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The Station Marine d'Endoume, Marseille: 150 years of natural history

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Abstract

When marine natural sciences began to be the concern of most European scientists, in the middle of the 19th century, Marseille, in southern France, was no exception. The creation, ca. 150 years ago, of the first Zoology Laboratory of the Faculty of Sciences of Marseille took place in 1868. Under the leadership of Antoine-Fortuné Marion, it soon led to the creation of the Station Marine d'Endoume (SME) in 1889. Marion's pioneering work survived both world wars and was then taken to another dimension by Jean-Marie Pérès, head of the marine station from 1948 to 1983. This institution is still alive to date. We here inventoried all the taxa described by SME scientists (1870 to 2021) and arranged them in a public database. Three main periods of activity at the SME are described, as well as the focus made through time to different groups of taxa, selected ecosystems, or biogeographic areas. Through many examples, it was possible to document how these naturalistic, taxonomic descriptions contributed to a broader scientific knowledge within this period. Finally, we discussed trends in taxonomic and naturalistic research, based on the SME experience.

Key words: Biodiversity, history, taxonomy, ecology, marine, database

Introduction

« Nomina si nescis perit cognitio rerum »

In his "*Critica Botanica*", Linnaeus (1737) resurrected this century-old Latin quote by Elizabethan jurist Edward Coke (1628): "If you do not know the names of things, the knowledge of things themselves perishes". How well this applies to taxonomy!

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Marseille (south of France) has been one of the main cradles of marine science in the Mediterranean region. As early as 1706, samples collected in the Gulf of Marseille were studied by Luigi Ferdinando Marsigli, the Italian scientist and precursor of modern oceanography, who produced wonderfully illustrated plates in his "*Histoire physique de la mer*" (Marsigli 1725; Faget 2011). A few decades later, a similar initiative was undertaken by Filippo Cavolini (1785) and Carl von Salis-Marschlins (1793) in the Gulf of Naples. Biologists of the 19th century undoubtedly built their knowledge on these early contributions and carried on discovering new marine species and ecosystems within a new research framework. In Marseille, at the end of the 19th century, the study and observation of the underwater flora and fauna occurred in the broader context of the advent of modern oceanography in Europe. Indeed, in the wake of the pioneering works of Jean-Victor Audouin (1797–1841), Henri Milne Edwards (1801–1885), and their disciples Henri de Lacaze-Duthiers (1821–1901), Armand de Quatrefages (1810–1892) and Charles Robin (1821–1885), the need was soon felt to establish permanent places for studying and experimenting in the close vicinity of the sea. Escaping the constrained framework of the ancient academies, brand-new universities offered naturalists a protective status providing more human and material resources to identify unknown forms of life. The organization of marine sciences was thus overturned along the European coasts by a series of inaugurations of marine stations dedicated to natural history (Kofoïd 1910; Faget 2011). This new framework significantly increased the ambitions of emerging marine sciences, thanks to the development of facilities such as aquaria and research vessels.

The first French marine station (1859) was founded on the Atlantic coast, in Concarneau (Brittany) followed by Arcachon (1867) and Roscoff (1872) which has celebrated 150 years in 2022 (Not *et al.* 2022), but such research structures also multiplied along the Mediterranean coast of France after 1870. These laboratories were usually attached to large universities. The Sète station, the first to be set up on the southern coast, was created in 1879. It was followed in 1882 by the Banyuls-sur-Mer laboratory, then by the Villefranche-sur-Mer station in 1884, and finally Marseille (Endoume) and La Seyne-sur-Mer were added to this already extensive list of establishments in 1888 and 1891, respectively. Driven by university professors holding chairs in zoology, this expansion resulted in an increasing number of doctoral theses devoted to the study of marine species. However, it also had a political backdrop. Indeed, in marine science as in other research fields, the war defeat of 1870 convinced the French elites of the need to catch up with the German science. Therefore, marine biology laboratories deployed along the Mediterranean Sea during this period also had a diplomatic dimension and corresponded to a certain strategy to realise the best scientific achievements and also to control the maritime space opened towards southern countries and colonies. In their great majority, marine scientists hopefully did not play this nationalistic game. In addition to the circulation of their respective journals, the laboratories welcomed a large number of foreign researchers, forming a virtual republic united by their passion for science. For instance, the frequent visits to Marseille and Naples of Russian and German biologists, such as Alexander Onufrievich Kowalewsky (1840–1901), August Weismann (1834–1914) and Carl Friedrich Wilhelm Krukenberg (1852–1889), demonstrates this fraternal solidarity across borders. By the late 1910s, a network of marine stations covered the Mediterranean from Mallorca to Castiglione (Bou Ismaïl, Algeria), from Sfax to Trieste. These laboratories offered oceanologists coming from all over the world access to their aquariums and scientific vessels, thus stimulating descriptions of the marine biodiversity.

In Marseille, the first zoology laboratory was created by the Faculty of Sciences in 1868, 20 years before the opening of the marine station (Romano 1998; Aillaud *et al.* 2002). In this laboratory, Alphonse Derbès (1808–1894) and Adolphe Dufossé (1809–1871) developed their work on sea urchin embryogenesis and on the hermaphroditism of Mediterranean Serranidae fishes. Then, it is the increasing number of new organism descriptions under the leadership of Antoine-Fortuné Marion (1846–1900) which convinced the university authorities to build a marine station (Fig. 1). The building was delivered to Marseille's zoologists in 1888, while the overall taxonomic fever driving most European teams was also fuelled by an almost daily concern with the so-called 'impoverishment of the seas' (Faget 2014). Forged by the recent awareness of the devastating effects of benthic trawling on the infralittoral and circalittoral bottoms, the discourse on marine resources decline became dominant among all those working at sea. One scientific response was thus to explore aquaculture techniques in parallel to more fundamental research. The dream of a 'cultivation of the seas' (Roché 1898), in the wake of Saint-Simonian thoughts (Faget 2011), led marine station scientists to multiply experiments in the rearing and reproduction of various species (Faget 2007). The destruction of some trophic compartments through overexploitation or the effects of pollution finally led scientists to develop innovative management plans, as for instance the model carried out by Marion for the Gulf of Marseille (Marion 1883a, b; Gourret 1897). Between 1872 and 1879, he organised major fishing and deep-dredging campaigns in the Gulf of Marseille and off Algeria (Marion 1876, 1878). Before the expeditions carried out by

Lacaze-Duthiers off the Banyuls-sur-Mer station (Jacques & Desdevises, 2021), Marion's work shortly preceded cruises by the oceanographic vessel '*Travailleur*' in the Mediterranean Sea in 1881 and the one organised in the same year on the '*Washington*' by Battista-Magnaghi (1839-1902). At the beginning of the 1880s, Marion and his school produced what is still a reference for the entire scientific community today, the "*Esquisse d'une topographie zoologique du golfe de Marseille*", a monograph giving the first description of benthic communities of the area from shallow to deep waters (Marion 1882, 1883a, b).

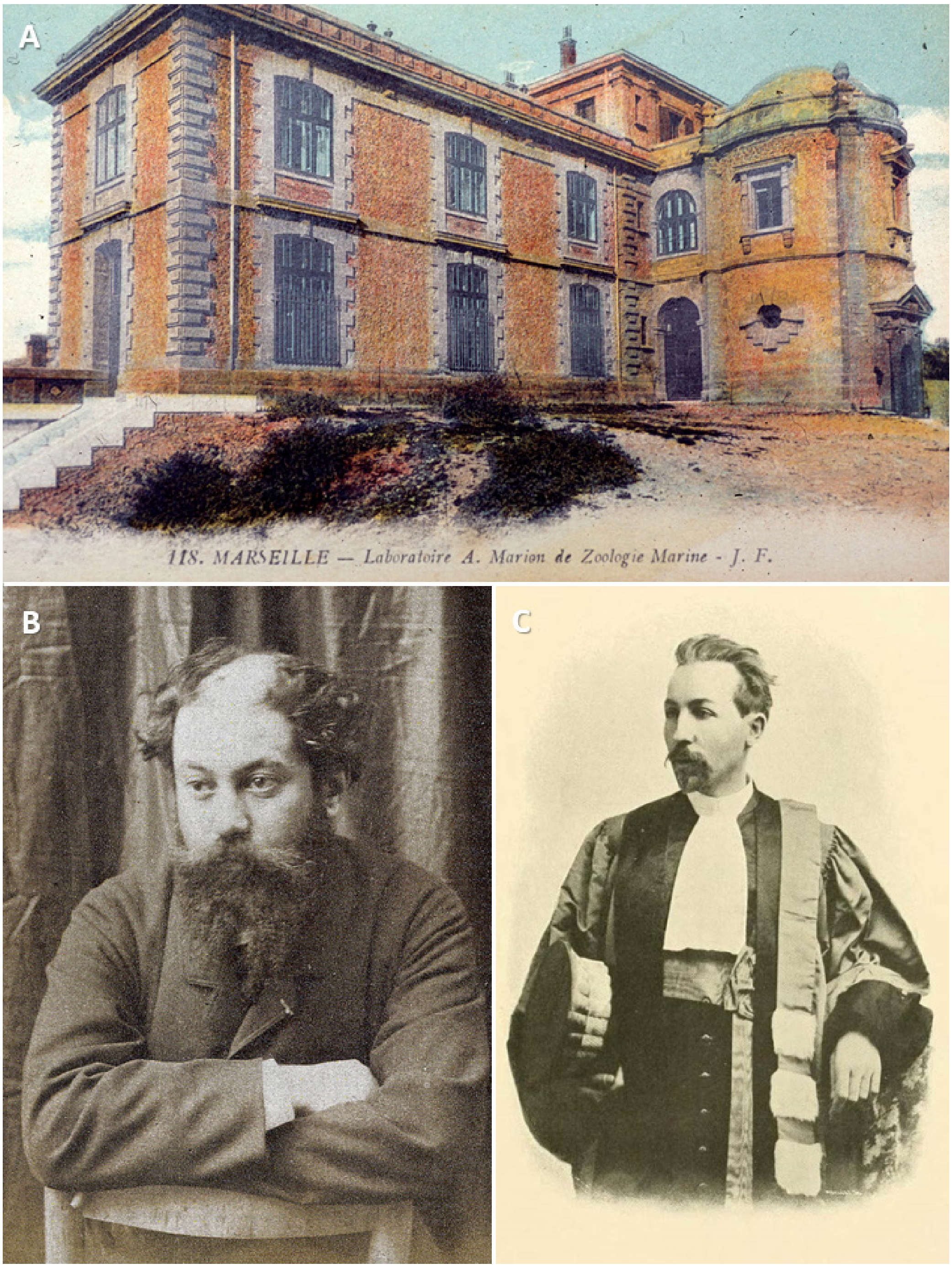

FIGURE 1. A) The Station Marine d'Endoume (SME) soon after its inauguration in 1889, B) Antoine-Fortuné Marion and C) Paul Gourret.

Before anything else, Marion was a true naturalist who defended his doctoral thesis entitled "*Nématoïdes errants du golfe de Marseille*" (Marion 1870) and then described species within several animal phyla (Nematoda, Annelida, Cnidaria, Mollusca, *etc*.; Marion 1873, 1874a, b) and even fossil algae with his friend, palaeobotanist Gaston de Saporta (Saporta & Marion 1881).

Marion gathered around him a group of researchers who soon tried to find the keys to understanding evolution. Among the various scientists who animated the "era of Marseille's naturalists" (1870–1930), Paul Gourret (1859–1903) was among the most dynamic (Fig. 1c). This orientation, giving an essential place to the identification of marine invertebrates, aimed at ensuring the definitive victory of the evolutionary doctrine, by demonstrating the existing links between the embryonic developments of vertebrates and invertebrates. Their tireless endeavour to classify the marine world was made possible by the organisation of great exploration cruises at the end of the 19th and early 20th century. Those of the Prince Albert of Monaco and his '*Hirondelle*' are the most emblematic, conducted mainly in the Mediterranean Sea and the NE Atlantic, together with those of the '*Challenger*' which made a circumnavigation across the globe.

The marine station created in Marseille has been called "*Laboratoire Marion*" after his death, and until World War II. Gourret passed away very young, only three years after Marion, and although many other collaborators remained, some of them taking the lead of the marine laboratory, the dynamism of this school diminished until the arrival of active leaders.

Just before World War II, the marine station was officially named "*Station Marine d'Endoume*" (SME). The arrival of Georges Petit (1892–1973) at its head in 1939 restored a certain dynamic, in spite of the collapsing funds resulting from the context. During the war, he invested a lot of energy in developing research in the Camargue wetlands which were already partly included in a protected area at this time. Soon after the end of the war, in 1947, Petit left Marseille to lead the Banyuls marine station, but the new rhythm implemented was maintained and then significantly increased. With the arrival of Jean-Marie Pérès (1915–1998) at its head in 1948, the SME gained three new buildings during the 1960's and became the largest French marine laboratory during the 1970's, with about 100 permanent staff. However, before becoming one of the leaders of French oceanography, Pérès was, like Marion, a naturalist who worked a lot on the systematics, biology and ecology of ascidians. With the collaboration of Jacques Picard (1925–2015) and Roger Molinier (1927–1991), he quite completed Marion's work by proposing, after a 10 year-long sampling effort in the Marseille area, a first accurate description of Mediterranean benthic communities (Pérès & Picard 1964), which was later re-published in English to reach a wider audience (Pérès, 1967). Their proposed vertical zonation and typology of species assemblages, from the ecosystem to facies level, remain nowadays a reference not only for the Mediterranean Sea but also for the world ocean. It can be seen as one of the very early precursors of habitat "systematics" such as EUNIS (https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification). In the meantime, from the late 1950s to the 1970s, Pérès regularly assigned taxonomic research objectives to the new generation of marine biologists. Following Pérès' will to develop the taxonomic skills of the "Endoume school", numerous young student scientists started working on sponges, corals, bryozoans, polychaetes, molluscs, or crustaceans, and were sent across the globe (Indian Ocean, Antarctic, Pacific, Tropical Atlantic, *etc.*) to participate in major oceanographic expeditions or in establishing new marine laboratories abroad (*e.g.* Brazil, Madagascar). In such a manner, new knowledge on marine biodiversity was acquired while the following generation of taxonomists was offered training opportunities (Fig. 2). At the same time, the 'macroalgae' side was held by Roger Molinier and his students.

The creation of scientific journals such as the *Annales du Muséum d'Histoire Naturelle de Marseille*, the *Bulletin du Muséum d'Histoire Naturelle de Marseille* (which became *Mésogée* in 1986), the *Recueil des Travaux de la Station Marine d'Endoume* (which became *Téthys* in 1969) by Marion, Petit and Pérès, respectively, was an answer to the need to publish as fast as possible all the knowledge acquired by the scientists hosted at the SME. The edition of these publications also allowed to exchange journals with other French and foreign marine laboratory libraries to increase the number of bibliographic references available for the SME researchers.

Very few institutions worldwide provided a sum of marine naturalistic knowledge such as the SME. Some of them, such as the Smithsonian Institution provide inventories and allow access to all publications written by their researchers. This contributes to the scientific influence of an institution, and sheds light on ancient bibliographic references which can exist in various languages and are not always recorded in public databases. The aim of the present work is thus to provide an extensive inventory of all the taxa described by SME scientists, from 1870 to 2021, in all the aquatic ecosystems and biogeographic areas investigated, with information on their current taxonomic status. Our objective is also to show how these descriptions of taxa contributed to the improvement of a broader scientific knowledge (organismal biology, ecosystem functioning, evolutionary history, *etc*.), sometimes overturning established concepts. Finally, we intend to discuss putative trends, a certain level of specialization, the loss or gain of scientific skills, changes in the prioritization and motivation to conduct taxonomic research.

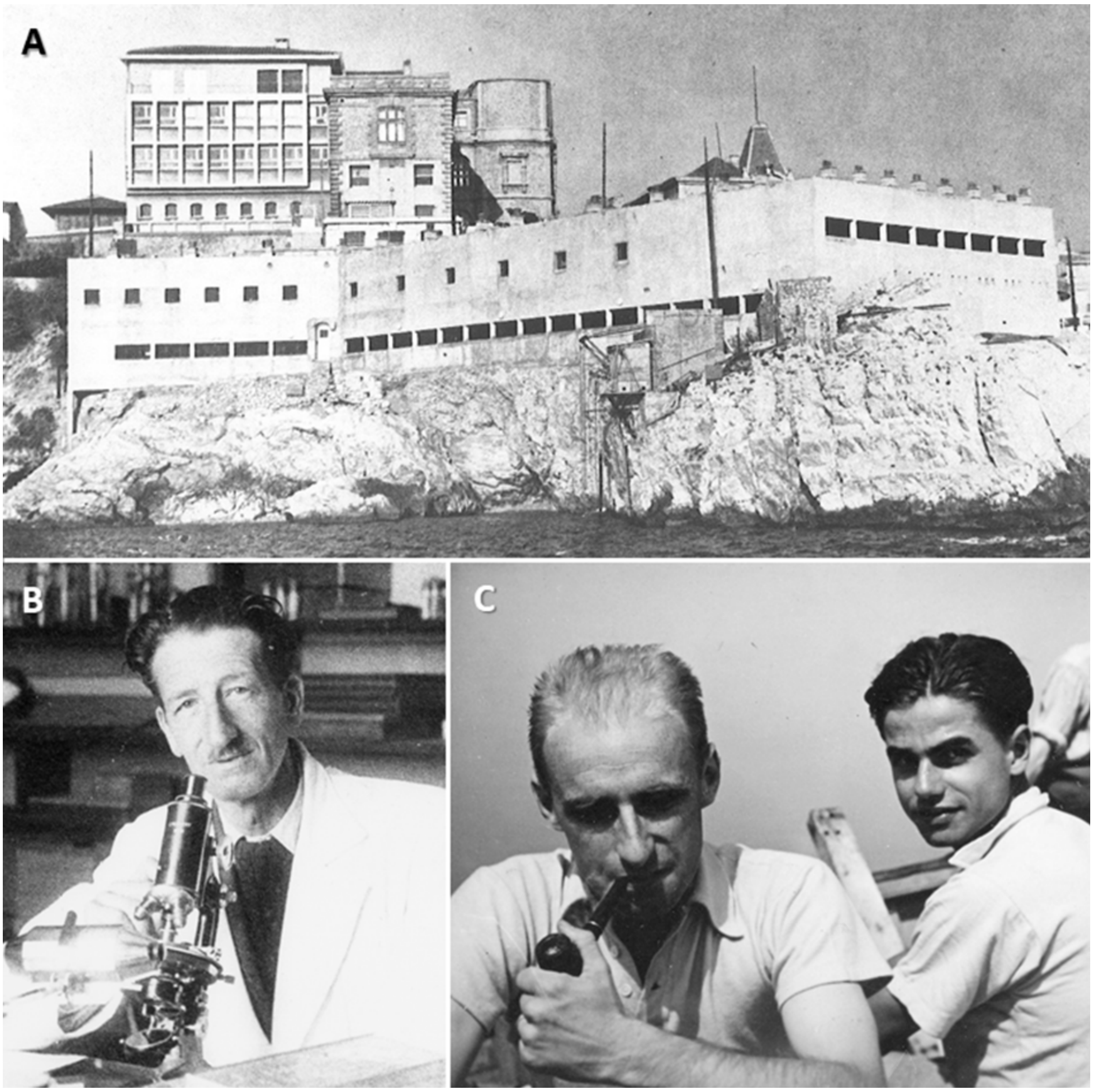

FIGURE 2. A) The Station Marine d'Endoume (SME) after the construction of three new buildings during the 1960s, B) Georges Petit, C) Jean Marie Pérès (left) and Jacques Picard (right).

Material and methods

Establishing the inventory of species described by SME researchers required an approach combining naturalistic science and history. Three distinct periods were considered: (i) the period of the SME founders led by Antoine-Fortuné Marion, from 1870 to 1924, (ii) the period of the "Endoume school", from 1937 to 1990 which has seen an explosion of specialized taxonomic works mainly motivated by Jean-Marie Pérès and Jacques Picard, and finally (iii) starting in the 1990's, the period of integrative taxonomy, with a new generation of naturalists who combined genetics with the analysis of various phenotypic traits.

Historical and biological sources

The biographies of SME directors Marion (Jourdan *et al.* 1901; Petit 1941; Pérès 1983; Reynaud 1993), Paul Gourret (Martin 1903), Etienne Jourdan (Vayssière A. 1931), and Albert Vayssière (Vayssière P. 1975) allowed to obtain a list of the researchers of the earlier period. For the second period, the biography of Pérès (Arnaud P. 1998) as well as the memory of several of us (JV, DBS, GB, JGH) and some unpublished reports (Zibrowius, Lesbros, pers. comm.) allowed to obtain a very precise list of researchers. From this list, we gathered authors who participated in the description of new taxa, selecting any SME member (permanent staff and students) who described at least one taxon as leading author (first, last or corresponding author) (Table 1).

Every publication describing a new taxon was checked, which was made easier by the extensive collections of the library of the SME. The macroalgal library at the '*Plateforme macrophytes'*, hosted on the Luminy campus in Marseille, a structure directly derived from the historical SME, also constituted a valuable source of information. Some of the journals created and edited by the SME (*Annales du Muséum d'Histoire Naturelle de Marseille*, *Bulletin du Muséum d'Histoire Naturelle de Marseille, Mésogée*, *Recueil des Travaux de la Station Marine d'Endoume, Téthys*) are not available online but fully accessible at the SME library, and were used as important bibliographic resources.

Other important resources were Gallica, the digital library of the French National Library (www.gallica.bnf.fr), and the Biodiversity Heritage Library (www.biodiversitylibrary.org). The World Register of Marine Species (WoRMS, www.marinespecies.org) also provided access to original taxa descriptions, when digitized. For references not already digitized, PDFs were created from originals in order to feed our database (see thereafter).

Update of taxonomic status

The current taxonomic status of the taxa listed from the literature was checked in WoRMS (2022) as flawed as it may be for some rather unstable taxonomic ranks. This database, hosted at the Flanders Marine Institute, provides an authoritative and comprehensive list of marine species names, including synonymy. Many species, especially from the earliest periods, were initially not present in the database and thanks to the WoRMS data management and the collaboration of many editors, we succeeded in resolving most issues involving missing names or taxa (Table 2,). We deposited in WoRMS the PDFs of original description papers by SME researchers that were missing, with the help of the different section editors.

SME Database

All the taxa described at the SME also fed a local database, available at sme-taxa.imbe.fr.

The database visualization application is divided in three services distributed on three different servers. The front-end, developed in Angular, is a user interface allowing data sorting, adding and modifying. This interface requests a Node.js API (Application Programming Interface) which is responsible for making the link with the MySQL database. This distributed architecture facilitates maintenance, indeed, if one of the services breaks down, only this service has to be fixed, the others remaining operational. This structure also allows for a greater flexibility of update since we do not have to modify the code of the whole application to improve one of the services. We opted for the Angular and Node.js languages because they are known to offer a certain developmental flexibility as well as a good execution speed. This last point seemed essential to us because of the large amount of data that will be displayed in the interface.

The database allows access to the revised list of species described at the SME and to their related publications (original description and potential revisions), and to make checklists of taxa of various ranks, or attributed to one specific author.

Data analysis

Data from the SME database were extracted and sorted according to their taxonomic rank. Only the species rank was considered in the following analyses, whatever the acceptation status of taxa. The species extracted were grouped according to their geographic origin at the time of their description into one of the following main regions of the world ocean: Antarctic/Subantarctic, Atlantic, Indian, Mediterranean, Pacific. The few fossil species were considered apart as a special group. The relative frequencies of species per phylum within the different world ocean regions were generated in R (R Core Team 2021) with the help of the *mgsub* (Ewing 2020), *tidyverse* (Wickham *et al.* 2019) and *ggplot2* (Wickham 2016) packages. For the Mediterranean species, the localisation within one of 15 subregions (see Fig. 3) was also documented. For practical reasons and to evaluate this geographical level, we discriminated species described from the Marseille area (here considered from the Gulf of Fos to La Ciotat) from the ones described in the Gulf of Lion (from Banyuls-sur-Mer to Camargue) and in Provence (here from La Ciotat to the Italian border). Only phyla with >10 species per Mediterranean subregion were represented. The relative frequencies of species descriptions per phylum and per global geographical area were also generated in R using the *maps* and *ggplot2* packages (Fig. 4). The temporal trend of species described per phylum was elaborated in Excel 16.61.1 (Fig. 5). Only species still valid nowadays were considered in these analyses.

TABLE 1. Extensive list of SME researchers (with dates of birth and death when available), main taxonomic groups, number of taxa described (and currently accepted) per period; three periods: 1870–1924 (**1**); 1938–1990 (**2**); 1990–2021 (**3**). Abbreviations: sp: species; g: genus; f: family; ord: order; sc: subclass; abs: absent from WoRMS. Phyla are according to WoRMS. The last column indicates the year of the 1st and last descriptions of new species during research period at the SME.

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Period 1: 1870–1924				
Marion, A.-F. 1846–1900	Nematoda	24 sp, 11 g	14 sp, 4 g	1870–1906
	Cnidaria, Anthozoa	13 sp	8 sp, 1 abs	
	Cnidaria, Hydrozoa	2 sp	2 abs	
	Annelida	26 sp, 4 g	12 sp, 3 g	
	Hemichordata	2 sp	2 sp	
	Arthropoda, Amphipoda	1 sp	1 sp	
	Arthropoda, Decapoda	1 sp	0 sp	
	Bryozoa	1 sp	0 sp	
	Mollusca	7 sp	4 sp	
	Nemertea	2 sp	2 sp	
Jourdan, E. 1854–1930	Cnidaria, Anthozoa	6 sp	5 sp	1880–1895
Gourret, P. 1859–1903	Arthropoda, Mysida	2 sp	1 sp	1883–1891
	Arthropoda, Decapoda	9 sp	2 sp, 1 abs	
	Arthropoda, Isopoda	11 sp	4 sp	
	Arthropoda, Leptostraca	1 sp	Abs	
	Arthropoda, Copepoda	2 sp	2 sp	
	Chaetognatha	1 sp	0 sp	
	Brachiopoda (fossil)	1 sp	Abs	
	Mollusca (fossils)	23 sp.	3 sp, (20 abs)	
	Ciliophora	45 sp, 6 g	10 sp, 1 g (31 sp, 4 g abs)	
	Myzozoa, Dinophyceae	51 sp, 3 g	31 sp (14 sp, 1 g abs)	
	Protozoa	5 sp	0, 2 doubtful	

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Roule, L. 1861–1942	Chordata, Ascidiacea	8 sp, 3 g	4 sp (1 abs), 1 g	1884–1886
Vayssière, A. 1854–1942	Mollusca, Gastropoda	63 sp, 10 g, 1 f	27 sp, 5 g	1892–1930
	Plathyhelminthes	3 sp, 1 g	2 sp, (1sp, 1 g abs)	
Period 2: 1937–1990				
Petit, G. 1892–1973	Arthropoda, Copepoda	1 sp	1 sp	1943
Pérès, J.-M. 1915–1998	Chordata, Ascidiacea	43 sp, 2 g	29 sp, 1 g, 3 abs	1949–1959
Picard, J. 1925–2015	Cnidaria, Hydrozoa	9 sp, 3 g, 2 f	7 sp, 2 g, 1 f	1951–1960
Amar, R.	Arthropoda, Isopoda	11 sp, 3 g	10 sp, 2 g	1948–1978
	Arthropoda, Tanaidacea	1 sp	1 sp	
Bourdillon, A.	Arthropoda, Pycnogonida	1 sp	1 sp	1955
Huvé, P. & Huvé, H.	Rhodophyta	3 sp	2 sp	1962–1972
	Endoume School from 1955			
Arnaud, F.	Arthropoda, Pycnogonida	9 sp, 1 g	8 sp, 1 g	1971–1978
Arnaud, P.	Mollusca	2 sp	2 sp	1984
Bellan, G.	Annelida	9 sp	9 sp	1960–2003
Bellan-Santini, D.	Arthropoda, Amphipoda	106 sp, 9 g, 1 f	98 sp, 7 g, 1 f	1972–2018

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Berland, B.	Dinophyceae	1 sp	1 sp	1995
Bodin, P.	Arthropoda, Copepoda	37 sp, 1 g	36 sp, 1 g	1964–1971
Boudouresque, C.-F.	Chromista	2 sp	1 sp	1971–2017
	Rhodophyta	17 sp, 3 g	16 sp, 2 g	
Boury-Esnault, N.	Porifera	56 sp, 12 g, 9 f, 5 ord, 2 sc	55 sp, 12 g, 9 f, 5, 1 sc	1985–2017
Brunet, M.	Platyhelminthes	57 sp, 9 g	57 sp, 8 g	1965–1979
Cazaubon, J.-P.	Arthropoda, Tanaidacea	1 sp	1 sp	1978
Chrétiennot-Dinet, M.-J.	Chromista	1 sp, 1 g	1 sp, 1 g	1979
Dinet, A.	Arthropoda, Copepoda	20 sp, 1 g	20 sp, 1 g	1970–1981
Dumay, D.	Arthropoda, Isopoda	1 sp	1 sp	1972
Emig, C.	Hemichordata	1 sp	1 sp	1977
Gaillande, D. de	Annelida	1 sp	1 sp	1966–1970
	Arthropoda, Decapoda	1 sp	1 sp	
Gaudy, R.	Arthropoda, Copepoda	5 sp	3 sp	1963–1973

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Gautier, Y.V.	Bryozoa	16 sp, 3 g	16 sp, 3 g	1954–1962
Gravier, R.	Chordata, Ascidiacea	3 sp	1 sp, 1 abs	1955
Griessinger, J.-M.	Porifera	13 sp, 2 g	13 sp, 2 g	1971
Guérin, J.-P.	Annelida	1 sp	1 sp	1990
Harmelin, J.-G.	Annelida	5 sp, 2 g	4 sp, 2 g	1964–2021
	Bryozoa	82 sp, 5 g, 1 f	81 sp, 5 g, 1 f	
Harmelin-Vivien, M.	Chordata, Actinopteri	2 sp	2 sp	1977
Herberts, C.	Cnidaria, Anthozoa	2 sp, 1 g, 1 f	2 sp, 1 g	1972
Hipeau-Jacquotte, R.	Arthropoda, Decapoda	2 sp, 1 g	2 sp, 1 g	1965–1971
Kaïm-Malka, R.A.	Arthropoda, Amphipoda	24 sp, 1 g	24 sp, 1 g	1976–2018
Lagardère, F.	Annelida	1 sp	0 sp	1971
Lagardère, J.-P.	Arthropoda, Amphipoda	5 sp, 1 g	5 sp, 1 g	1966–1983
	Arthropoda, Decapoda	1 sp	1 sp	
	Arthropoda, Mysida	11 sp, 2 g	11 sp, 2 g	
Le Campion, T.	Fungi	1 sp		1971
	Cyanobacteria	1 sp		

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Ledoyer, M. 1937-2015	Arthropoda, Amphipoda	295 sp, 22 g, 3 fam, 2> fam	286 sp, 20 g, 3 fam, 2> fam	1965–1993
	Arthropoda, Cumacea	46 sp, 2 g	45 sp, 2 g, 1 abs	
	Arthropoda, Decapoda	2 sp	2 sp	
	Arthropoda, Leptostraca	6 sp	6 sp	
	Arthropoda, Mysida	11 sp, 2 g	11 sp, 1 g	
Leveau, M.	Arthropoda, Ostracoda	1 sp	0 sp	1966
Patriti, G.	Cnidaria, Siphonophorae	5 sp	1 sp	1965–1970
Picard, C.	Annelida	2 sp	2 sp	1974
	Chromista	1 sp	1 sp	
Pichon, M.	Cnidaria, Anthozoa	1 sp, 1 g	1 sp, 1 g	
				1971
Plante, R.	Ctenophora	1 sp, 2 g	1 sp, 2 g	1966–1971
	Chordata, Ascidiacea	3 sp	3 sp	
Pouliquen, L.	Porifera	2 sp, 1 g	2 sp, 1 g	1970–1972
Reys, J.-P.	Echinodermata	3 sp	1 sp	1959–1967
	Annelida	1 sp	1 sp	
Reys, S.	Arthropoda, Ostracoda	3 sp	3 sp	1961
Roman, M.-L.	Arthropoda, Isopoda	8 sp, 2 g	4 sp	1974–1991
	Arthropoda, Tanaidacea	1 sp, 1 g	1 sp, 1 g	

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Thomassin, B.	Annelida	9 sp, 2 g	9 sp, 1 g	1970–1998
	Arthropoda, Decapoda	2 sp	1 sp	
Vacelet, E.	Ciliophora	13 sp	11 sp	1960–1961
Vacelet, J.	Porifera	188 sp, 33 g, 8 f, 4 ord	184 sp, 24 g, 7 f, 4 ord	1958–2021
	Foraminifera	1 sp	1 sp	
Vasseur, P. 1935-2022	Chordata, Ascidiacea	6 sp	5 sp	1965–1976
	Porifera	50 sp, 4 g	47 sp, 3 g	
Vicente, N.	Mollusca, Gastropoda	7 sp	4 sp	1962–1975
Verlaque, M.	Chromista	1 sp	1 sp	1977–2017
	Rhodophyta	6 sp	5 sp	
Vitiello, P.	Nematoda	140 sp, 5 g	136 sp, 5 g	1967–1977
Vivier, M.-H.	Nematoda	5 sp	5 sp	1974–1985
	Gastrotricha	1 sp	1 sp	
Zibrowius, H.	Annelida	32 sp, 4 g	29 sp, 4 g	1967–2016
	Arthropoda, Tanaidacea	1 sp, 1 g	1 sp, 1 g	
	Bryozoa	3 sp	3 sp	
	Cnidaria, Anthozoa	45 sp, 3 g	43 sp, 3 g	
	Cnidaria, Hydrozoa	20 sp, 1 g	20 sp, 1 g	
Period 3: 1990–2021				

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TABLE 1. (Continued)

Names	Kingdom/Phylum, Class/Order	**Described taxa**	**Accepted taxa**	**Period**
Chenuil, A.	Echinodermata	3 sp	3 sp	2020
Chevaldonné, P.	Arthropoda, Decapoda	1 sp	1 sp	2004–2021
	Arthropoda, Mysida	5 sp	5 sp	
	Arthropoda, Thermosbaenacea	1 sp	1 sp	
	Annelida	6 sp	6 sp	
	Porifera	5 sp	5 sp	
Ereskovsky, A.	Porifera	15 sp	15 sp	2006–2016
Gazave, E.	Porifera	2 sp	2 sp	2012–2013
Grenier, M.	Porifera	1 sp	1 sp	2020
Pérez, T.	Porifera	47 sp, 7 g, 2 sc	46 sp, 7 g, 1 sc	1998–2021
Ruiz, C.	Porifera	12 sp, 1 g	12 sp, 1 g	2015–2020

TABLE 2. In the column "Species": the number of taxa described. The number in parentheses gives the number of taxa currently accepted and the number of taxa absent from WoRMS. sp = species; g = genus; f = family; ord = order; sc = subclass; acc = accepted in WoRMS; abs = absent of WoRMS.

Kingdom	Phylum	Class (Order)	Species	Authors
Protozoa	**Amoebozoa**	Tubulinea	5 sp (abs)	Gourret P.
Chromista	**Ciliophora**		59 sp (21 acc, 30 abs) 6 g (1 acc, 4 abs)	Gourret P., Vacelet E.
		Heterotrichea	3 sp	Vacelet E.
		Karyorelictea	1 sp	Vacelet E.
		Litostomatea	7 sp (1 acc, 4 abs)	Gourret P., Vacelet E.
		Nassophorea	1 sp	Vacelet E.
		Oligohymenophorea	12 sp (3 acc, 9 abs)	Gourret P.
		Oligotrichea	2 sp 2 g (1 acc, 1 sp + 1g abs)	Gourret P.
		Phyllopharyngea	11 sp (5 acc, 6 abs)	Gourret P., Vacelet E.
		Prostomatea	3 sp (2 acc, 1 abs)	Gourret P., Vacelet E.
		Spirotrichea	11 sp, 1 g (2 sp acc, 3 abs, 1 g acc)	Gourret P., Vacelet E.
	Foraminifera	Monothalamea	1 sp	Vacelet J.
	Myzozoa	Dinoflagellata	52 sp (32 acc, 14 abs), 3 g (0 acc, 1 abs)	Gourret P., Berland B.
	Ochrophyta	Dictyochophyceae	1 sp 1 g	Chrétiennot-Dinet M.J.
		Phaeophyceae	2 sp (1 acc)	Boudouresque C.-F., Verlaque M.
Plantae	**Rhodophyta**	Florideophyceae	23 sp (19 acc) 2 g	Huvé P., Huvé H., Boudouresque C.-F., Verlaque M.
		incertae sedis	1 sp, 1 g	Boudouresque C.-F.
Animalia	**Annelida**	Polychaeta	92 sp (73 acc) 12 g (10 acc)	Marion A.-F., Bellan G., Chevaldonné P., Harmelin J.-G., Guérin J.-P., Gaillande D. de, Lagardère F., Picard C., Reys J.-P., Thomassin B., Zibrowius H.
	Arthropoda	Pycnogonida	10 sp (9 acc) 1 g	Arnaud F., Bourdillon A.
		Malacostraca	597 sp (526 acc) 46 g (39 acc)	
		Amphipoda	396 sp (351 acc) 30 g (27 acc) 3 f	Marion A.-F., Ledoyer M., Bellan-Santini D., Kaim-Malka R.,
		Malacostraca Decapoda	18 sp (10 acc) 1 g	Marion A.-F., Gourret P., Ledoyer M., Chevaldonné P., Hipeau-Jacquotte R., Gaillande D. de & Lagardère J.-P., Thomassin B.
		Malacostraca Isopoda	29 sp (18 acc) 5 g (2 acc)	Gourret P., Amar R., Roman M.-L., Dumay D.

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TABLE 2. (Continued)

Kingdom	Phylum	Class (Order)	Species	Authors
		Malacostraca Tanaidacea	3 sp 2 g	Amar R., Cazaubon J.-P., Roman M.-L., Zibrowius H.
		Malacostraca Cumacea	46 sp (45 acc, 1 abs) 2 g	Ledoyer M.
		Malacostraca Mysida	29 sp (28 acc) 4 gen (3 acc)	Gourret P., Lagardère J.-P., Ledoyer M., Chevaldonné P.
		Malacostraca Thermosbaenacea	1 sp	Chevaldonné P.
		Malacostraca Leptostraca	7 sp (6 acc, 1 abs)	Gourret P., Ledoyer M.
		Copepoda Harpacticoida	57 sp (56 acc) 2 g	Bodin P., Dinet A.
		Copepoda Calanoida	6 sp (4 acc)	Gaudy R., Petit G.
		Copepoda Cyclopoida	2 sp	Gourret P.
		Ostracoda	4 sp (3 acc)	Reys S., Leveau M.
	Bryozoa	Gymnolaemata	78 sp (77 acc) 8 g 1 f	Marion A.-F., Gautier Y., Harmelin J.-G.
		Stenolaemata	19 sp 1 g	Harmelin J.-G.
	Chordata	Ascidiacea	60 sp (41 acc 8 abs) 5 g (2 acc)	Roule L., Pérès J.-M., Gravier R., Vasseur P.
		Actinopteri	2 sp	Harmelin-Vivien M.
	Cnidaria	Anthozoa	67 sp (59 acc) 4 g 1 f	Marion A.-F., Jourdan E., Pichon M., Zibrowius H.
		Hydrozoa	36 sp (28 acc) 4 g (3 acc) 2 f (1 acc)	Marion A.-F., Picard J., Patriti G., Zibrowius H.,
	Ctenophora	Tentaculata	1 sp 2 g	Plante R.
	Echinodermata	Ophiuroidea	5 sp (3 acc)	Reys J.-P., Chenuil, A.
		Holothuroidea	1 sp	Reys J.-P.
	Hemichordata	Enteropneusta	2 sp	Marion A.-F.
		Graptolithoidea	1 sp	Emig C.
	Gastrotricha		1 sp	Vivier M.-H.

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TABLE 2. (Continued)

Kingdom	Phylum	Class (Order)	Species	Authors
	Mollusca	Bivalvia	3 sp (2 acc)	Marion A.-F., Arnaud P.
		Gastropoda	70 sp (31 acc) 10 g (5 acc) 1 f (0 acc)	Vayssière A., Vicente N.
		Solenogastres	5 sp (4 acc)	Marion A.-F.
		Fossils	23 sp (4 acc, 16 abs)	Gourret P.
	Nematoda		169 sp (155 acc) 16 g (9 acc)	
		Chromadorea	111 sp (106 acc) 7 g (6 acc)	Marion A.-F., Vitiello P., Vivier M.-H.
		Enoplea	57 sp (48 acc) 9 g (2 acc)	Marion A.-F., Vitiello P.
		incertae sedis	1 sp 1 g	Marion A.-F.
	Nemertea	*incertae sedis*	2 sp	Marion A.-F.
	Platyhelminthes	Rhabditophora	59 sp (58 acc 1 abs) 10 g (8 acc 1 abs)	Brunet M., Vayssière A.
		incertae sedis	1 sp	Brunet M.
	Porifera	Calcarea	37 sp 16 g 9 f (8 acc) 3 ord	Boury-Esnault N., Pérez T., Pouliquen L., Vacelet J.
		Demospongiae	189 sp (182 acc) 24 g (15 acc) 2 f 4 ord 2 Sc (1 acc)	Boury-Esnault N., Pérez T., Chevaldonné P., Ereskovsky A., Griessinger M., Vacelet J., Vasseur P.
		Hexactinellida	4 sp	Boury-Esnault N., Chevaldonné P., Vacelet J.
		Homoscleromorpha	35 sp 2 g	Boury-Esnault N., Pérez T., Gazave E., Grenier M., Pouliquen L., Ruiz C., Vacelet J.
Total	**1929 species**	**1605 accepted**		

Results and discussion

From 1870 to 2021, SME researchers have contributed to the description of 1929 species, among which 1605 are still accepted to date. The corpus of species described by SME researchers extends over 20 phyla from eukaryote protists (kingdoms Alveolata, Rhizaria, *etc.*) to Subphylum Vertebrata (with the Actinopteri class), including fossils. Among the 20 phyla studied, Arthropoda was the most represented with 289 species from the Indian Ocean (particularly Madagascar), 131 species from the Mediterranean Sea and 117 from the Atlantic Ocean. Porifera (264), Nematoda (169), Cnidaria (103), Annelida (92), Bryozoa (78), Mollusca (78), Chordata (62) (including Tunicata and Vertebrata), Platyhelminthes (60), Ciliophora (59), Myzozoa (52) were the main contributing taxa after crustaceans with at least 50 described species per taxon (see Fig. 4; Table 2).

Over 150 years, 66 taxonomists were involved in this work. The number of species described per taxonomist is quite heterogeneous ranging from one species to 391 for Michel Ledoyer (see thereafter). Some of the researchers have spent their entire career at the SME, while others only a few years. For the latter, the species included here only encompass their stay at the SME. In the same way, some researchers had a continuous effort describing taxon diversity along their carrier, and thus had a great influence on their taxonomic groups. Some of them were only marginally involved in taxonomic works while others only had a very temporary naturalistic activity (Table 1). Today, none is devoted entirely to taxonomy.

Three periods with varying researcher profiles

The first period of pioneering naturalists (1870–1924) accounted 5 researchers, with only Antoine-Fortuné Marion and Paul Gourret being true naturalists able to describe species from various phyla.

Marion described 97 species belonging to 8 phyla. His first great contribution occurred in 1870 with his Doctoral thesis, where 24 species and 11 genera of Nematoda were described, about 50% of them still accepted nowadays. Soon after this first achievement, he conducted several dredging expeditions to obtain a first overview of the benthic communities off Marseille, and thereby further described 26 species and 4 genera of Annelida, 15 species of Cnidaria and 7 of Mollusca. These sampling campaigns along the southern French coasts made a decisive contribution to the contemporary scientific knowledge of the Mediterranean marine fauna (*e.g.* Marion 1883a).

However, the greatest contributor of this period was Gourret, a student of Marion, with 151 species and 9 genera described, belonging to 7 phyla (Table 1). With his Doctoral thesis and related publications (see for instance Gourret 1883; Gourret & Roeser 1886), Gourret made a huge leap forward in the challenging taxonomy of the so-called protists (a polyphyletic group), with the description of 45 species and 6 genera of Ciliophora and 51 species and 3 genera of Dinophyceae (kingdom Alveolata) (Table 1). The second great contribution of Gourret was his revision of the Malacostraca of the Gulf of Marseille, which was followed by an attempt to propose a phylogenetic classification of Crustacea. He described 25 crustacean species belonging to 5 different orders, with a special attention paid to parasites (*e.g.* Gourret 1887a, b, 1891). Then, he devoted his research to the development of "applied zoology", a discipline which aimed at rationalizing the exploitation of marine resources, through a better knowledge of population dynamics and the establishment of protected areas. This re-orientation of his research led to the publication in 1894 of a work that is still a reference for contemporary researchers: "*Les pêcheries et les poissons de la Méditerranée*" (Gourret 1894).

The period of specialized taxonomists (1937–1990) accounted 54 researchers, 8 of which are still active nowadays, who were usually specialized in one phylum or one order. For example, the Arthropoda phylum has been investigated by different specialists of Pycnogonida, Amphipoda, Copepoda, Mysidacea, Cumacea, Isopoda, *etc.* The first impulse was given by Petit who wanted to promote systematics**:** *« Une conséquence de l'essor de l'écologie, c'est la nécessité de remettre à l'honneur la systématique (…). Sans une systématique précise (…) l'écologie se perd d'elle-même et reste sans efficacité* », which translates as: « *A consequence of the rise of ecology is the need to put systematics back in the spotlight (...). Without an accurate systematics (...) ecology loses itself and remains ineffective* ».

However, Petit soon left the SME to head the marine laboratory of Banyuls-sur-mer (Jacques & Desdevises, 2021). He was replaced by Jean-Marie Pérès, who had the same philosophy about ecology and taxonomy. First almost alone, Pérès soon succeeded in giving an extraordinary impulse to the laboratory, with the addition of several collaborators. Among them was Jacques Picard, a zoologist with an encyclopaedic knowledge and a great enthusiasm for taxonomy. Together, Pérès and Picard undertook to update the unique, first description by Marion of the marine benthic communities of the Marseille area, which required numerous collections of specimens. Moreover, they developed annex laboratories where they also stimulated research on marine biodiversity, such as in La Rochelle (French Atlantic coast) and overseas at Tuléar, currently Toliara (Madagascar). As a specialist of Ascidiacea, Pérès described himself 45 taxa (*e.g.* Pérès 1948, 1951, 1952), while Picard, specialist of Cnidaria, described 15 taxa (*e.g.* Picard 1950, 1958). But, for three decades, their main action in taxonomy at the SME has been to encourage the emergence of vocations for marine natural history and to obtain the appointment on permanent positions of new specialists of Annelida, Amphipoda, Porifera, Copepoda, Bryozoa, Nematoda, Cnidaria, *etc.* In 1954, Pérès obtained the creation of specialized teaching in oceanography, mostly at the SME, with a special attention to benthic communities ("biocoenoses"), with Picard in charge of practical work at sea. One of their main purposes was to have a specialist for every taxonomic group in the laboratory. Hiring of numerous young scientists was helped by the CNRS (*Centre National de la Recherche Scientifique*) and by the emergence of CNEXO (*Centre National pour l'Exploitation des Océans*, which later became IFREMER: *Institut Français de Recherche pour l'Exploitation de la Mer*), in which Pérès was a main actor.

The most productive taxonomist of this period was undoubtedly Michel Ledoyer who described 391 taxa of crustaceans belonging to 5 different orders (Amphipoda, Cumacea, Leptostraca, Mysida, Decapoda). What is particularly remarkable about Ledoyer's naturalist work, achieved well before the molecular biology era, is that only a few species that he described are no longer valid today: only 9 Amphipoda out of 295 and 1 Cumacea out of 46. Ledoyer worked mostly on the Indo-Pacific (especially Madagascar, *e.g.* Ledoyer 1972) and the Antarctic/Sub-Antarctic (*e.g.* Bellan-Santini & Ledoyer 1974), but also on the Mediterranean (*e.g.* Ledoyer 1963, 1966a, c).

Following the example of Marion, Pierre Vitiello described 140 species and 5 genera of Nematoda by studying bathyal muds, mostly of the Marseille area (*e.g.* Vitiello 1970a, b, c; Vitiello 1971; Vitiello & Haspeslagh 1972; Aissa & Vitiello 1977). Among his descriptions, 97% remain valid taxa nowadays, and the pioneering use of Nematoda as marine bioindicators by Vitiello has inspired many scientists across the world (Aissa & Vitiello 1984; Mahmoudi 2007).

During this period, Helmut Zibrowius also deserves a special attention, as his boundless knowledge extends far beyond the taxonomic groups on which he has published. As a specialist of Annelida (mainly Serpulidae, *e.g.* Zibrowius 1968; 1973), Zibrowius described 32 species and 4 genera, and as a specialist of Cnidaria, he described 45 species and 3 genera of Scleractinia (*e.g.* Zibrowius 1974; 1980) and 20 species and one genus of Stylasteridae (*e.g.* Cairns & Zibrowius 2013). Of these taxa, 95% remain valid. Zibrowius' generalist skills were much sought after on European oceanographic cruises, and when he could not be on board, a special box labelled "Zibrozoans" gathered all organisms that could not be identified by the scientific crew. Today, he remains active, dedicated and committed to saving the natural heritage he has built, sorting out and distributing his biological collections to new specialists and museums over the world.

The third period, from 1990 to present, accounting 15 researchers, saw the continued participation of 8 taxonomists from the previous (2nd) period, whereas 7 were new additions to the SME. The period saw the advent of molecular techniques, later leading to the "integrative taxonomy" concept (see below and Cárdenas *et al.* 2012 for instance). During this period, new descriptions regularly combined analyses of morphologic and cytological traits, the development of various molecular markers, and the use of natural products chemistry and then metabolomics. This approach required collaboration of researchers from different disciplines, or mastering different techniques, and consequently authorship included more contributors than in the previous periods. During this period, researchers dedicated only a little part of their time to taxonomy, which focused mainly on Bryozoa, Crustacea and Porifera. However, they maintained some of the main original traits that gradually had become the trademark of marine research at the SME: the extensive use of SCUBA (most of them being also professionally-certified divers) for research, and the focus on hard substrate benthos (see below).

The temporal trend in species description (Fig. 5) clearly reflects the three pre-cited periods and the associated demography of taxonomists at the SME. The period of pioneering naturalists is productive but relies on very few persons with a strong specialization on some phyla. The following period of specialized taxonomists (1937–1990) is synonymous of exponential growth in species description with a boom in descriptions of Arthropoda, Porifera and Nematoda over the 1970s and 1980s. Since then, there has been a serious slowdown in the rate of species descriptions. Taxonomy and systematics gave way to new approaches in marine sciences that attracted more attention and funding. There were a few decades gap at the SME before the advent of integrative taxonomy allowed new species descriptions to be in the spotlight again. For phyla such as Porifera, species descriptions never stopped thanks to the taxonomic interest of natural products chemists all along the 1980s and 1990s (*e.g.* Aknin *et al.* 1990;

Barnathan *et al.* 1993; Loukaci *et al.* 2004; Vergne *et al.* 2006; Gabant *et al.* 2009). In return, from the 2010s, chemistry and metabolomics became a usual addition to poriferan and cnidarian taxonomy (Ivanišević *et al.* 2011; Cachet *et al.* 2015; Ruiz *et al.* 2015).

A few species are still described every year within some groups of Crustacea (Kaïm-Malka *et al.* 2016; Wittmann & Chevaldonné 2017; Wagner & Chevaldonné 2020; Wittmann *et al.* 2021), Bryozoa (Harmelin *et al.* 2019; Harmelin 2020; Taylor *et al.* 2021), Annelida (Borda *et al.* 2013; Stiller *et al.* 2013), but only one phylum, Porifera, has maintained a powerful and diverse group of researchers that is recognized worldwide.

Newly hired researchers brought new approaches to the SME, notably chemical and molecular ecology. Some "by-products" of these approaches have been the use of DNA and specialized metabolites to come in support of the more traditional approaches of taxonomy (Ivanišević *et al.* 2011; Cachet *et al.* 2015; Ruiz *et al.* 2015). This led to the practice of integrative taxonomy, particularly adapted to difficult phyla, such as sponges (Cárdenas *et al.* 2012; Ruiz *et al.* 2015; Klautau *et al.* 2022). With the increasing use of these methods, SME researchers have often discovered groups of cryptic species, only distinguished from each other by their DNA divergence, within supposedly well-defined and well-known taxa (Ereskovsky *et al.* 2011; Cachet *et al.* 2015; Greff *et al.* 2017). Although the finding of cryptic species leads only too rarely to the proper description of each uncovered species, this clearly contributes to a better knowledge of the studied biodiversity and to a new form of systematic description. It becomes only fully operational when integrated with other approaches (*e.g.* morphology, metabolomics) which are still practiced at the SME. This is the only way to render valuable modern approaches such as the metabarcoding of environmental samples. Metabarcoding alone would not help in describing species diversity, it would barely help evaluate our lack of knowledge. In future years these methods, when properly applied, will likely uncover a bounty of new species, even in supposedly well-described areas such as the NW Mediterranean.

The oceanic areas and the ecosystems covered

The greatest part of the described taxa was from the Mediterranean Sea (736 species, 44.3%), which clearly represents the main playground of the SME naturalists over the last 150 years (Fig. 3 and 4). The Indian Ocean and the Atlantic (24.7 and 19.7%, respectively) represent also two productive areas for species description (Fig. 4). The Pacific Ocean (7.5% of described species) was not much invested in spite of the occurrence of former French colonies such as Indochina, and the overseas territories of New Caledonia and French Polynesia. Antarctic and Subantarctic regions have been marginally explored (2.7%), while the 23 fossil species (1.4%) highlight the marginality of paleontological taxonomy at the SME (Fig. 4).

In the Mediterranean only (Fig. 3 and 4), which is by far the region that SME naturalists focused on the most, Arthropoda and Nematoda were the two most described taxa with respectively 126 and 147 species, followed by Porifera with 84 species then a cluster of taxa with >50 species described each (Annelida, Bryozoa, Ciliophora, Myzozoa). It is interesting to note that a strong geographic heterogeneity exists among the different Mediterranean subregions for these groups and the others. Porifera are for example the main described group from the Levantine Sea, Alboran Sea and the Adriatic while Nematoda were mainly described from the French metropolitan coast (see Fig. 3). Bryozoa is the only group with species described from all but one of the 15 subregions of the Mediterranean.

Due to sampling easiness and facilities, and certainly due to a better environmental knowledge, the number of species described is of course much more important in the Marseille area (493 species) and the nearby French coasts (Gulf of Lion, Provence and Corsica, with 37, 33 and 52 species, respectively) (Fig. 3). Surprisingly, the number of species in the other Mediterranean subregions never exceeds 18 species (in the Levantine Sea) reflecting at the same time political constraints and sampling opportunism through collaborations with foreign Mediterranean colleagues.

In the "*Esquisse d'une topographie zoologique du golfe de Marseille*" and in "*Considérations sur les faunes profondes de la Méditerranée d'après les dragages opérés au large des côtes méridionales de France*", Marion (1883a, b) provided a description of all ecosystems from the supralittoral to the bathyal zone. He drew detailed pictures of all species present in the different areas of the Gulf of Marseille. He gave a particular attention to the fauna present in the ports, describing very carefully, along 20 pages, the species distributed among the various areas of Marseille harbour. The second part was dedicated to the description of the fauna of the littoral zone. Starting by the semi-submersed zone, he carefully described the fauna of the seagrass beds, of the coralligenous bioconstructions, and of sandy and muddy bottoms found at different depths in the Gulf of Marseille. In the above-mentioned work especially devoted to the deep-water fauna Marion (1883a) explored the bathymetric range from the circalittoral to the lower bathyal zone (70–2020 m). The amount of data gathered with such "primitive" sampling techniques is really impressive. Marion's successors will considerably diversify the different habitats concerned by taxonomic works with a clear apparent dominance of species descriptions from deep sea habitats, reefs and to a less extent soft bottoms (Fig. 6). However, hard substrates from shallow and coastal zones (categorized in Fig. 6 as coral reef, diverse hard bottom, detritic, coralligenous, other biogenic substratum, cave) account for an extensive part of described species. In summary, about one third of described species were from the deep sea, another third from coastal hard bottoms and finally one third from soft bottoms, reflecting the all-out taxonomic works of SME researchers over time.

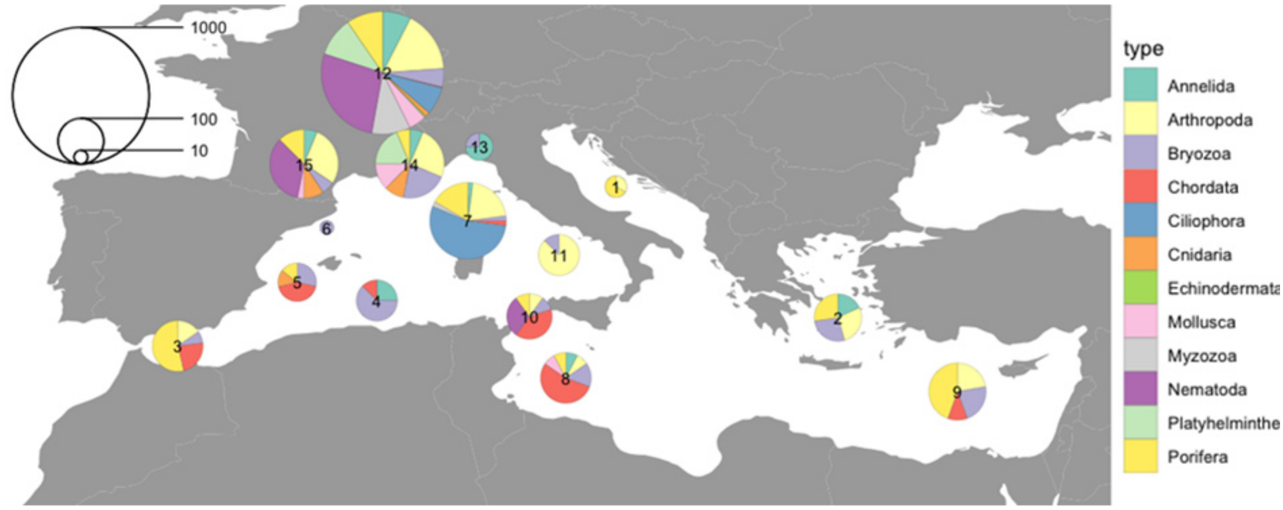

FIGURE 3. Distribution of new species discovered in the Mediterranean (type locality) by SME researchers. The size of pie charts is scaled according to the number of species. Only phyla with >10 species described per region are represented. 1: Adriatic Sea, 2: Aegean Sea, 3: Alboran Sea, 4: Algerian Basin, 5: Balearic Islands, 6: Catalonia, 7: Corsica, 8: Gulf of Gabès/Tunisian Plateau, 9: Levantine Sea, 10: Strait of Sicily, 11: Tyrrhenian Sea, 12: Marseille area, 13: Ligurian Sea; 14: Provence, 15: Gulf of Lion.

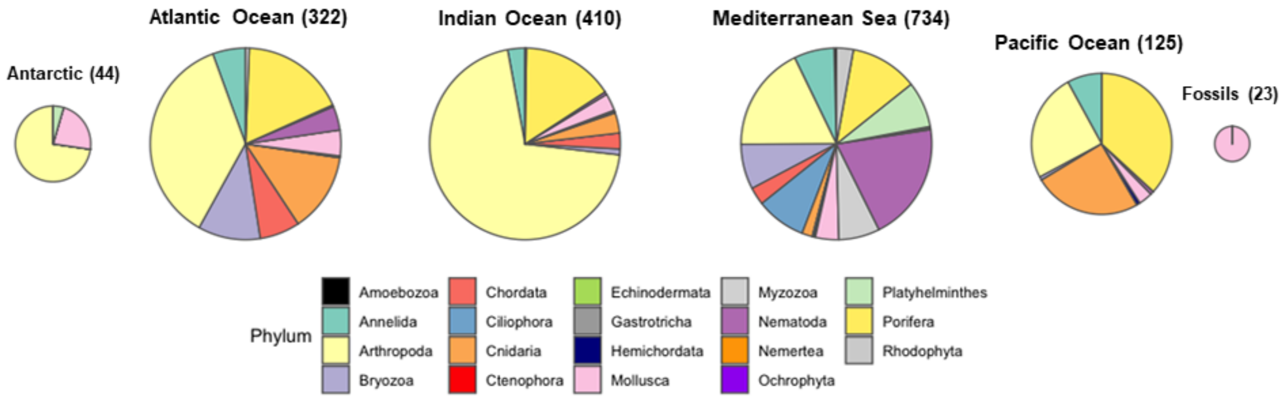

FIGURE 4. Geographical origin (type locality) and phylum (including fossils) distribution of valid species described by SME researchers. The size of pie charts is scaled according to the number of described species indicated between brackets.

Whereas Marion's work was essentially focused on the Marseille area, the "*Nouveau manuel de bionomie benthique de la Mer Méditerranée*" (Pérès & Picard 1964), had the ambition to draw a synthetic view of all biocoenoses and ecosystems of the Mediterranean Sea. Pérès and Picard recognized several biogeographic units which were characterized by their benthic communities, from West to East: Alboran Sea with a mixture of Atlantic & Mediterranean species, the Western Mediterranean divided in three entities (Algerian Basin, Central sector and Northern sector), the Adriatic Sea and the Eastern Mediterranean (Levantine Sea, Aegean Sea). In spite of obvious differences between the studied areas, they considered the Mediterranean benthic communities as relatively homogenous. They underlined that the bathymetric zonation proposed by Marion was mainly based on the light intensity rather than to a particular depth. For instance, the coralligenous extends to shallower depths in the Western part of the Gulf of Lion, where the light intensity is affected by the turbidity of the Rhône River plume, than in the Eastern Basin (Laborel 1961). This essential synthetic "*Manuel*", of course could not have existed without, and much relied upon, the detailed contributions achieved by all SME taxonomists (*e.g.* Bellan 1959; Bellan-Santini 1962; Brunet 1965; Bellan-Santini, 1965; Gautier 1962; Vacelet 1959) and ecologists (*e.g.* Molinier 1960). The Mediterranean still remains today a hotspot of taxonomic species description for SME researchers; Marseille, Provence and adjacent areas such as the Ligurian Sea and Corsica remain their favourite playground (Fig. 3).

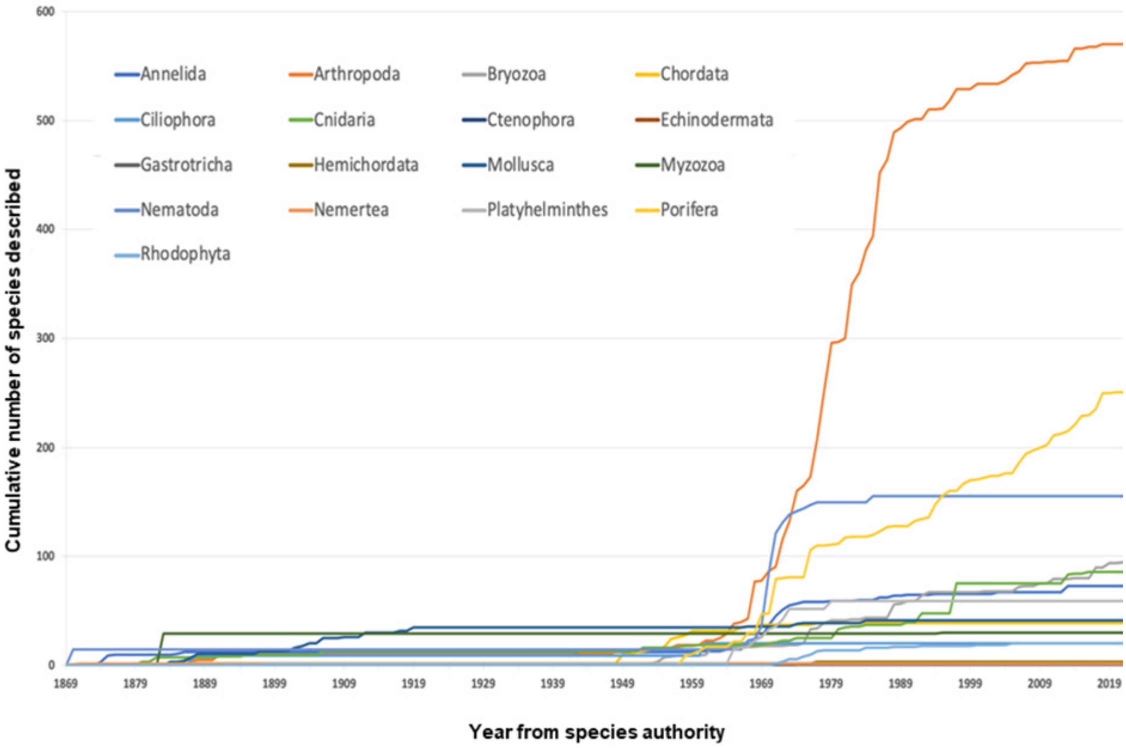

FIGURE 5. Cumulative number of species described per phylum at the SME over time. The year used corresponds to the year of description according to the species authority. Only still valid species were considered.

However, the geographic area covered by the SME researchers, was not limited to the Mediterranean, and other regions such as the Indo-Pacific and the Atlantic were intensively explored (Fig. 4), especially because Pérès was very active at the international level. For example, a big expedition, the first of such a scale in this region, was organized by the SME aboard Captain Cousteau's R/V *Calypso* along the Atlantic coast of South America, with the participation of CNRS and the MNHN (*Muséum National d'Histoire Naturelle de Paris*). A key member of this expedition, Jacques Laborel, had been sent by Pérès in Recife in 1961 where he later worked on his doctoral thesis (Laborel 1970). This was a very significant contribution to the knowledge of Atlantic coral reef ecosystems by the SME researchers (Nonato & Pérès 1961; Laborel 1970; Laborel-Deguen *et al.* 2019). It was also the beginning of a long-lasting collaboration with Brazilian researchers, a collaboration still active today.

In the same period, Pérès also initiated tropical studies in Madagascar. From 1961, regular expeditions were organized to Tuléar (Toliara, SW Madagascar), which achieved precise descriptions of the biodiversity of the local tropical reef ecosystems, with 227 taxa described (*e.g.* Vacelet 1967; Ledoyer 1969; Vasseur 1969; Gravier *et al.* 1970; Thomassin 1970; Arnaud F. 1971; Vacelet & Vasseur 1971; Vacelet *et al.* 1976; Harmelin-Vivien *et al.* 1982). Many of the results of such expeditions were published in "Supplements" of the *Recueil des Travaux de la Station marine d'Endoume*.

From the late 1960s, an important development occurred with the participation for a period of about 20 years of Patrick Arnaud to regular expeditions in the Antarctic and in Sub-Antarctic islands: Terre Adélie, Kerguelen, Crozet, St Paul & Amsterdam. His pioneering work led to the description of the benthic ecosystems of Terre Adélie, and of about 40 new taxa (e.g. Arnaud F. 1971, 1972; Arnaud P. 1972; Vacelet & Arnaud, 1972; Bellan-Santini & Ledoyer 1974; Ledoyer 1977a, b, 1990, 1995).

During this 2nd period summarized above, the popularization of SCUBA diving (Laborel & Vacelet 1958; Laborel 1961; Ledoyer 1966a, b, c), the technical development of manned submersibles (Pérès & Picard 1955, 1956; Pérès 1958; Laborel *et al.* 1961; Augier & Boudouresque, 1979) as well as of a fleet of French oceanographic vessels, allowed huge progress to be made with the study of the biodiversity of hard bottoms. This is especially the case for deep-sea canyons with submersibles (Vacelet 1969), and to underwater marine caves with SCUBA (Laborel & Vacelet 1958; Ledoyer 1963; Harmelin *et al.* 1985). These technical advances would have had long-lasting consequences on the still ongoing special interest SME taxonomists have of remote and dark habitats, and on the benthic vs. pelagic realm.

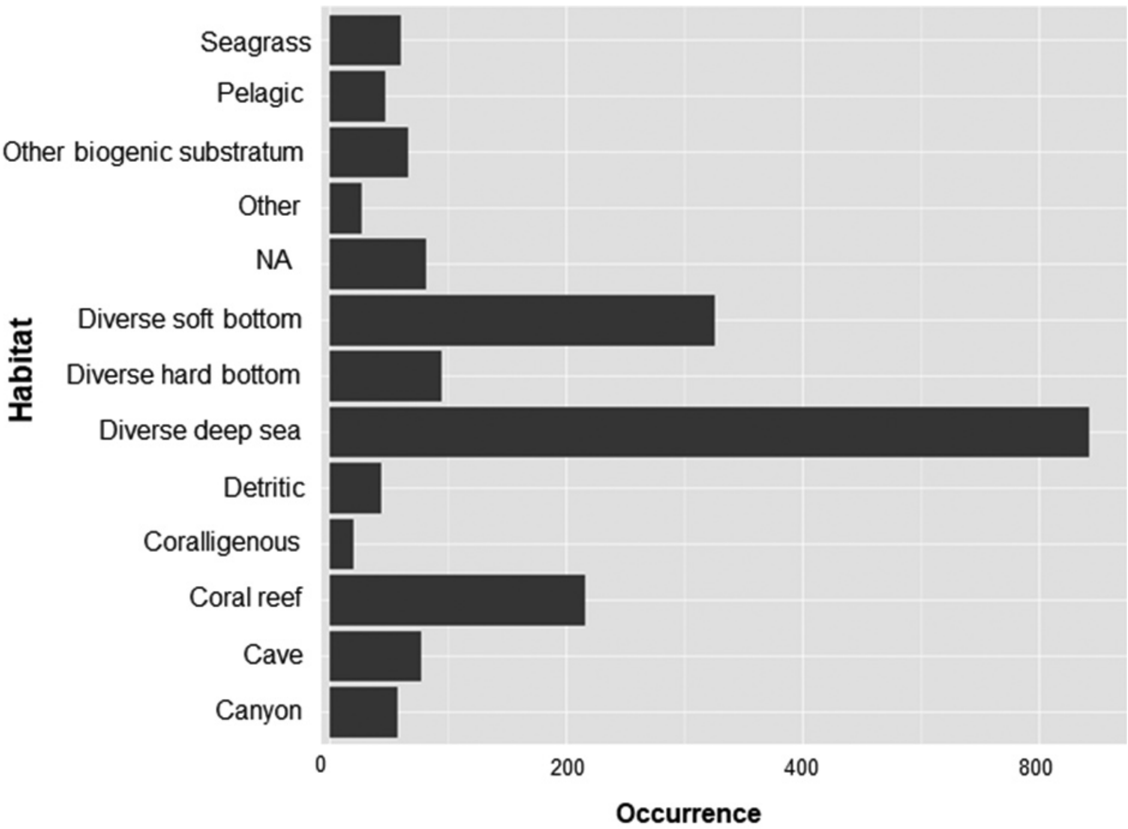

FIGURE 6. Occurrence of species described at the SME according to their habitat. Should a species be reported from several habitats at the same time in the original description paper, it was accounted for each of the habitats. NA: data not available.

The 3rd period, starting in the 1990s and currently still ongoing, saw a clear retreat of taxonomy and systematics at the SME. Many of the prominent specialists of the previous period had disappeared or retired and the rare new recruits were not hired on the basis of their taxonomic skills. With much fewer scientists playing a role in describing new species, the SME lost its expertise in some ecosystems and habitats. Notably, the soft-bottoms expertise virtually disappeared and entire phyla were no longer considered locally. Several researchers also carried on working on deep-sea hydrothermal vent taxa for a while (*e.g.* ten Hove & Zibrowius 1986; Bellan-Santini & Thurston 1996; Bellan-Santini 2005, 2006, 2007; Borda *et al.* 2013; Stiller *et al.* 2013), but this particular deep-sea extreme habitat is no longer within the area of expertise of the SME today. Gradually, the SME expertise reduced to seagrass meadows and hard substrates, especially underwater caves and deep-water rocks and canyons. This specialization resulted in an international workshop organized at the SME in 2018 on Deep-Sea and Cave Sponges which has allowed the publication of a special volume in *Zootaxa* (Klautau *et al.* 2018; Boury-Esnault 2018) to celebrate 60 years of cave research (*e.g.* Cárdenas *et al.* 2018; Lage *et al.* 2018).

The discovery of a littoral cave with bathyal environmental conditions, the 3PP cave, at the beginning of this period gave a new impulse to the study of caves and allowed the discovery of Hexactinellida at 25 m deep (Vacelet *et al.* 1994), followed by the description of the 1st carnivorous sponge (Vacelet & Boury-Esnault 1995) as well as deep-sea bryozoans (Harmelin 1997) or poorly known ascidians (Monniot & Zibrowius 1999). The exploration of caves along Mediterranean-Atlantic coasts as well as in the South Pacific or Antarctic has demonstrated that they shelter an original species diversity (Logan & Zibrowius 1994; Harmelin *et al.* 2003; Calado *et al.* 2004; Pérez *et al.* 2004; Zibrowius & Taviani 2005; Bakran-Petricioli *et al.* 2007; Chevaldonné *et al.* 2015; Grenier *et al.* 2020; Wittmann

& Chevaldonné 2021). Also, the exploration of Mediterranean deep canyons was revived thanks to institutional conservation efforts to extend marine protected areas to the deep sea. This led to a series of research cruises and to an overview of the biodiversity at deep canyons and offshore rocks of the French Mediterranean (Boury-Esnault *et al.* 2015, 2017; Fourt *et al.* 2017; Grinyo *et al.* 2021), and also in remote overseas territories (Chevaldonné & Pérez 2016; Pérez *et al.* 2016).

Key taxa descriptions and their contribution to a broader scientific knowledge

The above statistics do not reflect the qualitative contribution of the different species described at the SME over 150 years and how some of them contributed to great scientific advances in various fields of natural sciences. Thereafter, we selected emblematic species or group of species which represent the SME trademark.

Glandiceps talaboti **(Marion, 1876) (Fig. 7): a deep-sea worm with affinities to echinoderms and chordates (Hemichordata, Enteropneusta, Spengelidae)**

In July–October of 1875, Antoine-Fortuné Marion had undertaken a dredging inventory of the deep-sea bottom to the south-east of the Bay of Marseille, to complete his previous studies of the littoral zone (Marion 1873). These dredging efforts were realized thanks to the financial support of a group of his friends (Talabot, Benet, Renouard, Meilhac, Mazel, Gallas and Martin). Among the most interesting discoveries he made was a new enteropneust species from yellowish sticky mud at 350 m depth in the area then called "Plateau Marsilli". First Enteropneusta from Provence at this time, it was shortly described by Marion in 1876 as *Balanoglossus talaboti*, to honour one of his friends and sponsors. Later, he gave a very complete description of the species, pink-coloured, cylindrical and composed of a short anterior and conical proboscis, a collar where the mouth opens, and a trunk (Marion, 1885, 1886). Marion could observe the animal alive, crawling on the sediment surface of an aquarium for several weeks and noticed the emission of thick mucus with iodine smell when the animal was disturbed. Later, Spengel (1893) studied the enteropneusts of the Bay of Naples and subdivided the genus *Balanoglossus* in four genera, assigning Marion's species to the genus *Glandiceps*, even becoming its type-species. The Enteropneusta, although not species-rich, are part of the Hemichordata and as such have a major evolutionary interest due to their close relationships with both Echinodermata and Chordata.

Glandiceps talaboti is a Mediterranean endemic species. It was later collected in bathyal mud of the Cassidaigne and Lacaze-Duthiers canyons (DPR096 cruise, see photo, Zibrowius personal communication), possibly along Egyptian coasts near Alexandria, and also recently off Turkey (Çevik & Erguden 2005).

Hemimysis speluncola **Ledoyer, 1963 (Fig. 8): an unexpected model for Mediterranean climate change and evolutionary ecology**

Being among the first SME researchers to use SCUBA, in 1958 Laborel & Vacelet (1958) reported of surprisingly dense swarms of a small red mysid (Crustacea: Mysida) in the darkest reaches of a small underwater marine cave of the Bay of Marseille at Niolon. Closely resembling the well-known Atlantic species *Hemimysis lamornae* (Couch 1856), it was later recognized that such swarms were common in dark caves of the Marseille area, and that some of them were made of a new species, *Hemimysis speluncola* Ledoyer, 1963. For twenty years (1966–1986), the new species then became a model for behavioural ecology and ecophysiology, as it was found relatively easy to maintain in aquarium (*e.g.* Macquart-Moulin & Patriti 1966; Gaudy *et al.* 1980; Bourdillon & Castelbon 1983; Passelaigue & Bourdillon 1986). Among other things, *H. speluncola* displayed original horizontal circadian migrations in and out of caves to feed, in a way similar to the vertical migrations of deep-sea zooplankton. Suddenly, in the late 1990s, concomitant with the first marine heat wave and invertebrate mass mortalities recorded in the NW Mediterranean, Chevaldonné & Lejeusne (2003) provided evidence that, in most of its known geographic range, *H. speluncola* had vanished, gradually being replaced by the more thermophilic *Hemimysis margalefi* Alcaraz, Riera & Gili, 1986. This was the first documented Mediterranean warming-induced species shift and it triggered a series of studies on the *Hemimysis* species (many of which cryptic) present in the Atlantic-Mediterranean area, to investigate their molecular phylogeography and evolutionary history. Today, cave-dwelling *Hemimysis*, including the now-endangered *H. speluncola*, have become a model to study the effect of natural habitat fragmentation on population connectivity (Lejeusne & Chevaldonné 2006; Rastorgueff *et al.* 2014).

FIGURE 7. *Glandiceps talaboti*: Upper and lower left, respectively dorsal and ventral drawings of *G. talaboti* observed in vivo by Marion, 1886. Right, recent photograph from a specimen collected in Lacaze-Duthiers canyon during the DPRO96 cruise at 534–634 m. (Coll. H. Zibrowius, Photo by Dieter Fiege). Scale: 2 cm.

Peyssonnelia rosa-marina **Boudouresque & Denizot, 1973 (Fig. 9): an unsuspected Mediterranean rose garden**

It is perhaps one of the most abundant seaweeds in the Mediterranean Sea, since it thrives from the infralittoral to the widely extended and widespread coastal detritic bottoms, in the circalittoral, where it is often dominant. It is also a particularly elegant macrophyte, resembling a calcified rosebud, hence its name, *Peyssonnelia rosa-marina*. Like many red algae, this seaweed can live in rather low irradiance down to ca. 100 m depth; it is an important producer of carbonate sediment and is furthermore an ecosystem engineer that takes a significant part in the construction of the coralligenous beds so characteristic of the Mediterranean. Yet, it has long been confused with its sister species, *Peyssonnelia polymorpha*, until the 1970s. It was then very surprising to realize that such an abundant, conspicuous, and well-characterized species, both by its morphology and anatomy, had been overlooked for so long.

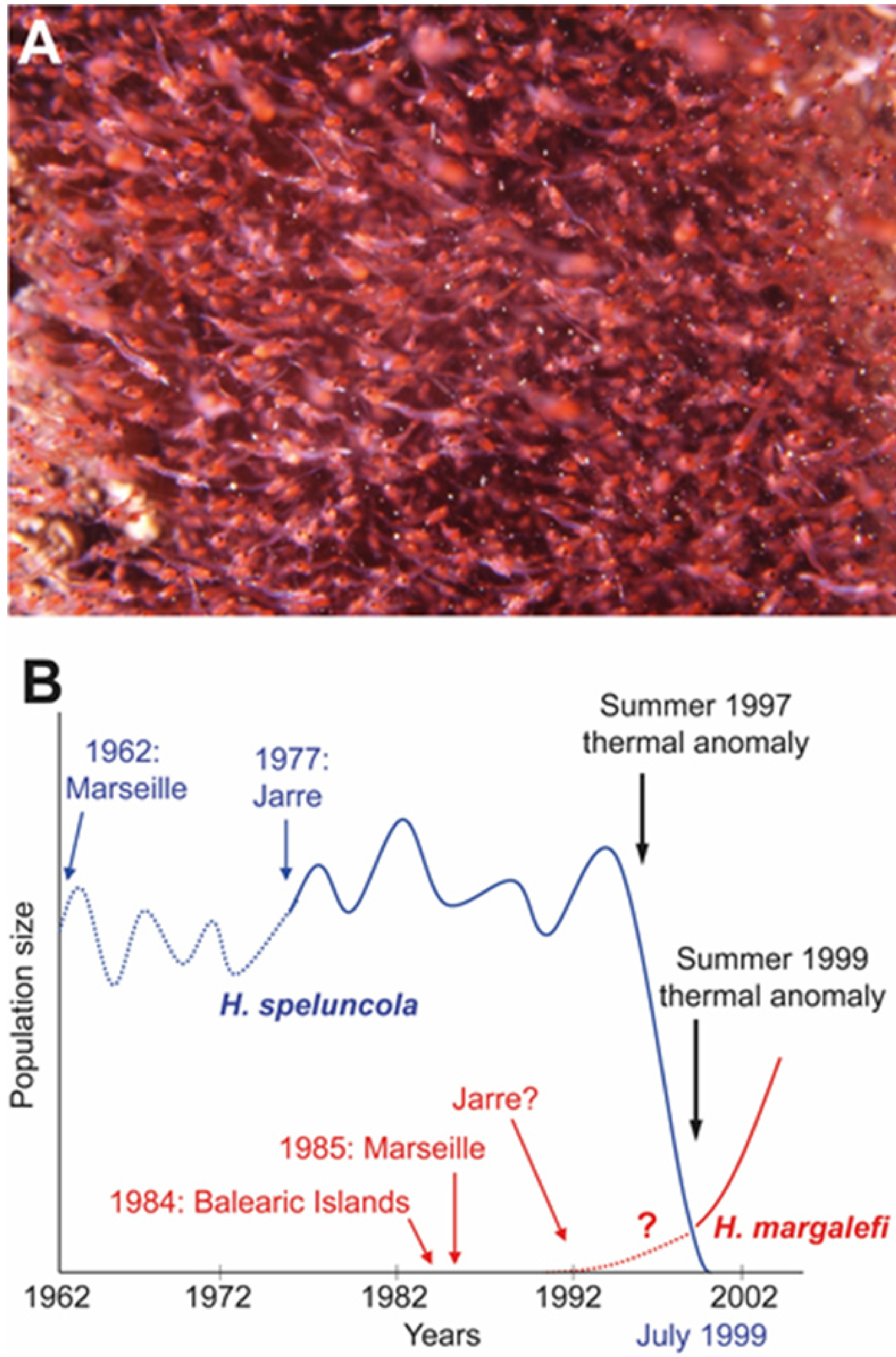

FIGURE 8. *Hemimysis* mysids: A) The currently dominant swarming *Hemimysis* species, the thermophilic *H. margalefi* in Jarre cave near Marseille, S. France (Photo J.-G. Harmelin). B) Schematic representation of changes that occurred in the populations of the two Mediterranean species of *Hemimysis* in Jarre cave until the occurrence of marine heat waves at the turn of the century. Modified from Chevaldonné & Lejeusne (2003).

FIGURE 9. *Peyssonnelia rosa-marina* in its habitat on the Calanques coast, Figuerolles (Provence), 13 m depth. Photo Jean-Pierre Miquel. Total length ca. 5 cm.

***Paracheilinus hemitaeniatus* Randall & Harmelin-Vivien, 1977 (Fig. 10): the half-banded flasherwrasse of mesophotic habitats off Madagascar**

Paracheilinus hemitaeniatus is a rare brightly colored fish species sampled for the first time in 1972, at 45 m depth on the outer slope of the barrier-reef off Toliara, SW Madagascar. Created in 1961 as a branch of the SME, the marine station of Toliara (Tuléar) hosted many scientists who studied the coral reef communities and described a number of new species of marine organisms, contributing largely to improve our knowledge on coral reef diversity. The half-banded flasherwrasse is known only from the south-west of the Indian Ocean, Madagascar and Comoro Islands, where this elusive and beautiful species remains a 'holy grail' for photographers. It belongs to the Labridae, a highly diversified fish family, where sexual dimorphism is so pronounced that males, females and juveniles have often been described as separate species by early ichthyologists! Such color dimorphism is viewed as an adaptation to sexual selection and life in coral reefs, where it is more conspicuous than in other environments. Labrids play an important role in the trophic functioning of coral reefs due to their high abundance and diverse feeding behaviors, from small zooplanktivores, crustacean and mollusk feeders to large-sized piscivores. *P. hemitaeniatus* is a small (<12 cm) species feeding mainly on tiny planktonic crustaceans and participating with other species to the carbon transfer from the water column to mesophotic coral reef habitats.

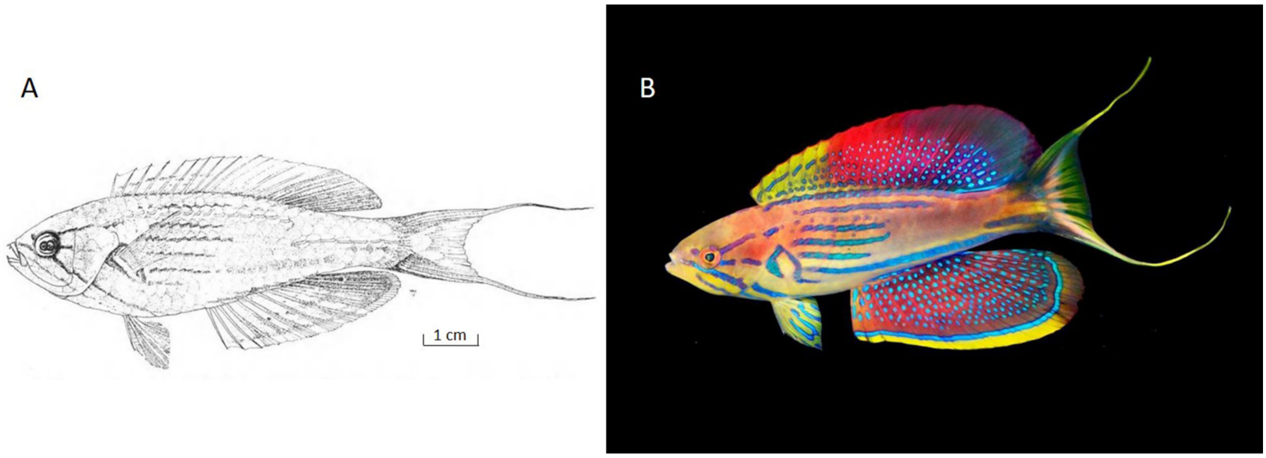

FIGURE 10. *Paracheilinus hemitaeniatus*: A) Original drawing by M. Harmelin-Vivien. B). Underwater picture from Madagascar, author unknown.

The poorly-known Spionidae genus *Lindaspio* (Annelida: Polychaeta) and the finding of *Lindaspio sebastiena* Bellan, Dauvin & Laubier, 2003 (Fig. 11), from an oil-field off Congo (Western Africa)

The genus *Lindaspio* was created by Blake & Maciolek (1992), to accommodate two original spionid polychaetes species recovered from two different sedimented deep-sea hydrothermal vent areas in the Pacific. Later, polychaete material obtained from sediment at 150 m depth near an oil platform of the offshore oil field of N'Kossa, Congo (Central Western Africa), yielded a third species, *Lindaspio sebastiena* Bellan, Dauvin & Laubier, 2003. Other reports of this genus are very rare, the last one being a yet undescribed *Lindaspio* species from a whale-fall site on the São Paulo Ridge (Sumida *et al.* 2016). The four species therefore appear to share a preference for reducing environments such as deep-sea sediments rich in decaying organic matter or hydrothermal fluids. Among their peculiarities, these species display unusually large gills, likely an adaptation to life in low-oxygen environments; in *L. sebastiena*, gills even display a "felting" that may be useful in further increasing gill surface area.

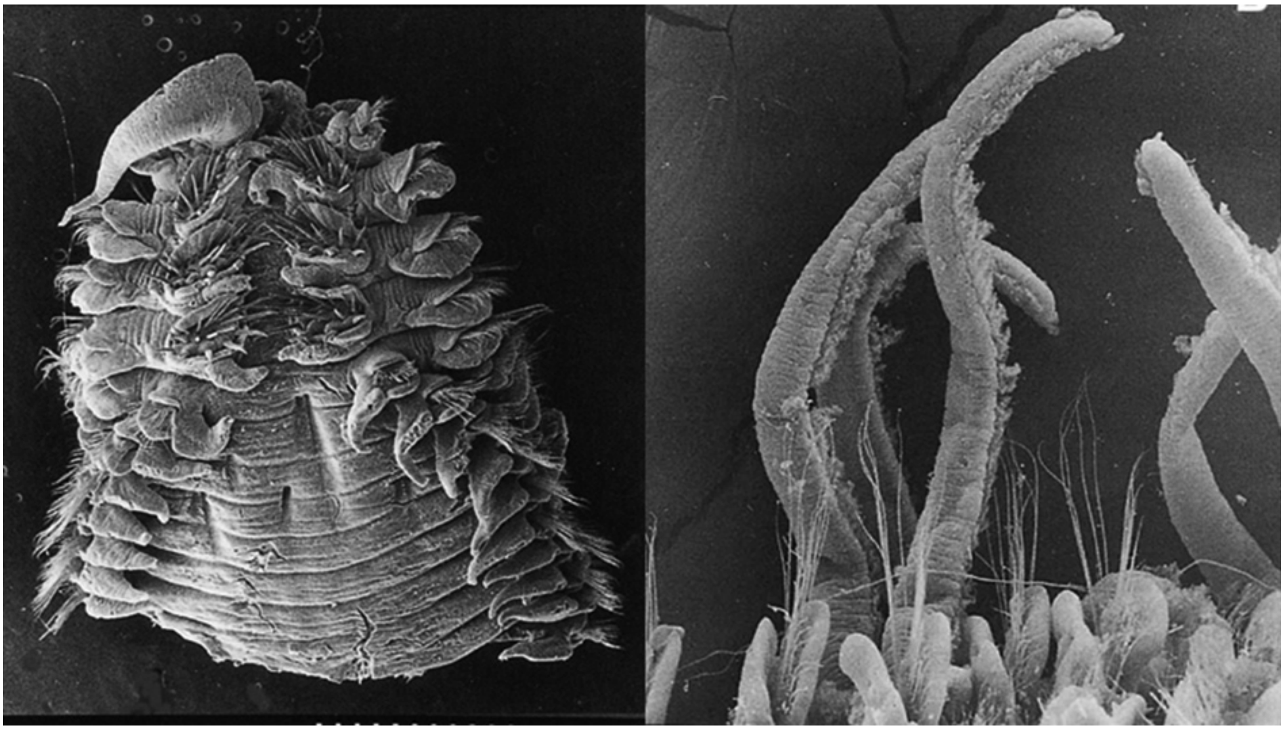

FIGURE 11. *Lindaspio sebastiena*: Left, anterior part. Right: "Felting" visible on notopodial branchiae. Modified from Bellan *et al.* (2003).

The *Rhachotropis* species (Fig. 12) of Mid-Atlantic Ridge deep-sea hydrothermal vents: *R. flamina, R. licornia, R. pilosa* Bellan-Santini, 2006

SME taxonomists also have taken part in the major adventure started with the 1977 discovery of deep-sea chemosynthetic animal communities. In the vicinity of hydrothermal vents of the Mid-Atlantic Ridge, 3 new species of *Rhachotropis* (Crustacea: Amphipoda: Eusiridae) were collected by sediment traps at 1700–2750 m depth: *Rhachotropis flamina* Bellan-Santini, 2006, *Rhachotropis licornia* Bellan-Santini, 2006, and *Rhachotropis pilosa* Bellan-Santini, 2006.

With 63 species (Horton *et al.* 2021) this genus is found in all oceans with a large bathymetric distribution (0–7160 m) (Lörz *et al.* 2018). It is the most common amphipod genus in bathyal and abyssal zones.

Morphologically, *Rhachotropis* have a delicate body with slender pereiopods, long antennae and sometimes dorsal processes. However, some of them display antennae bearing complex and puzzling structures called calceoli (present in *R. pilosa* and *R. licornia*) that are believed to be part of sensory organs. Cuplike receptacles, arranged serially on the antennae, would act as non-visual sensory organs, ensuring the perception of sound and vibration stimuli by the amphipods. These likely mechanoreceptors are found in several amphipod species (Hurley 1980, Lincoln & Hurley 1981, Bellan-Santini 2015); some could be involved in the detection of mates, others to detect preys. However, at hydrothermal vents, they could also be a good way to locate active fluid emissions.

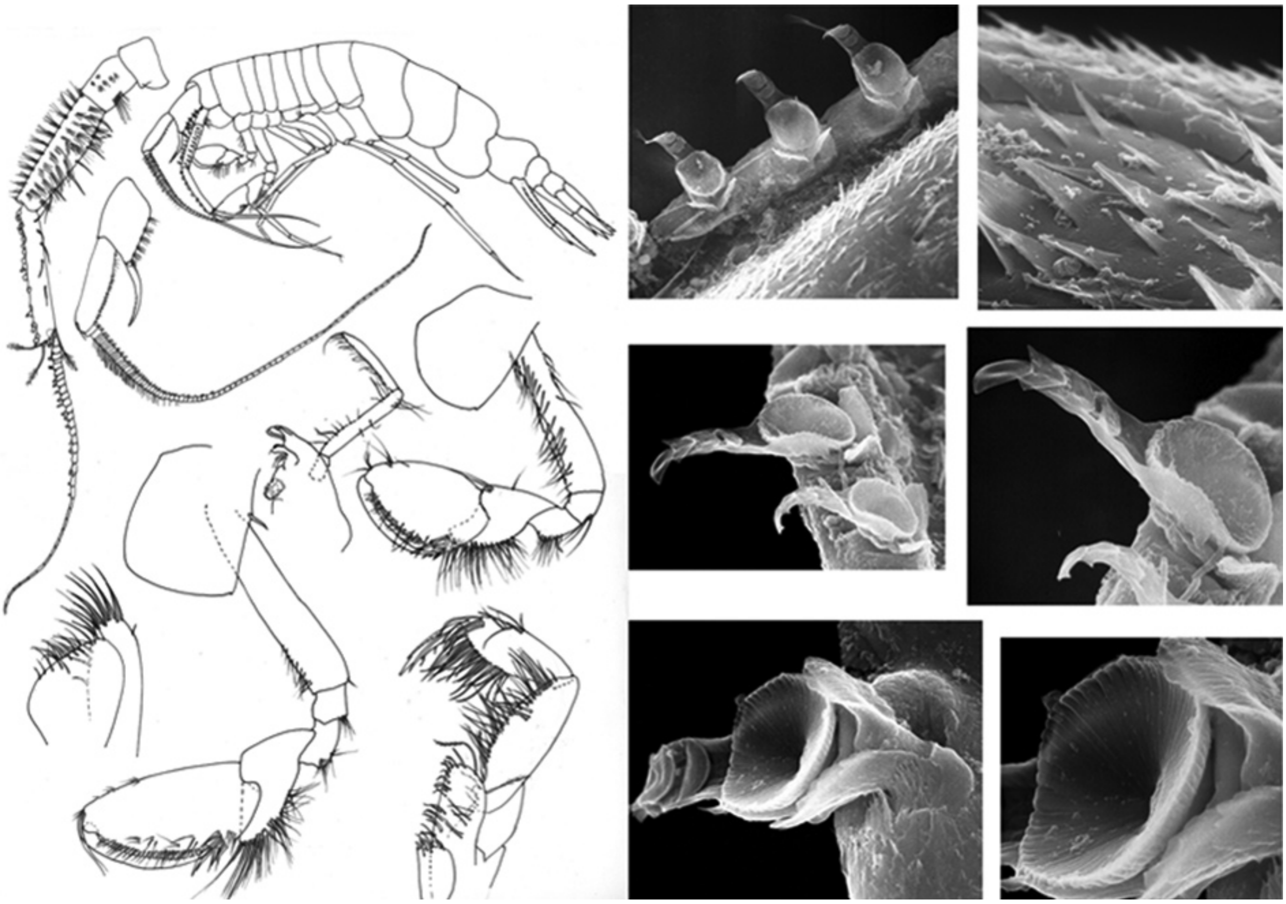

FIGURE 12. *Rhachotropis licornia* female holotype (10 mm): Left: habitus, antenna 1 and 2, mandibles, maxilla, maxilliped and gnathopods. Right: Scanning Electron Micrographs of antenna 1 with calceoli, and surface of antenna 1, different magnifications and views of calceoli. Modified from Bellan-Santini (2006).

***Schizoretepora hassi* Harmelin, Bitar & Zibrowius, 2007 (Fig. 13): a mysterious bryozoan from the East**

Schizoretepora hassi is a cheilostomate bryozoan belonging to the Phidoloporidae, i.e. the family of the beautiful reteporid *Reteporella grimaldii* (Jullien, 1903), the so-called "lace coral" well-known of Mediterranean divers and which has been the first bryozoan in the world to be illustrated in the literature, by Rondelet in 1554. Among the bryozoans described from the material collected during surveys of the Station Marine d'Endoume, *S. hassi* is not the most spectacular and its features are only but typical of the family. It lives in shaded rocky habitats of the Lebanese littoral zone and has not yet been found anywhere else. What is surprising is that a Mediterranean species living in the shallow coastal zone with large, conspicuous colonies, had not been described before. The question of its status, steno-endemic of the Levantine Basin or Erythraean immigrant introduced in the Mediterranean, remains open. It was dedicated to Dr Hans Hass, Austrian biologist who was both a famous diving icon and a pioneer in scientific diving and underwater photography. In 1948, he also had written a thesis on the Mediterranean reteporids, collected by diving.

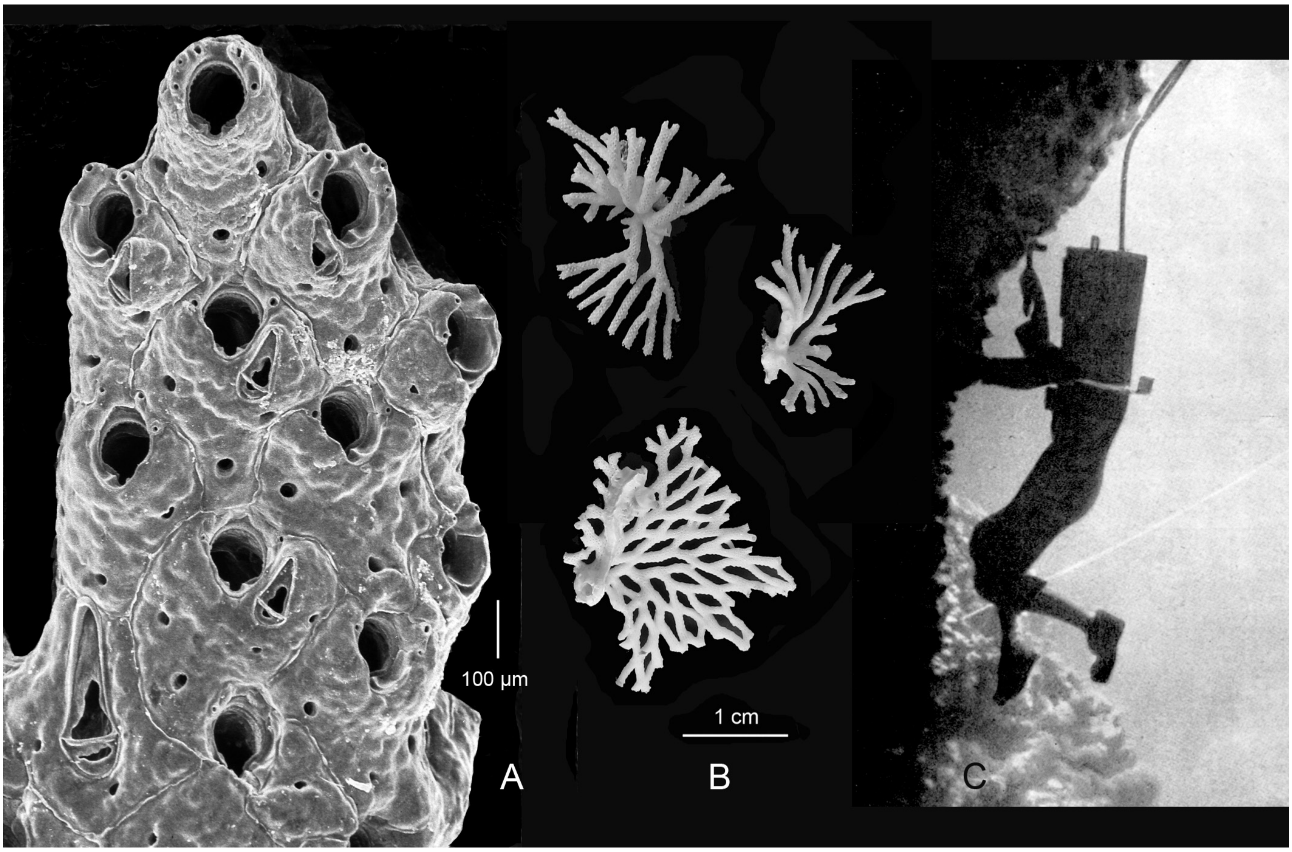

FIGURE 13. *Schizoretepora hassi*: A & B, samples from Lebanon (A: scanning electron micrograph). C: Hans Hass collecting bryozoans in the 1940s in Greece (From Hass, 1952).

Cave-dwelling wonders (Fig. 14), the actors of a perpetual revolution in sponge biology

The exploration of submarine caves is probably the practice that has enabled SME researchers to make among the most groundbreaking discoveries in zoology. In this marine habitat, sponges, the oldest metazoans, widely distributed on the planet, dominate in terms of biomass and diversity (Harmelin *et al.* 1985; Grenier *et al.* 2018).

During the earliest cave explorations (Laborel & Vacelet 1958), it appeared that a strange calcareous sponge had not only calcareous spicules, but also a massive "hypercalcified" skeleton. The discovery of *Petrobiona massiliana* Vacelet & Lévi 1958 shed a new light on ancient reef builders which were common in the Mesozoic, but rare at present. The dense populations of this hypercalcified sponge in Mediterranean caves prompted their search in other refuge habitats (coral reef caves, bathyal cliffs) leading to the discovery of unexpected survivors of important Mesozoic reef builders such as chaetetids or stromatoporoids, thought to be Cnidarians before the 1970s (Hartman & Goreau 1970; Vacelet *et al.* 2010). One hypercalcified sponge of the Indo-Pacific, *Vaceletia crypta* (Vacelet 1977), proved to be a survivor of the sphinctozoans, believed to be extinct since the end of the Cretaceous and of uncertain affinities. The surviving species shed new light on the likely sponge nature of archaeocyaths, the first reef-builders of Cambrian times.

Cave-dwelling sponge biodiversity became the specialty of two generations of SME researchers who developed skills to study unusual body plans. Among well-represented singularities of underwater caves, skeleton-less sponges have been one of the greatest challenges, as the absence of fundamental characters of sponge taxonomy required attention to other phenotypic traits. Allowing the description of various new genera (*e.g. Myceliospongia* Vacelet & Pérez, 1998; *Thymosiopsis* Vacelet & Pérez, 1998; *Vansoestia* Díaz, Thacker, Redmond, Pérez & Collins, 2015;

Pseudocorticium Boury-Esnault, Muricy, Gallissian & Vacelet, 1995; *Aspiculophora* Ruiz, Muricy, Lage, Domingos, Chenesseau & Pérez, 2017) and species belonging to clades of spiculate sponges (*e.g.* Tetractinellida, Plakinidae), a new kind of taxonomy developed at the SME: the integrative taxonomy.

Homoscleromorpha is one of such groups containing many skeleton-less species. About 50% of the species of this group have been described over the last 40 years only as a result of increasing research in caves. A first consequence of this high rate of new descriptions has been a profound overturning of the Homoscleromorpha systematics, from a subclass within Demospongiae to a fourth class within Porifera. It also led to the recognition of two homoscleromorph families, originally supported by the absence (Oscarellidae) or the presence (Plakinidae) of a skeleton, now overturned by the description of several skeleton-less Plakinidae (see Boury-Esnault *et al.* 2013 and Ruiz *et al.* 2017). A second consequence was the acknowledgment of some fundamental phenotypic traits of the Eumetazoa in sponges (*e.g.* true epithelium) which made one representative of this class, *Oscarella lobularis*, a new model species in evolutionary biology (Ereskovsky *et al.* 2009).

However, the most extraordinary discovery from a dark submarine cave was undoubtedly the carnivorous sponge *Lycopodina hypogea* (Vacelet & Boury-Esnault, 1996). The description of this species has indeed revolutionized the definition of sponges found in all dictionaries around the world: a sponge that does not have the common sponge body plan, which does not pump and filter seawater, but feeds on living animal prey without any digestive tract (Vacelet & Boury-Esnault, 1995)! These sponges, belonging to the family Cladorhizidae, were known only from deep-sea ecosystems, and the discovery of this cave representative thus allowed revealing their true nature. Following this, an increased interest for deep-sea sponges led to a high rate of new descriptions in this family over the last 25 years. Today, 223 carnivorous species are known from deep-sea ecosystems, 33 of which described by SME researchers (de Voogd *et al.* 2022).

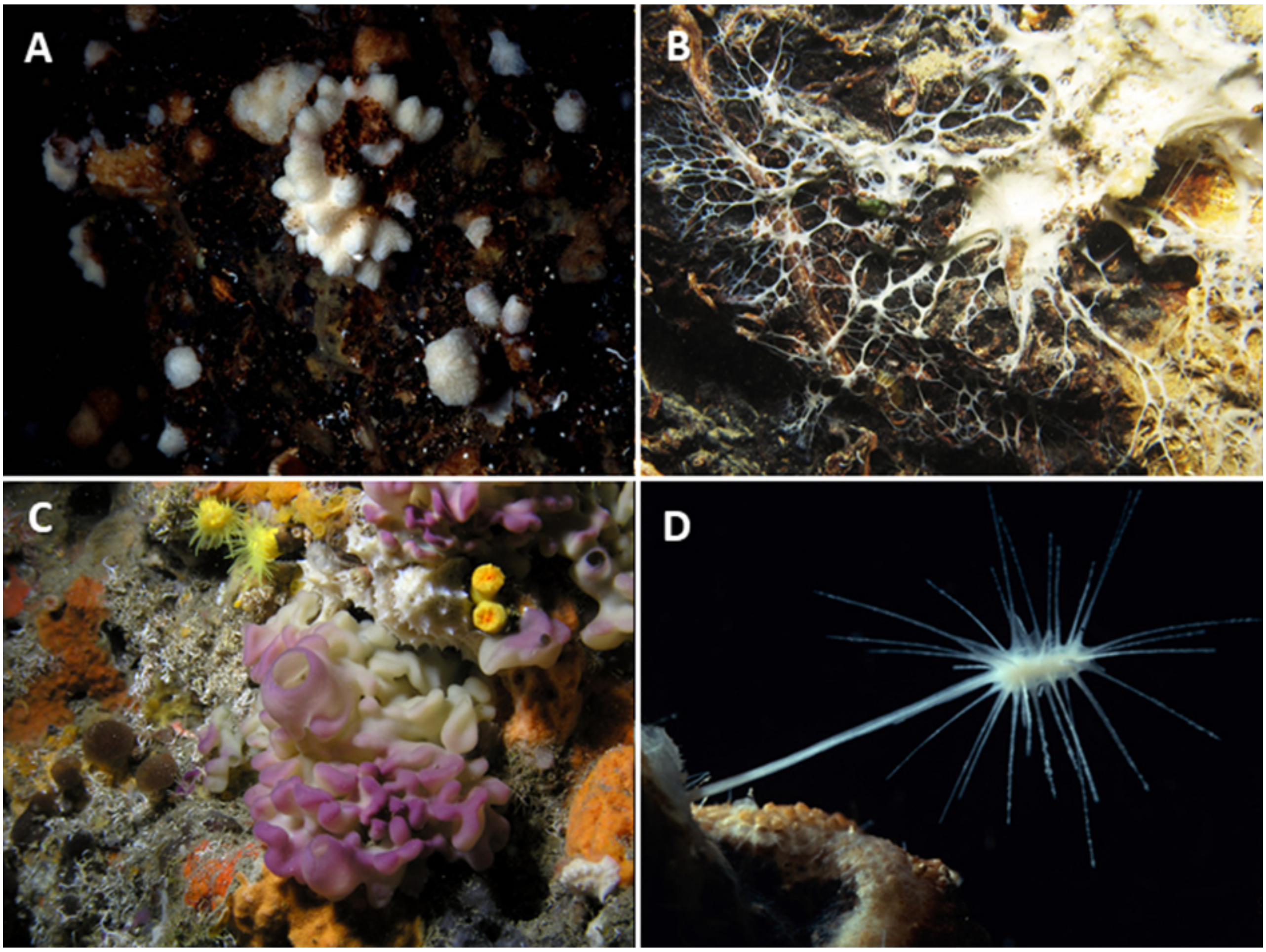

FIGURE 14. Cave-dwelling sponges: A) the Mediterranean hypercalcified sponge *Petrobiona massiliana*, B) *Myceliospongia araneosa,* a skeleton-less Demospongiae that long remained *incertae sedis*, C) *Oscarella lobularis*, an homoscleromorph sponge which became a model in Evo-Devo, D) The carnivorous sponge *Lycopodina hypogea*.

Conclusions

The turn of the century has seen taxonomy being abandoned in favor of holistic approaches allowing the assessment of genetic or functional diversity of environments believed to be perfectly known (Rogers *et al.* 2022). However, in geographical areas such as the Mediterranean, where ecosystems have been studied by naturalists for more than two centuries, species diversity is far from being acceptably known and there are still many macroscopic species to be described (Bianchi *et al.* 2012). Genomic assessments of this diversity, using environmental DNA approaches, have multiplied, but the alpha biodiversity remains unidentified and many ecological functions in the ocean have not been discovered yet. As a result, there is nowadays a new demand for taxonomic expertise, particularly now that the "biodiversity crisis" is widely acknowledged (Boero 2001), to contribute to large international initiatives to sequence marine genomes or hologenomes, but also to define marine ecosystem services and how they may be altered by global change (Doney *et al.* 2012). Unfortunately, there is no longer a research organization, in France or abroad, capable of meeting all taxonomic needs. During the second period studied here, SME taxonomists brought together this expertise, and together they were able to comprehensively study several ecosystems in a given geographical area. Today, biodiversity inventory programs bring together specialists from all over the world in workshops. SME specialists are sometimes called upon for their knowledge of a taxonomic group, mainly sponges, or of a specific ecosystem, such as underwater caves for example.

Unfortunately, taxonomy or the use of identification keys are no longer taught at university (Guidetti *et al.* 2014). To save the naturalist expertise of our laboratories, specific training courses, like those of the Smithsonian Tropical Institute, are organized worldwide. Through the organization of several taxonomy training schools targeted for young researchers, the dissemination of systematic and taxonomic knowledge of SME has been maintained. For instance, a "Taxonomic Course on Porifera" was organized in Marseille in 2005 to answer the need of a formation combining field, laboratory, and theoretical work. 40 participants from 18 different countries have participated to this course, organized within the framework of the EU Network of Excellence "MARBEF". Later on, SME field courses focussing on Porifera have had a lot of success, such as in La Martinique in 2013 and La Réunion in 2017 (*e.g.* Pérez *et al.* 2017).

The naturalistic interest in the study of the nearby Mediterranean Sea was the main driver for the creation of the Station Marine d'Endoume. It survived two world wars. Over the decades this interest has significantly grown at times, then was almost lost and carried away by bigger forces when conventional, governmental sources of funding openly disregarded natural history, systematics and taxonomy. However, awareness of the importance of knowing and naming marine biological diversity seems to have been growing recently, leaving hope that the SME will prevail and stand upfront to monitor the challenging times lying ahead of humankind for the next 150 years.

Acknowledgements

This hugely collective work has benefited from the still vivid memories of many SME researchers. Their memory could be efficiently supported by all the written works deposited at the SME library. We therefore thank Catherine Beaussier, the current documentalist of the "OSU Pytheas Institute", as well as Michèle Perret-Boudouresque, the librarian at the Luminy Campus "Plateforme Macrophytes". Our colleagues Richard Kaim-Malka and particularly Helmut Zibrowius have been essential in gathering small bits of information that were still fresh in their minds. Finally, we are grateful to the Data Management and the editors of the World Register of Marine Species (WoRMS).

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