* with *Spongilla plumosa* as the type species. Penney & Racek (1968) later redefined the genus. Manconi & Pronzato (2002) provided an update of generic diagnosis with description of its type species. Cândido *et al.* (2010) provide the latest review of this genus, with redescriptions of all five species. Indian records of *D. plumosa* include Mumbai (Maharashtra), Pulta (W Bengal), Hazaribagh (Bihar), Jodhpur, Jaipur and Udaipur (all from Rajasthan), Rambha (Orissa) (Annandale 1911; Soota 1991).

Dosilia plumosa was previously well illustrated using SEM (see Manconi & Pronzato 2002 and Cândido *et al.* 2010), however since those works were based on the preserved museum material, our recent field data and ecological observations of the Indian populations improve the understanding of the species. Our material of this species from western Maharashtra shows similar morphological characters under SEM as described by the previous authors. We provide here a colour photograph of live *D. plumosa* (Fig. 8D) and another picture of this sponge was published recently (see Fig. 4B in Kulkarni *et al.* 2015). In the field, dried sponges of this species can be differentiated by their typical skeletal structure with considerable amount of membranous spongin and conspicuously ovoid gemmules, which are more oval in shape than those of any other sponge studied here. Live sponges however could be confused with *Radiospongilla cerebellata* Bowerbank, as both these species appear very similar in life and show similar preferences for substrata (Fig. 8D) (as discussed below).

FIGURE 8. Freshwater Sponges (fresh, live material). A–C—*Corvospongilla lapidosa*. D—*Dosilia plumosa*. E—*Ephydatia meyeni*. F–J—*Eunapius carteri*. K–M—*Radiospongilla cerebellata*. N—Co-existence of two sponges; peripheral green S. *indica* and central grey C. *ultima*. O—Co-existence of two sponges; homogenous mass formed by fusion of growths of D. *plumosa* and R. *cerebellata*. Scale: A, B, G, I—Red mark on the scalpel measures 2 cm in length.

Ephydatia meyeni (Carter, 1849)

Fig. 8E, Table 1.

Material. Seven specimens were studied. For localities see Table 1.

Description. Sponge often forming thick, large encrustations or massive growths, having more or less even or undulated surface. Colour in life brown and green; dry sponges appear light brown. Skeleton anisotropic with long, vertical pauci- to multi-spicular tracts. Spongin moderate in quantity. Oscula visible only in larger specimens.

Megascleres smooth oxea $(345-\underline{389}-431 \text{ X } 14.7-\underline{16.5}-19.3 \text{ }\mu\text{m})$. Microscleres absent. Gemmuloscleres birotules $(26-\underline{35}-42 \text{ X } 4.9-\underline{6}-7.7 \text{ }\mu\text{m})$ with deeply notched rotules (diameter of rotules: $16.5-\underline{20.5}-25.5 \text{ }\mu\text{m}$), shaft rarely smooth, or bearing 1–6 erect spines. (For illustrations see Figs 8–10 in Jakhalekar & Ghate 2013)

Gemmules (diameter: $356-446-530 \mu m$) very numerous, found throughout the skeleton. Gemmuloscleres radially embedded in monolayer in moderately developed, granular pneumatic layer.

Distribution. India, Sumatra and China (Annandale 1911; Penney & Racek 1968; Manconi et al. 2013).

Remarks. Originally described as *Spongilla meyeni* Carter, 1849 from the Islands of Bombay, India (Carter 1849), this sponge was later widely recorded from the following Indian localities: Bhimtal and Roorkee (both from Uttarakhand), Renuka Lake (Himachal Pradesh), Rohtak, Panipat, Ottu Lake, Sirsa, Hissar (all from Haryana), Dudhwa National Park (Uttar Pradesh), Calcutta (now, Kolkata) and neighbourhood (W Bengal), Jodhpur, Udaipur and Kota (all from Rajasthan), Pune (Maharashtra), Travancore (now, Thiruvananthapuram, Kerala) and Cape Comorin (now, Kanyakumari, Tamilnadu) (Annandale 1911; Soota 1991). We have also received samples of *E. meyeni* from eastern Maharashtra, but those are not included in the current study. A photograph of live *E. meyeni* is provided here (Fig. 8E).

With a recently described species from the Neotropical region (Nicacio & Pinheiro 2015), genus *Ephydatia* Lamouroux now includes 15 valid species (van Soest *et al.* 2016).

Eunapius carteri (Bowerbank, 1863)

Figs 8F-J, Table 1.

Material. Sixty-nine sponges were collected and studied. Additionally, many specimens were studied in the field. For localities see Table 1.

Description. Sponges growing to large masses, in a variety of shapes ranging from thick encrusting to bulbous lobate (discussed below). Colour ranging from pale yellow-brown to lush green. Oscula well defined, mostly single or a few, large (up to 1.5–2 cm), or sometimes multiple small but conspicuous. Skeleton not very dense, reticulate with some vertical spicular tracts. Spongin in moderate quantity.

Megascleres smooth oxeas $(315-356-396 \times 15-16.5-18.2 \mu m)$. Microscleres absent. Gemmuloscleres smooth oxeas $(126-166-198 \times 4.3-5.8-8.6 \mu m)$. (For illustrations see Figs 11–13 in Jakhalekar & Ghate 2013.)

Gemmules (diameter: about 700–725 μ m) numerous, dispersed singly throughout the skeleton. Very well developed tri-layered gemmular theca with multi-layered and distinctly cellular thick pneumatic layer.

Distribution. One of the widely distributed freshwater sponge species. Known from India, Sri Lanka, Myanmar, SE China, Malaysia, Thailand, Indonesia, Philippines, Uzbekistan, Afghanistan, Kurdistan, Turkey, Iran, southern Russia, Hungary, Uganda, Sahara, Mozambique, Mauritius and Panama (Potts 1887; Mendis & Fernando 1962; Penney & Racek 1968; Manconi & Pronzato 2002; Manconi *et al.* 2008; Manconi *et al.* 2013).

Remarks. Carter (1849) originally found this sponge on the Islands of Bombay, India, but mistook it for *Spongilla friabilis* Lamarck. Later, Bowerbank (1863), after studying Carter's material, recognised its potential as a new species and formally described it as *Spongilla carteri*. Genus *Eunapius* Gray, 1867, upon rejection by Carter (1881), was restored as the sub-genus of *Spongilla* Lamarck by Annandale (1911) with *Spongilla carteri* Bowerbank as type species (by subsequent designation) and was later redefined and elevated to full generic rank by Penney & Racek (1968).

Eunapius carteri is the most common sponge species in Indian freshwaters and has been recorded from a large number of localities (given in Annandale 1911; Soota 1991). Annandale (1911) described a few varieties of *E. carteri* namely, var. *mollis*, var. *cava* and var. *lobosa*. These varieties however have been synonymised with their parent species by Gee (1932), a synonymy that was also supported by Penney & Racek (1968); nevertheless

Manconi *et al.* (2008) and Manconi *et al.* (2013) are of the opinion that *E. carteri* represents a potential species complex.

Manconi & Pronzato (2002), Manconi *et al.* (2008) and Manconi *et al.* (2013) provide recent descriptions with SEM illustrations of *E. carteri*. Our material of this species from localities in western Maharashtra, Lohgad Fort and Igatpuri, being closest from the type locality (i.e. Mumbai), 75 and 100 km in distance, respectively, exhibit the true characters of species as described earlier by Bowerbank (1863), Annandale (1911), Penney & Racek (1968) and Manconi & Pronzato (2002). Also, the field photographs of *E. carteri* showing different growth forms are provided here (Figs 8F–J) (more discussion below).

Radiospongilla cerebellata (Bowerbank, 1863)

Figs 8K-M, Table 1.

Material. Thirty-one specimens were collected and studied. Field observations from numerous live sponges were also recorded. For localities see Table 1.

Description. Large sponges, corrugated, often growing conspicuous, finger-like projections at the surface; smaller individuals, however, form shallow cushions, covered by minute pores, along with megascleres projecting individually from the surface. Small but discernible oscula. Colour in life pale brown to bright green, discolours in alcohol; dry sponges off-white to pale brown. Skeleton not dense, of moderate strength. Spongin sparse.

Megascleres smooth oxeas (284–<u>351</u>–418 X 8–<u>11</u>–13.2 μ m). Microscleres absent. Gemmuloscleres spined strongyles (72.7–<u>81.6</u>–88.9 X 4–<u>4.3</u>–4.7 μ m). (For illustrations see Figs 5–7 in Jakhalekar & Ghate 2013.)

Gemmules (diameter: about 578–606 μ m) abundant, white, perfectly spherical, spread throughout the sponge, less near the surface.

Distribution. Widely distributed species known from Indian sub-continent, Sri Lanka, Indonesia, Philippines, New Guinea, China, Japan, Russia, SE Europe, tropical and sub-tropical Africa, Texas (N America) (Mendis & Fernando 1962; Penney & Racek 1968; Poirrier 1972; Manconi *et al.* 2013).

Remarks. Originally described from Aurangabad, Maharashtra, India as *Spongilla cerebellata* Bowerbank, 1863, this species is well represented in India from several localities (given in Soota 1991). Number of varieties, sub-species and species, including *Spongilla lacustris reticulata* Annandale and *Spongilla proliferens* Annandale, have been treated as junior synonyms of *R. cerebellata* by Penney & Racek (1968); however Manconi *et al.* (2013) consider this species to be a potential species complex.

In the field, *R. cerebellata* can be distinguished from the species discussed here by distinct corrugated form or finger-like projections with minutely hispid surface and perfectly spherical whitish gemmules. In life, it resembles live *D. plumosa*; however the latter mostly shows lobate body form and markedly ovoid off-white to pale yellow gemmules. A series of photographs of different growth forms of *R. cerebellata* is presented here (Figs 8K–M), and another picture of a live sponge of this species was published recently (see Fig. 4A in Kulkarni *et al.* 2015).

Discussion

Ten species belonging to six genera of the family Spongillidae Gray were represented in 176 samples collected from 51 localities in the western region of the Maharashtra State of India. These 10 species have been originally described from India and of these, three species, namely *Corvospongilla lapidosa*, *C. ultima* and *Stratospongilla gravelyi* are known to be endemic to the Indian region. *Eunapius carteri* was the most frequently encountered species and was also present in majority of the localities (24), followed by *R. cerebellata* (18), *S. bombayensis* (11), and *C. lapidosa* (9), whereas *Eunapius crassissimus* was found most rarely.

As per the latest checklists published by Manconi *et al.* (2013) and Manconi & Pronzato (2015), the Oriental Region contains 40 species, 12 genera and three families of the order Spongillida Manconi & Pronzato, and the Indian freshwater sponge fauna includes 28 species in 10 genera belonging to the family Spongillidae Gray (27 species in 9 genera are from the mainland, one monotypic genus is found on the Andaman Islands). These 10 spongillid species covered in our earlier (Jakhalekar & Ghate 2013) and the present study therefore constitute 25% of the known freshwater sponge fauna of the Oriental Region and about 36% of the documented freshwater sponge

fauna of India. Field observations with colour photographs of all species and SEM illustrations of some are provided here for the first time. *Stratospongilla gravelyi* is rediscovered after a century. *Eunapius crassissimus* is reported from western India for the first time, and additionally many new localities are reported for all of the species studied here. These new findings clearly indicate the deficiency of work on Indian freshwater sponges subsequent to the times of Annandale.

Sponges were found in lentic as well as lotic freshwater habitats. Sponges were collected from 16 reservoirs, 15 ponds, 9 fort tanks, 7 rivers and 4 temporary pools (see Table 1). This pattern was also reflected in the total number of sponge samples collected from each type of habitat. The majority of our sponge samples were collected from reservoirs (55% of the total collection) and other freshwater habitats have yielded sponge samples in the following manner: ponds (23.4%), fort tanks (10.2%), rivers (9%) and temporary pools (2.4%). Species richness was also found to be highest in reservoirs (9), moderate in ponds (6), rivers (6) and fort tanks (4), and lowest in temporary pools (2). Thirty-four of the 51 localities showed presence of only one species, nine localities had two co-occurring species, and eight localities had three or more co-occurring species. Tringalwadi Dam and Talegaon Dam in Igatpuri region showed maximum co-occurrence of sponge species (5). Habitat-wise species co-occurrence was maximum for reservoirs (5), followed by rivers (4), ponds (3), fort tanks (2) and temporary pools (1). Congeneric species were also found to be occurring sympatrically, for example, three species of *Stratospongilla* co-occurred in the reservoir of Talegaon Dam at Igatpuri, two species of *Corvospongilla* were found growing on rocks in a pond at Khandala, Pune, and also in the reservoir of Tringalwadi Dam at Nashik, two species of *Eunapius* also co-existed in Municipality Dam at Igatpuri, Nashik.

Interestingly, some of the species appear to prefer particular types of habitats, for example, all samples of *Dosilia plumosa* came from ponds, most of the specimens of both species of *Corvospongilla* were found in reservoirs, *Ephydatia meyeni* was recorded from reservoirs as well as from fort tanks, *Eunapius crassissimus*, although rare in occurrence, were all found in reservoirs, all three species of *Stratospongilla* studied here have shown clear preference for reservoirs and riverine habitats, with just a couple of additional records of *S. bombayensis* from ponds and fort tanks. None of the above species occurred in temporary pools. Conversely, *Eunapius carteri* and *R. cerebellata* were present in all five types of habitats. Although these two species occurred more frequently in relatively stable aquatic environments like reservoirs and ponds, these were also found to be able to settle and survive successfully in the very fluctuating and harsh environment of short-lived temporary pools. In a local pond, which we regularly monitor for sponges, *Eunapius carteri* was found to rapidly colonise and dominate the habitat in a period of a couple of months. Ability to colonise different kinds of freshwater habitats with wide tolerance to their environmental conditions, shown by *Eunapius carteri* and *R. cerebellata* is remarkable and could be most likely the reason for their widespread distribution at the global scale.

Although we did not record the physical and chemical properties of water-bodies for all the collections, as many of the collections were done during the dry season, we did record the general qualities of sampled waterbodies and habitats. Potable water sources (reservoirs and ponds) without chemical or organic pollution have shown high species number. *Eunapius carteri* was the only species found to be able to survive in reservoirs with sewage pollution and in eutrophic water-bodies. Rivers also had good species number but only in the pristine stretches near their origins or near the dams; lengths of rivers flowing through towns are grossly polluted. Fort tanks being located at slightly higher altitude, and being relatively free from human disturbance, sustained fairly large population of sponges. Temporary pools which supported only two species, i.e. *Eunapius carteri* and *R. cerebellata*, had considerable amount of organic material in the form of decomposing leaves or dung of herbivores.

Substratum appears to be one of the crucial constituents of the microhabitat for the settlement and growth of freshwater sponges. Along with different kinds of substrata, many other ecological factors affect the colour, abundance, growth and external form of freshwater sponges (see Potts 1887; Annandale 1911; Pronzato & Manconi 1994; Gugel 2001). In the present study, out of the total collected sponge specimens, 90.4% were found attached to rocky substrata, 8.4% on aquatic plants and 1.2% were found growing on loose soil at the bottom of the ponds.

All members of *Stratospongilla* were exclusively found on rocks. Large encrustations of *S. bombayensis* were characteristically found on vertical or slanting surfaces of the rocks. Numerous but small encrustations of *S. gravelyi* were observed on very irregular surfaces of large rocks in River Venna at Medha, Satara, primarily on a side of the rock that did not directly face the current of water. *S. indica,* on the other hand, was found on stones facing the mild current of water and also at the shallow periphery of large reservoirs where there is some wave

action. Interestingly, *S. indica* in River Mutha was observed to surround another encrusting sponge, *C. ultima* (Fig. 8N). All *Stratospongilla* species were collected from unpolluted, potable waters of reservoirs, ponds, fort tanks and rivers, but not found in polluted waters. *Corvospongilla lapidosa* and *C. ultima* also showed clear preference for rocky substrata. However, in a reservoir at Hotagi, Solapur, a large mass of *C. lapidosa* was found attached to a sturdy stem of a dead plant. Substrata and environmental conditions have been known to alter the external form of sponges (Annandale 1911; Manconi & Pronzato 1991). The affinity shown by the members of genera *Stratospongilla* and *Corvospongilla* studied here, particularly for the rocky substrata with even surface, is perhaps due to the exclusive encrusting nature of these sponges.

Ephydatia meyeni was predominantly found on rocks, however a single specimen collected from Katraj Lake, Pune, was found growing on the stem of an aquatic plant. This sponge, while growing on rocks, usually forms thick encrusting growths, but the specimen attached to the plant stem was found to be spherical in shape. Dosilia *plumosa*, on the other hand, was found equally on rocks as well as on aquatic plants. The shape of this sponge was mostly lobate, however the smaller individuals attached to plant stems were spherical. Radiospongilla cerebellata was also found growing on rocks and aquatic plants, with a preponderance of the former. Additionally, some less common substrata like the shell of water-snail (*Indoplanorbis* sp.), dung of herbivores, iron piers of a bridge, and plastic debris were also recorded for this species. Radiospongilla cerebellata initially grows horizontally on the substratum and thus appears as shallow cushions when young (Fig. 8K). As growth continues, finger-like processes are produced as stubby projections at the surface which then grow prominently in length and somewhat in breadth to form an extremely corrugated surface in large-sized sponges (Fig. 8M). A turret-like raised osculum was observed in a young sponge of this species collected from a fort tank on Koraigad Fort in Lonavla region (Fig. 8L). Saller (1990), while reporting on the formation and settlement of asexual buds in R. cerebellata, depicts presence of a similar, prominently raised oscular tube in the newly settled buds of this species. On the stem of a water-plant (Ipomoea aquatica Forssk.) growing in the pond of SP Pune University, R. cerebellata and D. plumosa had fused to form such a homogenous mass (Fig. 8O) that only after spicular examination could it be revealed that two different species had grown together. Eunapius crassissimus was present on rocks and quite consistent in external morphology.

Eunapius carteri displayed a range of variation in external morphology. This species, more commonly occurred on rocks, but was also found on aquatic plants, loose soil, and some artificial substrata. Very large sponges (about 30 cm in diameter) attached to stones had lobate surface and considerably broad canals with wide external openings (Fig. 8F). Some of the medium-sized round sponges that had grown horizontally on the surfaces of stones at the bottom of a pond showed a large depression in the middle, thus resembling a 'doughnut' in general shape (Fig. 8G). Medium-sized sponges (about 15 cm in diameter) attached on vertical rocky walls and on the underside of concrete constructions were quite uniform looking and showed hemispherical or rounded conical growths with distinctly corrugated surfaces and one or two large oscula located near the centre (Fig. 8H). Sponges found on the soil (probably detached recently from rocky substratum) were not attached to it by any means and showed poor growth and abnormal appearance with laterally positioned oscula (Fig. 8J), whereas individuals of about the same size growing on rocks in their close proximity displayed much healthier growth and normal external appearance, with centrally located oscula.

Gemmules are resistant bodies produced by most freshwater sponges which act as dormant stages to overcome various adverse environmental conditions through cryptobiosis. They also serve as asexual propagules for dispersal of sponges in time and space (Simpson & Fell 1974 and references therein; Simpson 1984; Fell 1993; Pronzato & Manconi 1994; Cáceres 1997; Bilton *et al.* 2001; Manconi & Pronzato 2007, 2015, 2016b). In our study, all 10 spongillid species were found to produce gemmules. Species of genera *Corvospongilla* and *Stratospongilla* produced sessile as well as free gemmules, whereas all other species produced only free gemmules. Carpets of gemmules fixed to rocky substrata in species like *S. bombayensis* signified the permanence of such species in time, as these gemmules are most likely to germinate in the same habitat upon the arrival of favourable conditions. Gemmules produced in finger-like processes of *R. cerebellata*, or near the surface in *Ephydatia meyeni* or *Eunapius carteri* are more likely to be carried to distant locations by natural forces, such as wind or water currents, or by biological vectors like water-birds. Only the gemmules of *Eunapius crassissimus* were found to be produced singly.

Temperature and some other environmental factors are important in gemmulation as well as germination of

gemmules of freshwater sponges; however certain endogenous factors are also thought to be involved in these processes (Annandale 1911; Simpson & Gilbert 1973; Simpson & Fell 1974; Harsha et al. 1983; Simpson 1984; Fell 1993; Corriero et al. 1994; Pronzato & Manconi 1995; Gugel 2001). We did not study the phenology of gemmule formation for every species in detail here but we observed that the period of gemmulation varied to some extent in different species as well as in different types of habitats. The gemmules began to appear roughly at the onset of summer, i.e. between mid-February and early April (water temperature 25.3–28.5° C). This was the case primarily for sponges growing in stable environments like reservoirs and ponds. During the extreme summer (April and May), all submerged live sponges contained numerous gemmules, whereas in dried sponges gemmules were held in their skeletons. Sponges observed in the early rainy (monsoon) season (June to July) were of small size, suggesting their recent settlement. Sponges collected in rainy and winter seasons (June to January) showed vegetative growth and no apparent activity of gemmulation was evident (water temperature 19.9-23.7° C). Stratospongilla indica found in flowing water of a canal showed no external signs of gemmulation in mid-January (towards the end of winter, water temperature $19.8-22.8^{\circ}$ C), whereas the same sponges were full of gemmules near the end of April (in extreme summer, water temperature about 25.3° C). These sponges had extensive growth measuring several metres in length along the wall of that canal. Such huge encrusting growths might have occurred by fusion of sponges grown by germination of numerous neighbouring germules at the same time, as suggested by Pronzato & Manconi (1994). In temporary pools, however, sponges were observed to produce gemmules shortly after their settlement. Such interesting behaviour may greatly help these sponges to adapt to the rapidly changing environment of temporary pools (water temperature may raise as high as 33.7° C). Eunapius carteri and R. cerebellata growing in temporary pools had produced gemmules in June and September, respectively (water temperature about 24.4°C), in the months of the rainy season. On the contrary, gemmules were never observed in individuals of these species growing in stable environments like reservoirs and ponds during the months of the rainy season but were seen only after March, i.e. during the summer (water temperature $>25^{\circ}$ C) (Water temperature data by courtesy of M. Kulkarni). Our data suggests that the type of habitat and its environment influence the process of gemmulation. Germination of gemmules is also an equally complex and interesting phenomenon. Harrison (1974) reported germination of gemmules of Australian spongillid species after a dry period of 25 years. In a preliminary laboratory experiment (unpublished data), we observed that the dry preserved gemmules of C. lapidosa, D. plumosa and Ephydatia meyeni, which were collected 20 years ago from reservoirs and ponds in Hyderabad and Pune regions, germinated successfully in filtered and autoclayed pond water at temperature $26-28^{\circ}$ C. Phenomena such as ability of gemmules to remain viable for long periods of time and survival of species through cryptobiosis shown by these simple invertebrates are quite remarkable (see Manconi & Pronzato 2016b).

Formation of gemmules in freshwater sponges is fairly studied (Rasmont 1970, Simpson 1984, and references therein; Saller & Weissenfels 1985; Fell 1993, and references therein). Tolerance of gemmules to various conditions and the germination of gemmules though have been well studied (Simpson & Fell 1974; Harsha *et al.* 1983; Rader 1984; Simpson 1984; Fell 1993, and references therein; Pronzato *et al.* 1993; Pronzato & Manconi, 1995; Loomis *et al.* 1996; Reiswig & Miller 1998; Gugel 2001). These studies, however, focused primarily on sponges found in temperate climates, whereas the formation and germination of gemmules in freshwater sponges living in sub-tropical and tropical waters are comparatively understudied (Fell 1993, and references therein).

Organisms associated with Indian freshwater sponges have been discussed in detail by Annandale (1911). In our study, some organisms were found to be associated with *Eunapius carteri*. Large oscula and broad canal system of this species appear supportive to these life forms. Chironomid larvae and annelid worms were in moderate abundance in some of these sponges. Bugs associated with aquatic habitats (Heteroptera: Leptopodidae) were also found in the oscula of dead sponges of *Eunapius carteri* and *C. ultima*. Larvae of spongilla-flies (Neuroptera: Sisyridae) were found in *R. cerebellata*. An isopod found inside the canals of *Eunapius carteri*, was named *Tachaea spongillicola* by Stebbing (1907), due to its peculiar choice of habitat. Later reports have recorded it predominantly on freshwater prawns (Annandale 1911; Mariappan *et al.* 2003; Dev Roy & Mitra 2014). One of us (HVG, unpublished data), also observed *T. spongillicola* to be parasitic on prawns of the genus *Macrobrachium*, however, we have not found this isopod in sponges. A few small water-snails were found in sponge canals. Also, snails of *Lymnaea* sp. were found on the surface of live sponges. A freshwater bryozoan (Bryozoa: Phylactolaemata) was found growing on *Eunapius carteri* in a temporary pool inside a cave. A filamentous alga, which Annandale (1911) quotes as 'the most active and obvious enemy of freshwater sponges', was observed growing extensively on the surfaces of some encrusting sponges, particularly on *S. indica* and *S. gravelyi*.

Freshwater environments have been globally impacted by human activities, which has resulted in the change in abundance of sponges (Bell *et al.* 2015). Deterioration of local freshwater habitats by human activities, and associated decline in sponge populations, have been noted by one of us over the past four decades. Some 20 years ago, extensive encrustations of *Ephydatia meyeni* on the flat rocky beds of rivers flowing through Pune, like R. Mutha and R. Ramnadi, were common (HVG, unpublished data). Sadly, these rivers are now heavily polluted with domestic and industrial waste and sponges seem to be restricted to their upstream unpolluted stretches. Urbanisation has evidently affected many of the important freshwater habitats of sponges. Water-bodies in the metropolis of Mumbai, which is the type locality of six species of freshwater sponges, are now significantly altered. It must be noted here that we have not found the eight species of freshwater sponges that had been previously reported from this region (Annandale 1911; Annandale 1912; Annandale 1919; Ghate 2012). Such threats to freshwater habitats have greatly increased the risk of local extinction of sponges.

No freshwater sponge is presently recognised as a 'threatened species' (Manconi & Pronzato 2008; Bell *et al.* 2015), with an exception reported from Brazil (Manconi & Pronzato 2016b). But considering the high level of endemicity and the imminent threat to their habitats, freshwater sponges, as suggested by Manconi & Pronzato (2008), can be indirectly protected in freshwater habitats that are being conserved for 'more important' animals such as fishes and amphibians.

Out of the total 8500+ known species of sponges, 238 species in 47 genera of six extant families are present in the freshwaters of the world (Manconi & Pronzato 2007, 2015; van Soest *et al.* 2012; Manconi *et al.* 2013; van Soest *et al.* 2016). Freshwater sponges are found in all biogeographic regions except Antarctica and are known to inhabit various kinds of lentic and lotic freshwater habitats (Manconi & Pronzato 2008). One of the most remarkable adaptations of evolutionary significance in freshwater (and some marine) sponges is the formation of dormant bodies called 'gemmules', which are produced by members of three extant families of freshwater sponges, of which Spongillidae Gray is the most widespread and species rich family (Pronzato & Manconi 1994; Manconi & Pronzato 2002). Detailed studies on gemmules and their germination process are wanting for many Indian species; and very little is known about their biology. Serious efforts are required to study this neglected group in India.

At the scale of biogeographic regions, Oriental Region harbours 40 species of which about 42.5% are endemic (Manconi & Pronzato 2002, 2015, 2016a). The recent discovery of two new species from Thailand, with eastward extension of the range of the genus *Corvospongilla* Annandale and new record of the family Potamolepidae Brien to the Oriental Region, suggests that species diversity in this region is probably underestimated. There is thus a need for exhaustive fresh surveys in this region (Manconi *et al.* 2012; Ruengsawang *et al.* 2012; Manconi *et al.* 2013; Manconi & Pronzato 2015).

To achieve this goal, we strongly feel that earlier described species need to be described again with better illustrations to provide clear-cut or unambiguous diagnosis. Many Indian species have not been seen since their original description nearly hundred years ago, while some species have been synonymised without providing compelling evidences, for example, *Trochospongilla latouchiana* Annandale has been doubtfully synonymised with an Amazonian species of *Trochospongilla* (Soota 1991; Jakhalekar & Ghate 2014). Because of poor knowledge of Indian freshwater sponges, some temperate freshwater sponge species have been reported from south India in a dubious manner, without giving images or taxonomic details. We have tried to provide basic taxonomic data on 10 freshwater sponge species so that these species can now be more easily diagnosed and we hope to continue this work for the remaining freshwater sponge species found in India.

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