Where Topsent went wrong: *Aka infesta* a.k.a. *Aka labyrinthica* (Demospongiae: Phloeodictyidae) and implications for other *Aka* spp.

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Early descriptions for species of *Aka* were poor in detail, and the only spicule type that occurs in this genus does not vary much between species, which led to taxonomic confusion. Moreover, the type specimens of five species of *Aka* are lost, causing considerable problems. Mediterranean specimens of *Aka* were identified as *Aka labyrinthica* (Hancock, 1849) by Topsent (1900), even though this species was originally described from the Indo-Pacific. All following publications on Mediterranean *Aka* accepted Topsent's decision. We assessed this problem with new samples from the Ionian Sea. Our material consisted of only one specimen of *Aka*, and we had to rely mainly on spicule characters for comparison with other species. We developed a system for species recognition solely based on spicular characters and biometry, involving a combination of the parameters oxea length, width, tip form and angle of curvature. This approach was surprisingly accurate. Forming ratios of the above parameters was less helpful, but can sometimes provide additional information. We identified our sample as *Aka infesta* (Johnson, 1899), and describe it as a minute-fistulate species with large, multicamerate erosion traces and stout, smooth oxeas. Our data further imply that *A. labyrinthica sensu* Hancock has not yet been found in the Mediterranean. *Aka labyrinthica sensu* Topsent is a collection of different species not including *A. labyrinthica sensu* Hancock.

INTRODUCTION

Taxonomy of the excavating genus *Aka* (Demospongiae: Phloeodictyidae) is difficult. Skeletal characters alone have been regarded as of little assistance for species distinction of *Aka* spp., as the genus has only one spicule type, smooth oxeas. While they may be recognized as typical for *Aka* (e.g. Rützler & Stone, 1986), their form does not vary in an immediately obvious way between different species. Moreover, *Aka* oxeas have traditionally been considered to be very variable between sample locations (Topsent, 1900, 1904). Characters that may differ more clearly between species of *Aka*—e.g. tissue layering, the amount of mucus exuded from fresh samples, unicamerate vs multicamerate erosion, papilla size and fistule length as in <mm vs cm scale—were rarely mentioned in previous descriptions and are only patchily available, making a comprehensive, morphology-based comparison impossible (e.g. Desqueyroux-Faúndez & Valentine, 2002). General morphological characters have traditionally been poorly described (e.g. Johnson, 1899). In addition, early research provided spicule dimensions without giving information about the sample size, an error value or from which part of the body the spicules were taken (e.g. Hancock, 1849), which means that comparing 'mean' spicule dimensions and accepting them as similar may be a risky business. To make matters worse, the most important,

historical type specimens have been lost and cannot be used to confirm earlier statements, or for redescrptions employing modern methods: *A. labyrinthica* and *A. nodosa* (Hancock, 1849; as *Cliona*) were destroyed during bombing of the Hancock Museum in the Second World War, and *A. insidiosa*, *A. rodens* and *A. infesta* (Johnson, 1899; as *Acca*) during a fire in 1980 in the Lisbon Museum.

While the Hancock specimens themselves are lost, we still have access to spicule slide preparations at the Hancock Museum in Newcastle upon Tyne, UK (see Rützler & Stone, 1986). The slides are unavailable until early 2009, as the Hancock Museum is under reconstruction (D. Gordon, personal communication, curator of the collection). Also, the slides are preparations of acid-cleaned oxeas. Without developing a system purely based on characters of isolated spicules and providing additional criteria to the usual mean length and width measurements, the Hancock preparations may be assumed to be of little value.

As a consequence of the described difficulties, many of the existing identifications or reports of *Aka* species will have to be regarded with great care. One particular case illustrates the predicaments we have to expect within this genus: '*A. labyrinthica*' from the Mediterranean Sea and the Atlantic. Hancock (1849) described *A. labyrinthica* (as *Cliona*), but did not specify a type locality. However, he found this particular species in a giant clam (*Tridacna gigas*) that has a distribution

Table 1. *Compilation of previous records of 'Aka labyrinthica' in the literature. Apart from the original description by Hancock, all reports are from the Mediterranean and the North Atlantic and differ from Hancock's species.*

Author	Year	Sample locality	Sea	Country	Taxonomic decision
Hancock	1849	(Not stated, but found in <i>Tridactna gigas</i>)	Indo-Pacific	Unknown	HMN 4.15.45–4.15.48; <i>A. labyrinthica</i> , Hancock's original description: oxeas 109 µm long. Rützler & Stone (1986) for larger oxea size-class of type material: length 120 µm, width 10 µm, ratio 12, tips can be mucronate. These values best match our measurements of the first kind of oxeas found on the type slides (see Remarks).
Topsent	1888	(Refers to Hancock, 1849)	Indo-Pacific; in <i>Tridactna gigas</i>	Unknown	MNHN DT 2521; not <i>A. labyrinthica</i> , as oxeas too slim. Does not match the second kind of oxeas found in <i>A. labyrinthica</i> type series either, as tip shapes and angles of shafts differ. Unknown, probably undescribed species. Could be conspecific with the sample from the Costa Brava, and needs to be compared in detail to MNHN samples DT2533, DT2534 and DNBE 711.
Topsent	1900	Gulf of Lion	Mediterranean	France	MNHN DT2423; Topsent (1900) describes the oxeas with a length of 150–170 µm and a width of 9 µm, i.e. with a ratio of 17–19, which matches our measurements and is about half-way between the measurements for the two Johnson species <i>A. infesta</i> and <i>A. insidiosa</i> (PANGAEA®, see Table 3). Our biometric studies matched this sample to <i>A. infesta</i> (Tables 5–8). However, it has also pronounced similarities with spicules of <i>A. conolithophaga</i> , resembling its spicule form better than that of <i>A. infesta</i> .
Topsent	1904	Azores, 880 m	North Atlantic	Portugal	MNHN DT875; very likely a new species of <i>Aka</i> : Topsent describes the oxeas as 'remarkably robust' with acerate tips and a length of 150–170 × 12 µm, i.e. with a ratio of 13–14, which matches our measurements, but not the spicular characters of any known species of <i>Aka</i> (Tables 5–8).
Alander	1942	Trondheim Fjord, 85 m	Norwegian Sea, North Atlantic	Norway	Regrettably, Alander does not give a description of the spicules. The live fistules depicted in his pl. 6 are white or light-coloured, 1.9–2.1 mm in diameter and have a sieve-like, reticulated top. No sample material was available for the present study, and Alander's samples could not conclusively be matched to any particular species of <i>Aka</i> .
Melone	1965	Strait of Bonifacio	Mediterranean	Between Corsica and Sardinia	Her figures were drawn free-hand and are thus insufficient. Moreover, judging from the drawings, the sample contained immature oxeas that were obviously used in the measurements: the oxeas were described to be 48–128 × 1–4 µm, i.e. with a ratio of 48–32. The oxeas are thus far too slim to be indicative for either <i>A. labyrinthica</i> , <i>A. infesta</i> or Topsent's MNHN DT2423 (Melone thought latter to be conspecific with her samples). A tentative identification cannot be attempted with provided information, but if reference samples exist, they should be compared with <i>Aka</i> sp. from the Ligurian coast ('Portofino') and with <i>A. rodens</i> .
Barletta & Vighi	1968	Ligurian and Tyrrhenian Sea	Mediterranean	Italy	Their figure 2B shows slim oxeas with slightly angular curvature. If our photocopy is 1:1, mature oxeas are 93 × 4 µm, with a ratio of 23 and an angle of 164°. The oxeas are thus far too slim to be indicative for either <i>A. labyrinthica</i> or <i>A. infesta</i> . If reference samples exist, they should be compared with <i>Aka</i> sp. from the Ligurian coast ('Portofino'), of which oxeas have a similar shape, and to <i>A. rodens</i> .

Table 1. (Continued.)

Cruz & Bacallado	1983	Tenerife, Canary Islands, 100 m	North Atlantic	Spain	They described ' <i>A. labyrinthica</i> ' as yellow and rarely white, with papillae of 0.5 mm in diameter and 1 cm in height and oxeas of 100 to 120 µm length. As no figures or widths of oxeas were given, this material cannot be tentatively identified, but should be compared to characters of <i>A. rodens</i> , the only known Atlantic species with a similar spicule length. Cruz (2002) synonymized his samples with <i>A. infesta</i> and lists two other publications on the same species that were not available to us. The Zoological Museum in Amsterdam holds seven samples of <i>Aka</i> from T. Cruz collected at the Canary Islands that are labelled <i>A. insidiosa (infesta)</i> . A preliminary study of those samples yielded more than one species. The specimen ZMA 05194 was here analysed in more detail, and according to our data it is neither <i>A. labyrinthica</i> nor <i>A. infesta</i> . It will be described as a new species in a forthcoming study.
Pulitzer-Finali	1983	Ligurian Sea	Mediterranean	Italy	Just an account of occurrence, no taxonomic data provided. If reference samples exist, they should be compared with <i>Aka</i> sp. from the Ligurian coast (Portofino).
Corriero et al.	1997	Ligurian Sea	Mediterranean	Italy	No data provided to support a taxonomic decision. If reference samples exist, they should be compared with <i>Aka</i> sp. from the Ligurian coast (Portofino).
Calcinai et al.	2000a	Ligurian Sea	Mediterranean	Italy	No data provided to support a taxonomic decision.
Rosell & Uriz	2002	Palamós, Catalan coast	Mediterranean	Spain	According to their description, two 'morphotypes' occurred in their samples: one with oxea dimensions of 95–125 × 3–7 µm, i.e. a ratio of 31.7–17.9 and one with 110–140 × 3–10 µm, i.e. a ratio of 36.7–14 (no figures of spicules). Bioerosion traces differed between the two 'morphotypes' as well, with longer spicules matching larger excavation chambers, indicating that two different species may be involved, but figures and measures do not provide enough information to match their samples with any of the presently studied samples. However, the 'Costa Brava' material of our study needs to be compared to their specimens with smaller spicules and erosion traces. The samples with the larger measures may well be <i>A. insidiosa</i> , but this needs to be confirmed.
Calcinai et al.	2003	Not stated	Mediterranean	Not stated	Erosion traces of ' <i>A. labyrinthica</i> ' are displayed. As no other information is given on the sample, no tentative taxonomic decision can be made, but scar patterns resemble those in our sample ZMA POR 19927.

Figure 1. Morphological aspects of *Aka infesta* specimen ZMA POR 19927. (A) Overview of specimen of *Madrepora oculata* in which *A. infesta* was found. White arrows indicate the extent of spread of *A. infesta*. Shorter black arrow pointing towards the fracture surface of 1 B, D and E, longer black arrow towards the surface of C; (B) overview over fracture surface with *A. infesta* tissue (upper half); (C) empty

Table 2. Dimensions of *Aka* spp. oxeas presumed fully-formed.

Species	Minimum oxea width (µm)	Maximum oxea length: width ratio
<i>A. brevitubulata</i> (holotype)	4.5	34
<i>A. cachacrouense</i> (holotype)	6.5	32
<i>A. coralliphaga</i> forma <i>typica</i> (holotype)	6.0	24
<i>A. infesta</i> (ZMA POR 19927 and Johnson, 1899)	6.5	24
<i>A. insidiosa</i> (Johnson, 1899)	7.0	26
<i>A. labyrinthica</i> (holotype)	8.0	14
<i>A. maldiviensis</i> (paratype)	5.0	28
<i>A. minuta</i> (MRAC 1466)	4.5	28
<i>A. mucosa</i> (holotype)	9.5	22
<i>A. mucosa</i> (from the Great Barrier Reef)	7.0	28
<i>A. nodosa</i> (holotype)	10.5	18
<i>A. paratypica</i> (QM G32242)	5.5	26
<i>A. rodens</i> (Johnson, 1899)	3.5	28
<i>A. siphona</i> (USNM 24107)	3.0	54
<i>A. xamaycaense</i> (holotype)	4.5	28

restricted to the Indo-Pacific (ARKive and UNEP-WCMC webpages) and is phototrophic and thus occurs in shallow water. Nevertheless, '*A. labyrinthica*' is presently only known from the Mediterranean Sea and the North Atlantic and has been described from as deep as 880 m (Table 1). This distributional discrepancy has largely been overlooked. To date, it has generally been assumed that Hancock's types mostly stem from Great Britain (e.g. Desqueyroux-Faúndez & Valentine, 2002), and the occurrence of *A. labyrinthica* in the Mediterranean has not been questioned before.

In the present publication we attempt to resolve the identity for some of the Mediterranean and Atlantic samples of '*A. labyrinthica*', to provide some tentative synonyms and to deal with related taxonomic issues. New sample material of Mediterranean *Aka* was made available by M. Taviani (ISMAR, CNR, Bologna, Italy), allowing us to make a well-founded taxonomic decision. As the only available historical type series (Hancock, 1849) is merely represented by slide preparations, we strongly relied on oxea biometric data, which yielded some interesting results that appear to have general value for the genus and will help in future comparisons.

MATERIALS AND METHODS

Fresh sample material was collected during the CORSARO cruise (26 April–6 May 2006) on the RV 'Urania' as part of the programmes ESF Euromargins Moundforce and EU HERMES. A trawl on the Apulian

shelf at Santa Maria di Leuca, at the 'heel' of southern Italy (Ionian Sea, Mediterranean, trawl start: 39°37.48'N 18°39.00'E in 671 m; end: 39°38.01'N 18°40.38'E in 679 m) yielded a dead specimen of *Madrepora oculata* Linnaeus, 1758 (Figure 1A), in which one specimen of *Aka* was found (Figure 1B,C). The sample was fixed in 70% alcohol. We lodged it with the Zoological Museum, Amsterdam, access no. ZMA POR 19972.

Museums and colleagues provided further material: slide preparations of *Aka* spp., tissue fragments and photographic material of *Aka* oxeas with known scale (sample number acronyms as follows: BC—Barbara Calcinai's personal collection, CS—Christine Schönberg's personal collection, DNBE—sampled and/or determined by Nicole Boury-Esnault, DT—sampled and/or determined by Emile Topsent, HMN—Hancock Museum, Newcastle upon Tyne, LPB—Little Pioneer Bay, MD—Maldives, MNHN—National Museum of Natural History, Paris, MRAC—Royal Africa Museum, Tervuren, MSNG—Museum of Natural History, Genova, QM—Queensland Museum, Brisbane, USNM—American Museum of Natural History, Washington, ZMA POR—Porifera collection of the Zoologic Museum, Amsterdam).

Spicule preparations were made by digesting sponge tissue in heated, concentrated nitric acid (60–70°C). Freed spicules were washed in distilled water and dehydrated in ethanol. The spicule-ethanol suspension was burnt on the microscope slide and mounted with Eukitt (Riedel de Haën, Seelze, Germany). Arrangement of spicules in the new

cavity that contained *A. infesta* tissue and matches upper half of B; (D) close-up of *A. infesta* tissue. In the lower part of the photograph the tissue is shrinking back from the substrate; (E) spicule arrangement in a substrate canal, very close to the surface (upper left corner); detail of C, upper part; (F) tissue-spicule ring marking the site of a papillar structure, probably exhalant, on smallest fragment of *Madrepora*; (G) minute fistule on short stem, widening at the top, on smallest fragment of *Madrepora*; (H–J) pluck-squeeze preparations of tissue; (H) choanosomal tissue with loose and unordered arrangement of oxeas; (I) choanosomal tissue with loose arrangement of oxeas in parallel to each other; (J) fragment of papillar ring, clearly showing the layered arrangement of densely-packed oxeas at right angle to each other; (K) SEM photograph of papillar fragment in which the lower layer of spicules would correspond with the outer layer of the minute fistule or papilla; (L–M) distribution and size of substrate pores made by *A. infesta*. A colour version of this figure is available at doi: 10.1594/PANGAEA.658949—further details.

Table 3. *Aka* spp. examined, together with respective sample information, sorted by name on sample label. The last column provides the last six digits of doi numbers at PANGAEA® for further sample information and data derived from the present study (doi: 10.1594/PANGAEA.xxxxxx). The respective numbers refer to the following parameters: RD, raw data of the spicule dimensions length, width, length:width ratio, angle; BS, basic statistics of the above spicule dimensions; FD, frequency distributions of the above spicule dimensions.

Name of sample	Sample number	Sample site	Last six digits for links to PANGAEA® for further sample information
<i>Aka brevitubulata</i>	YPM 8717, holotype	Discovery Bay, Jamaica, Caribbean; 15 m	RD: 658959 BS: 659037 FD: 659065
<i>Siphonodictyon cachacrouense</i>	USNM 24094, holotype	Scotts Head Bay, Dominica, Caribbean; 35 m	RD: 658971 BS: 659049 FD: 659077
<i>Siphonodictyon coralliphagum</i> forma typica	USNM 24095, holotype	Discovery Bay, Jamaica, Caribbean; 25 m	RD: 658972 BS: 659050 FD: 659078
<i>Acca infesta</i>	Figure 4 in Johnson's publication	Madeira, North Atlantic; 'from deep water'	RD: 658975 BS: 659053 FD: 659081
<i>Aka infesta</i> (was measured twice)	ZMA POR 19927	Apulian Shelf, Ionian Sea, Mediterranean; 671–679 m	RD: 658942 and 658984 BS: 658949 and 659062 FD: 658948 and 659090 coloured image at 658942 – further information
<i>Aka infesta</i>	ZMA POR 05194	Tenerife, Canary Islands, North Atlantic; 3 m	RD: 658974 BS: 659052 FD: 659080
<i>Acca insidiosa</i>	Figure 1 in Johnson's publication	Madeira, North Atlantic; 'from deep water'	RD: 658976 BS: 659054 FD: 659082
<i>Aka labyrinthica</i>	CS collection, no number, 'Portofino'	Portofino, Ligurian Sea, Mediterranean; unknown depth	RD: 658970 BS: 659048 FD: 659076
<i>Aka labyrinthica</i>	BC collection, no number, 'Costa Brava'	Costa Brava, Spain, Mediterranean; unknown depth	RD: 658968 BS: 659046 FD: 659074
<i>Cliona labyrinthica</i> (contained two kinds of oxeas typical for <i>Aka</i> ; the doi digits on the left refer to original holotype material)	Photographs of spicules of holotype HMN 4.15.45–4.15.48 (Hancock's no. 30 for all slides)	In <i>Tridacna gigas</i> =Indo-Pacific, photic zone	RD: 658977 and 658961 BS: 659055 and 659039 FD: 659083 and 659067
<i>Cliona labyrinthica</i>	MNHN DNBE 711	Unknown sample location and depth	RD: 658969 BS: 659047 FD: 659075
<i>Cliona labyrinthica</i>	MNHN DT 875	Azores, North Atlantic; 880 m	RD: 658967 BS: 659045 FD: 659073
<i>Cliona labyrinthica</i>	MNHN DT 2423	Banyuls, Gulf of Lion, Mediterranean; unknown depth	RD: 658973 BS: 659051 FD: 659079
<i>Cliona labyrinthica</i>	MNHN DT 2521	In <i>Tridacna gigas</i> =Indo-Pacific, photic zone	RD: 658966 BS: 659044 FD: 659072
<i>Aka maldiviensis</i>	BC collection MD 101, spicule preparation of paratype	Kuda Rah, Maldives, Indian Ocean; 12 m	RD: 658978 BS: 659056 FD: 659084
<i>Aka minuta</i>	MRAC 1466	Inhaca, Mozambique, Indian Ocean; unknown depth	RD: 658981 BS: 659059 FD: 659087

<i>Aka minuta</i>	QM G322595	Little Pioneer Bay, Orpheus Island, Palm Island Group, central Great Barrier Reef, western Pacific; 1 m	RD: 658982 BS: 659060 FD: 659088
<i>Aka mucosa</i>	CS collection LPB-F19	Little Pioneer Bay, Orpheus Island, Palm Island Group, central Great Barrier Reef, western Pacific; 3 m	RD: 658958 BS: 651936 FD: 659064
<i>Aka mucosa</i>	CS collection LPB-F61	Little Pioneer Bay, Orpheus Island, Palm Island Group, central Great Barrier Reef, western Pacific; 3 m	RD: 658957 BS: 659035 FD: 659063
<i>Siphonodictyon mucosa</i>	USNM 23697, holotype	Iwayama Bay, Palau, Pacific; 0.9–6 m	RD: 658983 BS: 659061 FD: 659089
<i>Cliona nodosa</i>	Photographs of spicules of holotype HMN 4.16.11-4.16.13 (Hancock's no. 24 for all slides)	In <i>Tridacna gigas</i> =Indo-Pacific, photic zone	RD: 658960 BS: 659038 FD: 659066
<i>Cliona nodosa</i>	MNHN DT 2534	Pointe-à-Pitre, Guadeloupe, Caribbean, unknown depth	RD: 658979 BS: 659057 FD: 659085
<i>Cliona nodosa</i>	MNHN DT 2533	unknown sample location and depth ('in polypier')	RD: 658980 BS: 659058 FD: 659086
<i>Aka paratypica</i>	GM G322242	Little Pioneer Bay, Orpheus Island, Palm Island Group, central Great Barrier Reef, western Pacific; 1.7 m	RD: 658962 BS: 659040 FD: 659068
<i>Acca rodens</i>	Figure 2 in Johnson's publication	Madeira, North Atlantic; 'from deep water'	RD: 658963 BS: 659041 FD: 659069
<i>Siphonodictyon siphonum</i>	USNM 24107	End of Turtle Rocks, Bimini, Bahamas, North Atlantic, 1 m	RD: 658964 BS: 659042 FD: 659070
<i>Siphonodictyon xamaycaense</i>	MSNG 47907, holotype	Jamaica, Caribbean; 40–45 m	RD: 658965 BS: 659043 FD: 659071

sample was viewed in pluck preparations mounted with Gel/Mount (Biomed, USA).

Biometric studies on acid-cleaned spicules of all available species were conducted under a Leica DMBL phase contrast microscope with micrometer eyepiece (×2000 maximum magnification). Per slide, the first 50 oxeas along a randomly chosen path were measured as long as they were possible to focus, undamaged and not significantly malformed. We recorded their maximum length, maximum width and the inner angle (from the central point of the spicule to the actine points, with the 'central' point being slightly displaced towards one tip in asymmetrical forms; using the software analySIS 3.2 and a ColorView I digital camera). The same measurements were conducted with a ruler on figures where only photographs or drawings were available. From the first set of measurements and per sample, frequency distributions were plotted to assess the occurrence of immature spicules. Where histograms for spicule width and length:width ratios were clearly bimodal with one maximum in the thin range for width or one in the large range for the ratio, we omitted all measurements of the slimmer spicules and replaced missing values with secondary measurements of a random selection of spicules presumed mature. We accepted spicules as mature at a minimum width and maximum length:width ratio as indicated in Table 2. Length:width ratios were

calculated (Rützler, 1971), and a biometric index was formed, dividing the ratio by the inner angle of oxea. All obtained parameters were subjected to biometric studies, including frequency distributions (doi: 10.1594/PANGAEA.659091). Data were further compared with parametric statistics (MANOVA and Sheffé's post hoc tests for each parameter). Finally, counts of significant differences ($P < 0.05$) between pairwise comparisons of specimens were evaluated to detect putative conspecific samples.

For the description of our own Mediterranean sample, bioerosion traces were examined under a Wild Heerbrugg dissecting stereoscope and with scanning electron microscopy (SEM). The SEM was conducted on substrate fragments that were cleaned in desalinated water (Zeiss DMS 940) and on trace casts after vacuum embedding (CamScan®; Beuck & Freiwald, 2005). Embedded material was cut in parallel to the growth axis of the coral, and the carbonate substrate was dissolved in 10% CHOOH to free the casts. After obtaining morphological data on the new sample, we identified it by consulting respective literature and other samples as far as available. Comparison with Johnson's (1899) material was difficult, as neither specimens nor slides exist. We measured spicules from the figures of his publication. As they appear to be drawings, oxea lengths are probably more reliable than the widths and length:width ratios. We did not use

respective angles, because they are unlikely to be accurate in drawings.

At the end of our study we found ourselves with a good reference collection of *Aka* spicule slides and photographs, including some species that are not easily accessed. We created a database on spicule parameters through PANGAEA® (doi: 10.1594/PANGAEA.659091) that will also be used in forthcoming publications and will later be supplied with additional data and figures (C.H.L. Schönberg, unpublished data), in review and related publications). This database will represent a virtual reference collection for other users.

SYSTEMATICS

Class DEMOSPONGIAE Sollas, 1885

Order HAPLOSCLERIDA Topsent, 1928

Suborder PETROSINA Boury-Esnault & van Beveren, 1982

Family PHLOEODICTYIDAE Carter, 1882

Genus *Aka* (Johnson, 1899 as *Acca*) de Laubenfels, 1936

Aka infesta (Johnson, 1899)

(Figures 1–4)

Synonymies: Table 1

Material examined

The material we considered is listed in Table 3. Of this, 25 different specimens were suitable for biometric studies of the spicules. More detailed sample information for each specimen is available at PANGAEA® (see doi numbers in Table 3).

Diagnosis for *Aka infesta*

Aka with robust, well-silicified oxeas, only rarely with open tips or corroded axial canals (Figure 2). Oxea tips regular-tapering in appearance, usually very sharply pointed and without easily discernible telescoping or tendencies for mamillate points. Spicular arrangement in endosome confused, ordered and layered in minute fistules. Mucoid. Multicamerate erosion.

Description of *Aka infesta* from the Ionian Sea specimen ZMA POR 19927

Colour and morphology: endosome light moss-green in ethanol (Royal Horticultural Society colour chart: RHS152B; coloured images at doi: 10.1594/PANGAEA.658942). Fistular structures and drying endosomal tissue ochre-yellow (RHS 153C to 160B). Alcohol-preserved endosome slightly rubbery, shrinking away from erosion chamber walls when drying, leaving latter clean or adhering with minute string-like tissue extensions that eventually break (Figure 1D). Papillae near invisible, merely coating inner walls of canals, often not quite reaching substrate surface (Figure 1E). Larger openings with mere tissue-and-spicule rings, more or less flush with substrate surface (Figure 1F). Where present, fistules minute, brittle and delicate, one fistule observed with short stem of 2–3 mm in height, thin-walled, with widening apical part (Figure 1G). In papillar tissue rings and mini-fistules surface spicules arranged in parallel and following outer curvature of papillae or fistules, i.e. following superficial ring-like arrangement without discernible hispidity. Where tissue observed in substrate canals leading outward, spicules in dense aggregation, oriented in parallel to canal wall (Figures 1E & 3A). Choanosomal spicule arrangement loose

Figure 2. Oxeas of *Aka infesta* specimen ZMA POR 19927 with acerate to long-acerate tips and well-silicified axial regions. Upper row: first three oxeas immature elements. Oxeas in the middle of the row slightly biangular. Last oxea malformed with branches and tylar areas, second and third last with stylar modifications. Magnified oxeas below: uppermost oxea with enlarged axial canal, second oxea with drawn-out long-acerate tips, lowermost strongylar modification.

and largely unordered (Figure 1H), in some areas oxeas loosely aligned in parallel, reminiscent of rungs of a ladder (Figure 1I). Oxeas in papillar structures closely packed and arranged in parallel, clearly displaying two layers with oxeas oriented at right angle to each other (Figure 1J,K).

Spicules: only one spicule type and rare derivatives (latter less than 4% of all observed spicules, see Table 4). Megascleres smooth, for *Aka* comparatively robust oxeas (Figure 2). Most with longish, almost conical–hastate to asymmetrical–acerate tips, usually very sharply pointed, but occasionally slightly rounded in thicker oxeas and rarely very, very subtly stepped. Shafts usually softly curved, some shafts centrally slightly angulate. Occasional occurrence of very slightly asymmetrical oxeas (more common in straighter forms; Figure 2, 5th last oxea) and very slightly biangular oxeas (more common in oxeas with more pronounced curvature; Figure 2, 8th and 9th oxea). Mean dimensions for mature, endosomal oxeas: 149 µm in length, 9 µm in width, mean length:width ratio 16, mean angle of oxea curvature 168° (N=50), immature oxeas easily recognizable by width mostly under 5 µm (Figures 2 & 4). Mean dimensions of immature oxeas 129 µm in length, 4 µm in width, mean length:width

Figure 3. Erosion traces of *Aka infesta* ZMA POR 19927 in *Madrepora oculata*. (A–F) SEMs of trace casts; (G–I) SEMs of traces. (A) Chamber narrowing into connecting canal, partly chipped to reveal spicules inside; (B) erosion chamber merging with septal lumina of corallites of *M. oculata*; (C) apertural canal connecting erosion chamber with substrate surface; (D) pioneer threads transversing the substrate, with antler-like branching; (E) whip-like extension on apertural canal (enlargement of C); note comparatively oval form of scars on extension and ring-like sculpturing on scars on connecting canal; (F) very fine radiating extensions without sculpturing of scars; (G) distribution of scars and unprotected openings into chamber lumen; (H) scars and a minute aperture leading outwards; (I) concentric rings in the scars are very faint and often invisible.

Table 4. *Spicule dimensions of Aka infesta from the Ionian Sea, ZMA POR 19927. Dimensions are given as minimum–mean–maximum (plain print), standard deviation/coefficient of variance (italics). Please note very small sample size (N) for immature oxeas and styles and that only one strongyle was found.*

	Spicule dimensions				Frequencies	
	Length (µm)	Width (µm)	Length:width ratio	Inner angle (°)	N	%
Mature oxeas	130.0– 149.3 –168.8, <i>8.1/5.4</i>	6.5– 9.3 –11.3, <i>1.0/10.8</i>	13.3– 16.1 –20.4, <i>1.8/11.2</i>	158.1– 167.7 –178.0, <i>4.0/2.4</i>	50	89.0
Immature oxeas	120.0– 128.8 –135.0, <i>7.5/5.8</i>	3.8– 4.4 –4.8, <i>0.4/9.1</i>	27.8– 29.5 –32.0, <i>1.9/6.4</i>	167.3– 168.3 –170.1, <i>1.2/0.7</i>	4	7.3
Styles	120.0– 121.3 –122.5, <i>1.8/1.5</i>	10.0– 10.0 –10.0, <i>0.0/0.0</i>	12.0– 12.1 –12.3, <i>0.2/1.7</i>	164.8– 167.8 –170.7, <i>4.2/2.5</i>	2	2.4
Strongyle	100	11.3	8.9	166.6	1	1.2

ratio 30, mean angle of oxea curvature 168° (N=4; 7% of the amount of all observed spicules; Table 4). Oxea length and width very uniform (Figure 4). Rare derivatives in form of styles (2%, mean length 121 µm, mean width 10 µm, mean angle of curvature 168°, N=2; Figure 2; Table 4) and strongyles (1%, only one found: 100 µm long, 11 µm wide, angle of curvature 167°; Figure 2; Table 4). Rare malformations with very finely split axial threads and points, resulting in point duplication or branches (Figure 2, last oxea). Axial thread only faintly visible, most oxeas very well silicified (Figure 2).

Erosion patterns: multicamerate erosion traces. Big, rounded to lobate–elongated chambers following the branches of *Madrepora oculata*, occasionally merging with lumina of corallites (Figures 1B,C & 3B). Mean maximum diameter of erosion chambers 4.9 mm (N=10). Minute canals of 60 to 180 µm in diameter, in exceptions 400 µm in diameter (Figure 3C), connecting chambers and leading to surface pores. Externally, only minute pores visible (Figure 1L,M). Smaller ones about 0.2–0.4 (inhalants?), larger ones about 0.7 mm in diameter (exhalants?). Pioneer threads with antler-like branches (Figure 3D). Canal and chamber walls with numerous minute, unbranching apertural extensions radiating out into substrate, as typical for *Aka* (Figure 3E). Extensions 4.5–7.2 µm in diameter at bases. Smaller extensions without sculpturing of erosion scars (Figure 3F). Unable to locate dome-shaped sieves formed by remaining substrate material at endpoints of canals from surface entering erosion chambers (Figure 3A&G), as known for other species of *Aka*. Erosion scars in main chambers 15–60 µm in diameter (usually 45 µm), shallow, cup-shaped, oval to circular (Figure 3C&E,F). Scars of pioneer threads 25–35 µm, and of apertural extensions ≤15 µm, elongated (Figure 3E). Micropatterns in scars very faint, resembling circular grooves (Figure 3G&I), but smooth scars dominate (Figure 3I). Micropatterns occasionally more pronounced in trace casts (Figure 3E).

Remarks

The present sample from the Ionian Sea was identified as *Aka infesta* (Johnson, 1899). Four species of *Aka* were quickly discounted as possibilities, as their oxeas and fistules are too large, they are known for their mostly unicamerate erosion and they occur in disparate areas to the present samples (Caribbean and Pacific): *A. cachacrouense*, *A. coralliphaga*, *A.*

mucosa and *A. siphona* (Rützler, 1971). *Aka nodosa* has too long oxeas with an angular, markedly stronger bend than in the present sample. *Aka densa* also has too large oxeas (C.H.L. Schönberg, preliminary and unpublished data). In contrast, oxeas of the following species are too short to match the present sample and except for *A. rodens* occur in disparate regions: *A. labyrinthica*, *A. minuta*, *A. rodens* and *A. xamaycaense* (Indo-Pacific and Caribbean, *A. rodens* North Atlantic; Hancock, 1849; Johnson, 1899; Thomas, 1972; Pulitzer-Finali, 1986). *Aka terebrans*, *A. brevitululata*, *A. maldiviensis* and *A. paratypica* have a similar mean oxea length compared to the present sample, but much slimmer oxeas, and the latter three have larger fistules and unicamerate erosion, and all occur at disparate sample sites (Caribbean and Indo-Pacific; Pang, 1973; Fromont, 1993; Calcinai et al., 2000b; C.H.L. Schönberg, preliminary and unpublished data). *Aka paratypica* also has dome-shaped structures of remaining substrate in the erosion chambers (Schönberg & Tapanila, 2006) that were not found in the present sample. Remaining species have similar oxea dimensions compared to our sample. However, except for *A. infesta* they were dismissed on the following grounds. *Aka diagonoxea* has too long fistules (2–5 cm), too large chambers (2 cm in diameter), has dome-shaped structures in the erosion chambers and occurs in the Indian Ocean (Thomas, 1972). *Aka insidiosa*’s surface erosion pores appear to be larger in diameter than in the present sample, and we were unable to locate skeletal arrangements as pictured in Johnson’s (1899) figure 1. In contrast, Johnson’s (1899) figure 4 for *A. infesta* is remarkably similar to our findings for the present sample. Also, the stout, robust appearance of the spicules in Johnson’s figure 4 resembles what we observed for ZMA POR 19972. Despite the possible difference in colour and the slightly different sample region (Johnson: pale yellow in life and North Atlantic, ZMA POR 19972: light moss-green in ethanol and Mediterranean), characters of Johnson’s (1899) *A. infesta* are the most similar to those of the present sample, and we identified it accordingly.

Some of the decisions for excluding all of the above species but *A. infesta* were largely based on spicule dimensions that may vary (Wiedenmayer, 1977; Schönberg & Barthel, 1997; Uriz et al., 2003) or have previously been described with inadequate accuracy. Particularly where spicule width is involved (=strongly influenced by the occurrence of immature spicules), great care should be taken, especially as we have

Figure 4. Frequency distributions of *Aka infesta* ZMA POR 19927 spicule dimensions in detail. (A) Spicule lengths; (B) spicule widths; (C) length:width ratio of spicules; (D) angle of spicules. Black bars, mature oxeas; white bars, immature oxeas; dark grey bars, styles; light grey bars, one sytrongyle. Total N=57.

no information about the historic author's methodological approaches. Nevertheless, the present samples match other descriptive characters given for *A. infesta* (Johnson, 1899) as well and at least slightly differ from those of the species listed above. Our decision is therefore the best presently possible. As it may still be possible that our material represents a new species, rather than *A. infesta*, we recommend confirmation of our findings with sample material from Madeira that should be lodged in a museum as neotype.

RESULTS AND DISCUSSION

Biometric comparisons of spicule characters of Aka spp.

Frequency distributions of oxea dimensions for all studied *Aka* spp. yielded a good first impression of differences and similarities (doi: 10.1594/PANGAEA.659091). *Aka chachacrouense* and *A. mucosa* had extremely long oxeas with means around 200 μm. Another cluster of specimens shared very short oxeas between 90 and 130 μm on average, which were comparable with those of *A. labyrinthica*: the Mediterranean samples from the Costa Brava and Portofino; samples from the Indo-Pacific and Caribbean including *A. labyrinthica sensu* Hancock (1849), *A. minuta*, *A. xamaycaense*, MNHN DT2521 and MNHN DT2534; and samples of unknown origin, MNHN DNBE711 and MNHN DT2533. We recognized some differences in their oxea forms and it was clear that this cluster still contained more than one species, but just using the histograms did not facilitate adequate discrimination, MNHN DT875 had by far the thickest oxeas with a mean of close to 14 μm, unparalleled by any other species studied here. The thinnest oxeas of species not belonging to the cluster mentioned above belonged to *A. brevitubulata* and *A. siphona*, which were very distinct. Oxea angles generally displayed nice, bell-shaped distributions that did not differ much between species, mostly with means of about 165 to and 170°. *Aka xamaycaense*, MNHN DT2534 and an unknown species in the *A. labyrinthica* type material had comparatively straight oxeas with angles of >170°, whereas oxeas from *A. coralliphaga*, *A. labyrinthica sensu* Hancock (1849), *Aka paratypica*, ZMA POR 05194 and MNHN DT875 had a more pronounced curvature of <164.5°.

Our raw and biometric data were lodged with PANGAEA® (see Table 3) so that researchers can download them for future investigations. Statistical comparisons should be conducted only with randomly selected, mature spicules, and sample sizes and tissue fractions should match between compared data sets. The perception of an angle can be biased in tissue preparations, and it is essential to make sure that spicules rest on the side when measuring.

All measured parameters were here subjected to statistics and significantly differed between our samples of *Aka* spp. (overall df=125, $P=0.0001$, MANOVA; df=25, $P=0.0001$ for each separate dimension, length, width, angle, length:width ratio and oxea index). In a Scheffé's post hoc test, all samples were compared pairwise to investigate how well the present approach worked and whether conspecific material could be recognized in the sample pool, especially when focusing on the Mediterranean samples originally named '*labyrinthica*'.

Spicule length and width of mature oxeas proved to be comparatively sensitive parameters when considered separately without regarding any other characters. They

generated 84.3 and 79.7% significant and genuine differences between the studied sample pairs, respectively (Table 5). The angle of the oxea curvature by itself was the least helpful character and very uniform between the species: only 23.1% of the samples could be conclusively separated (Table 6). These results suggested that a combination of measured data was likely to be more useful. Working only with the oxea length:width ratio, the rate of significant differences was 75.4% (Table 6), i.e. still lower than when using either length or width. This was caused by joining different species that had the same oxea proportions, but still had different oxea lengths and widths. Using this ratio for taxonomic purposes may thus be hazardous, if this parameter is regarded as being superior to the others, but as additional character it can be useful (Rützler, 1971). Generating an oxea index and including the angle as well by dividing the length:width ratio by it, the significance rate reached only 73.2% (Table 7). Obviously, a different approach or an additional parameter was necessary. We tested categories of oxea tip form, roughly distinguishing between acerate (as in most *Aka* spp.), conical (as in sample ZMA POR 05194), conical-concave (as e.g. in *A. siphona*) and rounded-mamillate (as in *A. paratypica*). Tip form by itself only separated 40.6% of the samples as distinct from each other (Table 7). After trying different combinations of the above parameters, we found that the most reliable results were obtained, when working with count matrices of pairwise differences for length, width and tip form, rather than with the ratios (reaching 96.4%; Table 8). Oxea angle as additional information was helpful to stronger define a few differences and to separate a few samples that appeared to belong to difficult species (reaching 97.5% differences in our sample pool; Table 8).

With the latter approach, known identical and conspecific samples were recognized as the same thus validating the method (*A. infesta*, *A. minuta*, *A. mucosa* from the Great Barrier Reef; Table 8). The few other sample pairs grouping together will have to be re-investigated in more detail for possible conspecificity (MNHN DT2533 and 'Portofino', MNHN DT2533 and MNHN DT2534, *A. infesta* and MNHN DT2423, MNHN DT2521 and 'Costa Brava', *A. xamaycaense* and MNHN DNBE 711; Table 8). Specimen pairs that are displayed with only one difference generally appear to be different species, but some cases will have to be studied in more detail as well. If specimen pairs only differed by oxea width, they may still be conspecific (e.g. holotype of *A. mucosa* and Great Barrier Reef *A. mucosa*). Even when using only mature oxeas width it is a comparatively variable character that could not be measured with as much accuracy as the other parameters.

The study yielded a surprising result concerning the type material for *A. labyrinthica*. There appeared to be at least two species of *Aka* in the spicule preparation: (1) *A. labyrinthica sensu* Hancock (1849) with oxeas that somewhat resembled peeled bananas with short, acerate tips and soft, well-formed bends (Figure 5A); and (2) very straight oxeas that were slightly longer, but also thinner than in *A. labyrinthica sensu* Hancock (1849), and with comparatively longer tips (Figure 5B). It is presently unknown that any *Aka* spp. possesses two clearly different spicule types, yet these two kinds of spicules differed visually and biometrically (Figure 5; Tables 5–8). As

Figure 5. Spicule slide preparations of Hancock's (1849) *Aka labyrinthica* type material. (A) The stout oxeas of *A. labyrinthica sensu stricto*; (B) the second kind of *Aka* oxeas in the type material, which differ from *A. labyrinthica* oxeas by their longer shafts and their straight form; (C) a third type of oxeas in the type material is unlikely to belong to a third species of *Aka* and is here regarded as contamination. The scale is the same for A–C.

Table 6. Significance matrix for pairwise comparisons of Aka. spp. choanosomal oxea length:width ratio and oxea angle (Scheffé's post hoc test).

[illegible]

CAR, Caribbean; ATL, Atlantic; MED, Mediterranean; IP, Indo-Pacific; ? , unknown locality; shaded squares, no difference between pairs; S, significant difference ($P < 0.05$, mostly $P = 0.0001$); =, identical specimen measured from two different preparations.

Table 8. Frequencies of differences resulting from pairwise comparisons of chondosomal *Aka* spp. Where frequency is zero, species pairs were conspecific or required more information for distinction.

		YPM 8717	USNM 24094	USNM 24095	MNHN DT2534	USNM 24107	MSG 47907	ZMA 05194	MNHN DT875	ZMA 19927 1.x	ZMA 19927 2.x	BC 'Costa Brava'	CS 'Portofino'	MNHN DT2423	BC MD 101	HMN 4.15.45-48a	HMN 4.15.45-48b	MNHN DT2521	HMN 4.16.11-13	MRA 1466	QM G322595	USNM 23697	CS LPB-F19	CS LPB-F61	QM G32242	MNHN DNBE 711	MNHN DT2533	
CAR	<i>brevitubulata</i>		3		3	3	3	2	3	2	2	2	2	2	1	3	4	2	3	3	2	3	3	3	3	3	1	
CAR	<i>cacharouense</i>	3					3	3	2	2	2	2	2	2	3	2	2	2	3	2	2	2	1	1	3	3	3	
CAR	<i>cordiliplaga</i>	3	1		3	4	3	2	1	1	2	2	2	1	3	2	2	2	3	2	2	2	2	3	2	4	1	
CAR	' <i>nodosa</i> '	2	2	2			2	4	3	2	2	2	1	3	3	2	2	1	3	3	3	3	3	3	3	4	0	
CAR	<i>siphona</i>	2	3	3	2		3	4	4	3	3	2	3	4	2	4	3	2	2	4	3	3	3	3	3	2	3	
CAR	<i>xangayense</i>	2	2	2	2	3		4	3	2	2	2	1	3	2	3	1	2	3	1	3	3	3	2	2	4	1	
ATL	' <i>insidiosa</i> '	2	3	2	3	3	3		2	1	1	3	3	1	3	2	4	3	3	3	3	3	2	3	2	4	0	
ATL	' <i>labyrinthica</i> '	3	2	2	3	3	3	3	2	3	3	2	2	1	3	2	3	3	3	4	2	2	2	3	2	3	3	
MED	<i>infesta</i>	3	2	1	2	3	2	2		3	3	2	2	0	3	1	3	2	3	2	2	2	1	1	1	2	2	
MED	<i>infesta</i>	2	2	1	2	3	2	1	2		2	2	2	0	3	1	3	2	3	2	2	2	2	2	2	2	2	
MED	' <i>labyrinthica</i> '	2	2	2	1	2	1	3	2	2	2	2	2	2	3	2	3	0	3	2	1	2	2	2	2	2	1	
MED	' <i>labyrinthica</i> '	2	2	1	2	3	2	1	2	0	0	2	2	2	3	1	3	2	3	2	1	2	2	1	3	3	2	
MED	' <i>labyrinthica</i> '	2	2	1	2	3	2	3	3	3	3	3	2	3	3	3	3	3	3	2	2	2	3	3	3	1	3	
IP	<i>maldiviensis</i>	1	3	3	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	2	1	3	3	3	3	3	2	
IP	<i>labyrinthica</i>	3	2	2	1	3	2	2	2	1	1	2	1	1	3	3	3	3	3	2	2	2	2	2	3	3	1	
IP	sp. in <i>labyrinthica</i>	3	1	1	2	3	2	3	2	2	2	2	2	2	2	2	3	3	3	3	2	2	3	2	3	1	3	
IP	' <i>labyrinthica</i> '	2	2	2	1	2	2	3	2	2	2	0	2	2	3	2	2	3	3	3	2	2	2	2	3	1	1	
IP	<i>nodosa</i>	3	3	3	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	
IP	<i>minuta</i>	3	2	2	2	3	0	3	2	2	2	2	1	2	2	2	1	2	3	0	0	2	2	2	2	2	2	
IP	<i>minuta</i>	2	2	2	2	3	0	3	2	2	2	1	1	2	1	2	1	2	3	0	0	2	2	2	3	1	1	
IP	<i>mucosa</i>	3	1	2	2	3	2	3	2	2	2	2	2	2	3	2	2	2	3	2	2	2	1	1	3	3	2	
IP	<i>mucosa</i>	3	1	2	2	3	2	2	2	1	1	2	2	1	3	2	2	2	3	2	2	2	1	0	3	3	2	
IP	<i>mucosa</i>	3	1	2	2	3	2	2	2	1	1	2	2	1	3	2	2	2	3	2	2	2	1	0	3	3	2	
IP	<i>paratyptica</i>	2	3	2	3	3	3	2	3	2	2	3	3	2	1	3	2	2	3	3	2	3	3	3	3	4	2	
IP	' <i>labyrinthica</i> '	2	2	2	1	2	0	3	2	2	2	1	1	2	2	2	1	3	3	1	0	3	3	3	4	3		
?	' <i>nodosa</i> '	2	2	2	0	3	1	3	2	2	2	1	0	2	3	1	2	1	3	1	0	3	2	2	2	3	1	
?		2	2	2		3	3	3	2	2	2	1	2	2	3	1	2	1	3	2	1	2	2	2	2	3		
		COUNT of differences, considering length, width and tip form																										
		COUNT of differences, considering length, width, tip form and angle																										

CAR, Caribbean; ATL, Atlantic; MED, Mediterranean; IP, Indo-Pacific; ? , unknown locality; shaded squares, no difference between pairs; = , identical specimen measured from two different preparations.

the slimmer oxeas were longer on average and had a less well-pronounced angle than those regarded as typical for *A. labyrinthica*, we discounted the possibility of two size-classes and assumed that the sample was not monospecific. A third kind of oxeas in the *A. labyrinthica* type series was unlikely to belong to yet another species of *Aka*, because the actines tapered uncharacteristically along the entire length of the shafts, and their mean length surpassed presently known values in other *Aka* spp. (a mean of 245 µm, N=11; Figure 5C).

Of the two *Aka*-like oxea types in Hancock's material for *A. labyrinthica*, the first kind with well-formed bends matches Hancock's (1849) description better than the second and is presently regarded as the source material of the holotype (see Table 1). This material visually and statistically differed from those of all other specimens in the present study, including all Mediterranean samples (Table 8). Four samples differed with only one spicule character, but are here regarded as not conspecific with *A. labyrinthica*: samples *A. infesta* ZMA POR 19927 and '*A. labyrinthica*' MNHN DT2423 had too long oxeas, and '*A. nodosa*' MNHN DT2533 and 'Portofino' had simultaneously markedly slimmer oxeas with weaker bends. To our present knowledge, *A. labyrinthica* has not been sampled since its original description from the Indo-Pacific and has no confirmed record from the Mediterranean. The Mediterranean samples listed here differ from *A. labyrinthica*. Presently we can distinguish three or four Mediterranean species of *Aka*: the Ionian Sea sample ZMA POR 19927 of *A. infesta*, which may or may not be conspecific with MNHN DT2423 from the Gulf of Lion, and the samples 'Costa Brava' and 'Portofino' that differ from the above samples and from each other.

Despite obvious differences between known samples, *Aka* spp. from the Mediterranean have traditionally been called '*A. labyrinthica*'. Not having access to Hancock's and Johnson's type specimens, a number of authors apparently relied on previous decisions. The first person to err was Topsent (1900, 1904), who wrongly identified material from the Indo-Pacific, the French Mediterranean and on the Azores as '*A. labyrinthica*' (Table 1). Topsent lived at a time when decisions were mainly made by referring to the available literature, and sample exchange may have been a rare occasion. He did not have much choice between known species, as only five had been described by 1900—Hancock's and Johnson's—and in the beginning Topsent was not even yet aware of the Johnson species. Therefore, in Topsent's experience, his specimens were to be either *A. labyrinthica*, *A. nodosa* or a new species, and he chose to conform to the known species. He was a very thorough sponge taxonomist far above the average for his period. It is thus understandable that authors listed in Table 1 did not question his decisions and relied on the previous reports of '*A. labyrinthica*' from the Mediterranean and Atlantic, especially as it was an easy slip to assume that Hancock's (1849) samples were mostly from Great Britain (e.g. Desqueyroux-Faundez & Valentine, 2002). However, we now know that Topsent's conclusions were wrong and that his samples contained different, in part undescribed species. We therefore suggest that re-evaluation of all samples from the Mediterranean will be essential.

Our study revealed that there is more diversity in the genus *Aka* than previously thought and that a comparatively 'nondescript' spicule such as the oxea can impart a number of very useful characters. A combination of as few as four characters (spicule length, width, tip form and angle) can generate enough information to distinguish species at a high level of accuracy. The standardized procedure used here may be helpful in other genera with little spicular diversity as well, as long as one keeps in mind that data need to meet requirements for statistical evaluation and that environmental variation may occasionally influence them (e.g. Uriz et al., 2003).

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