Криптическое разнообразие рода Leucosolenia (Porifera: Calcarea) в Белом и Баренцевом морях

I.A. Ekimova, Fernanda Azevedo, Andrey Lavrov, A.S. Koynova, Alexander Ereskovsky

Cryptic diversity of genus *Leucosolenia* (Porifera: Calcarea) in the White Sea

Irina Ekimova[1], Fernanda Azevedo[2], Andrey Lavrov[3,4,5], Alexandra Koynova[4], Alexander Ereskovsky[4,6]

[1]Department of Invertebrate Zoology, Lomonosov Moscow State University, Russia; [2]Departamento de Zoologia, Federal University of Rio de Janeiro, Brazil; [3]Pertsov White Sea Biological Station, Lomonosov Moscow State University, Russia; [4]Department of Embryology, Saint-Petersburg State University, Russia; [5]Koltzov Institute of Developmental Biology RAS, Russia; [6]Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Université, CNRS, IRD, Marseille, France

Introduction. The Porifera represent one of the most diverse taxa of sessile invertebrates with over 9 000 extant species. Calcareous sponges of the genus *Leucosolenia* are an emerging model object for evolutionary developmental biology studies. However, recent studies on the class Calcarea, and in particular on the subclass Calcaronea, indicates the presence of high cryptic diversity within most genera.

Currently *Leucosolenia complicata* is the only species mentioned for the White Sea and shows wide distribution range in North Atlantic from Greenland to Norway. Our study was aimed on the comprehensive analysis of *Leucosolenia complicata* identity in the White Sea using molecular, morphological, embryological and ecological data.

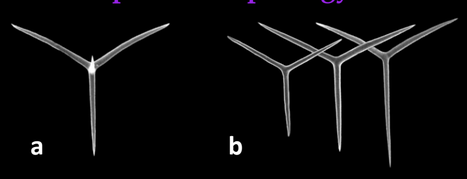
Material and methods. Material was collected during 2016-2018 summer seasons in environs of Pertsov White Sea Biological Station MSU (Russia) and of Station Biologique de Roscoff (France). External morphology, cytology, skeleton arrangement and spicule morphology were examined. Molecular study included analysis of C-region of 28S rDNA and partial Histone *H3*.

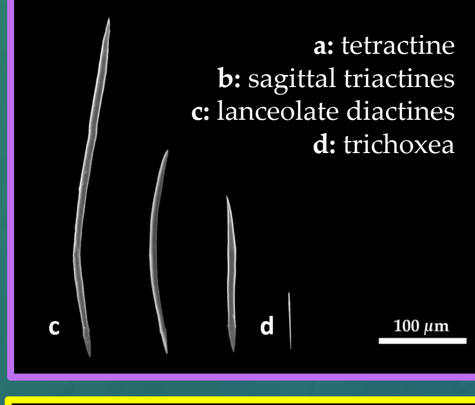
Leucosolenia complicata

External morphology: cormus small; multiple oscula lack lateral diverticula

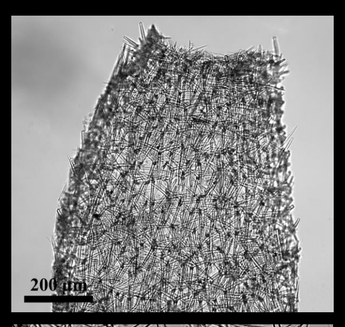
Skeleton: dense net predominantly formed by tetractines, triactines quite rare. Lanceolate diactines form small oscular crown and cover tubes surface, orienting in different directions and extending outside by lance-shaped tip. Trichoxeas sparsely distributed on outer surface.

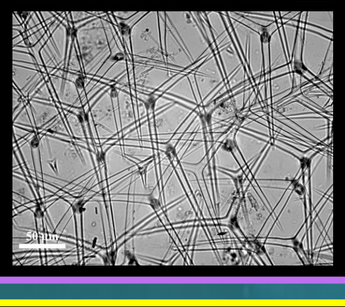
Spicule morphology:



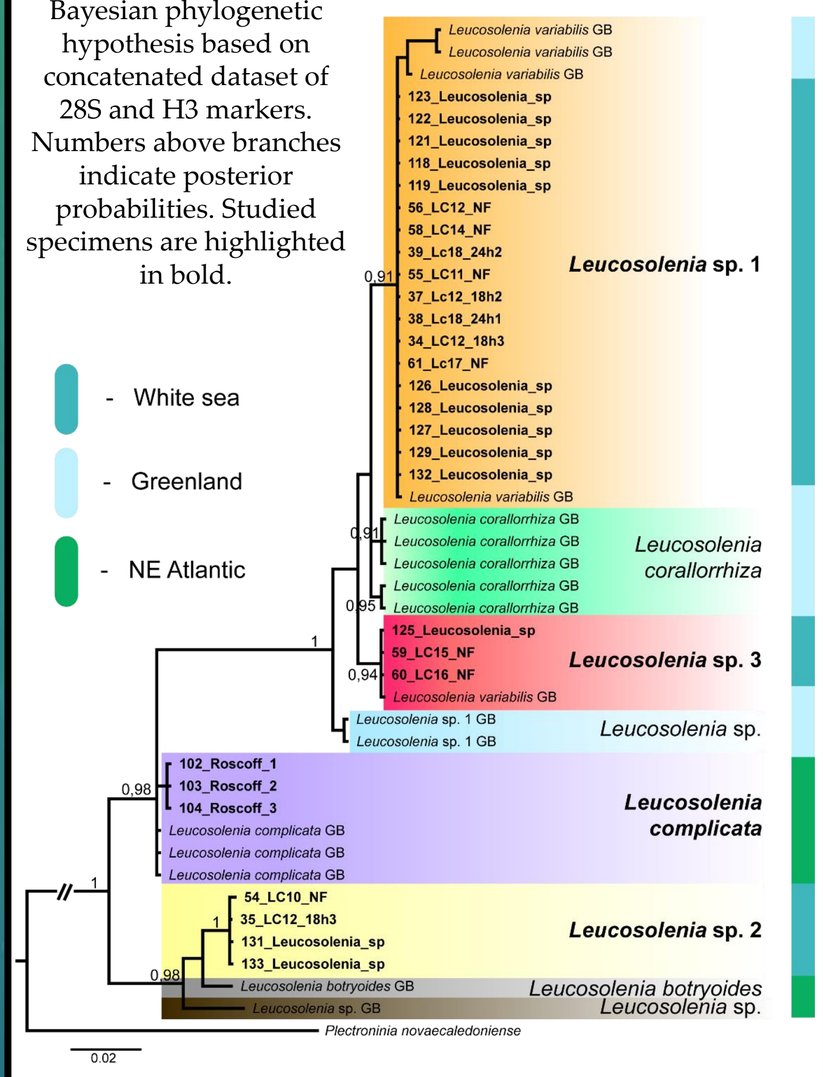


a: tetractine
b: sagittal triactines
c: lanceolate diactines
d: trichoxea





Bayesian phylogenetic hypothesis based on concatenated dataset of 28S and H3 markers. Numbers above branches indicate posterior probabilities. Studied specimens are highlighted in bold.

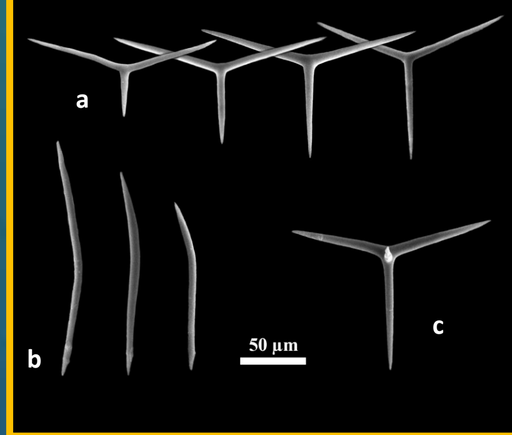


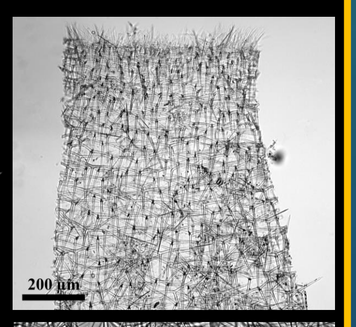
Leucosolenia sp. 1

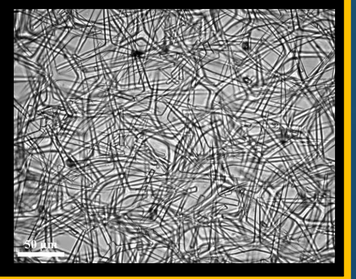
External morphology: cormus formed by basal reticulation of tubes, from which multiple erect oscular tubes arise, bearing lateral diverticula

Skeleton: Oscular skeleton predominantly formed by both T-shaped tri- and tetractines, while in cormus tetractines rare. Lanceolate diactines form small osculum crown and cover tubes surface, extending outside by lance-shaped tip.

Spicule morphology:
a: triactines; **b:** lanceolate diactines; **c:** tetractine

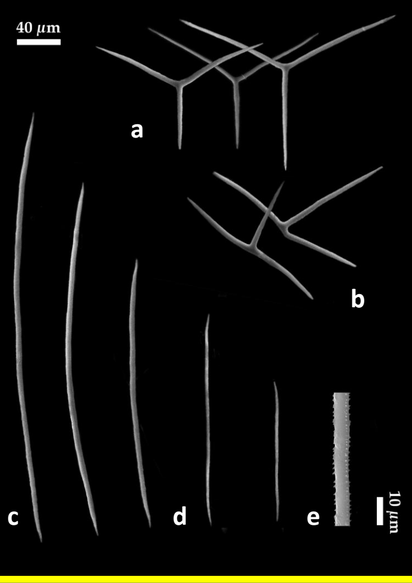


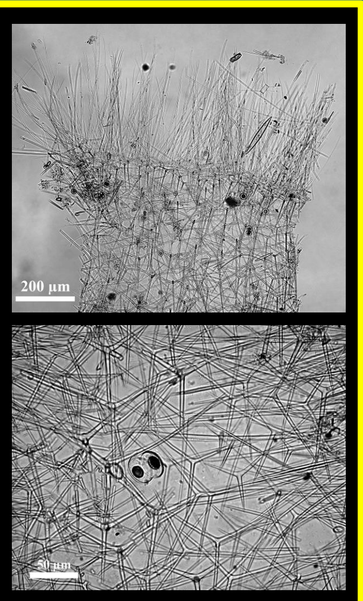




Leucosolenia sp. 2

Spicule morphology:
a: triactines; **b:** abmormal triactines; **c:** long trichoxeas; **d:** spined trichoxeas; **e:** details of spines



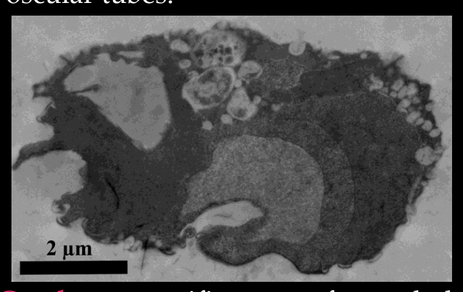


External morphology: cormus formed by creepy tubes; short oscular tubes possess prominent spicular crown and lack lateral diverticula

Skeleton: tetractines appear only in oscular rim. Trichoxeas form oscular crown and cover tubes surface, making it hispid.

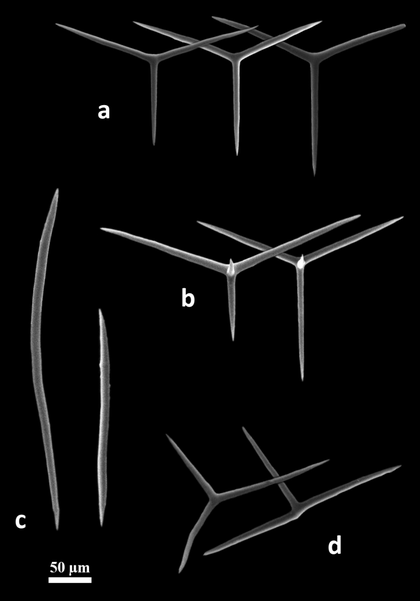
Leucosolenia sp. 3

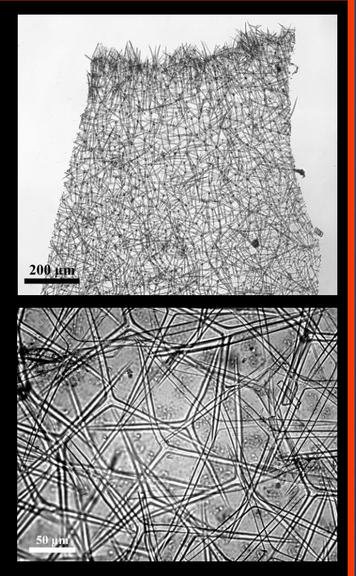
External morphology: cormus spherical with one or several long oscular tubes.



Cytology: specific type of mesohyl cell with inclusions

Spicule morphology:
a: triactines; **b:** tetractines; **c:** lanceolate diactines; **d:** abnormal triactines





Skeleton: dense net of tetractines and triactines. Lanceolate diactines form small osculum crown and cover tubes surface, extending outside by lance-shaped tip.

Mean measurements of triactines (in μm)

Species	Unpair actine		Pair actines		Angle
	Length	Width	Length	Width	
Leucosolenia sp. 1	70.5	6.5	82.8	6.6	142.9°
Leucosolenia sp. 2	80.7	5.4	94.9	5.8	131.1°
Leucosolenia sp. 3	122.3	8.1	128.0	8.3	137.7°
Leucosolenia complicata	113.5	6.3	95.0	6.9	120.1°

Mean measurement of tetractines (in μm)

Species	Unpair actine		Pair actines		Apical	
	Length	Width	Length	Width	Length	Width
Leucosolenia sp. 1	68.8	5.6	78.1	6.0	22.8	5.5
Leucosolenia sp. 2	85.1	6.2	94.9	6.5	25.6	5.2
Leucosolenia sp. 3	147.6	8.5	143.0	8.9	22.8	5.9
Leucosolenia complicata	109.3	6.7	93.2	6.8	23.8	5.4

Results and discussion. Molecular analysis of two independent markers revealed eight monophyletic species-level lineages. Surprisingly, *Leucosolenia complicata* was found only in the North-East Atlantic, where it shows stable diagnostic morphological traits: tri- and tetractines with unpaired actines commonly longer than paired ones and the presence of both lanceolate diactines and small trichoxeas. In contrast, in the White sea *Leucosolenia* diversity is represented by a complex of three pseudo-cryptic species, which differ in external features, cytology, skeleton arrangement and spicule morphology. *Leucosolenia* sp. 1 is characterized by lanceolate diactines and T-shaped tri- and tetractines with unpaired actines commonly shorter than paired ones. *Leucosolenia* sp. 2 possess smooth and spined trichoxeas, which form prominent spicular crown around oscula and cover cormus tubes, making them hispid. In addition its tri- and tetractines are thin, many of them are abnormal. Tetractines are rare, presented only in oscular rim. *Leucosolenia* sp. 3 is easily distinguished by voluminous spherical cormus with one or several long oscular tubes, presence of lanceolate diactines and T- or V-shaped tri- and tetractines, some of which are abnormal. In addition, we found peculiar type of mesohyl cells with specific inclusions, occurring in large number.

Leucosolenia sp. 1 and *Leucosolenia* sp. 2 are most common species in the White sea. In the upper intertidal zone they usually occurred sympatrically, while deeper waters are inhabited mostly by *Leucosolenia* sp. 1. *Leucosolenia* sp. 3 is also found in deep waters, but restricted to a single locality near Krestovye islands, which have specific fauna.

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