

FROM THE ARCHIVES

The History of Biological Exploration of the Bay of Villefranche



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Introduction

The Bay of Villefranche is a unique site. Protected by high hills, its relatively deep waters (in the outer parts 60–100 m) open out directly onto the mesopelagic depths of the N. W. Mediterranean Sea. These characteristics explain in large part the fact that it harbors a particularly rich marine life, especially with regard to planktonic forms. The early naturalists, François Péron and Claude Lesueur, contemporaries of Lamarck, were the first to describe new species from the bay finding meduse, ctenophores, pteropods (e.g., Fig. 1) and remarking on the diversity of forms (Lesueur 1813; Péron and Lesueur 1809). Fast forward to today—quite recently, another new species was described from the Bay of Villefranche, a dinoflagellate symbiont of radiolarians (Probert et al. 2014). Thus, for over 200 years the Bay of Villefranche has been a site of discovery of new life forms. It seems perhaps about time to review the discoveries and history of scientific exploration of the Bay. The total number of new forms described from the Bay of Villefranche (taxa presently considered valid) range in “age” from those recognized for 205 years to the one described a few months ago and numbers 103 by my count. The life forms described represent an

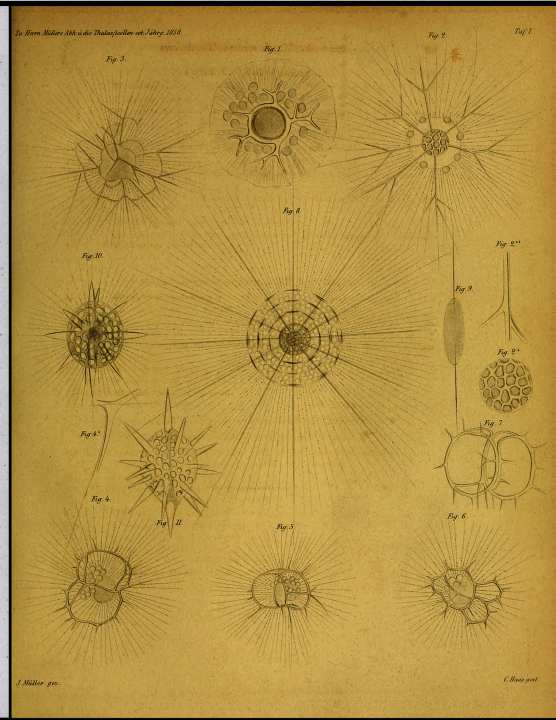
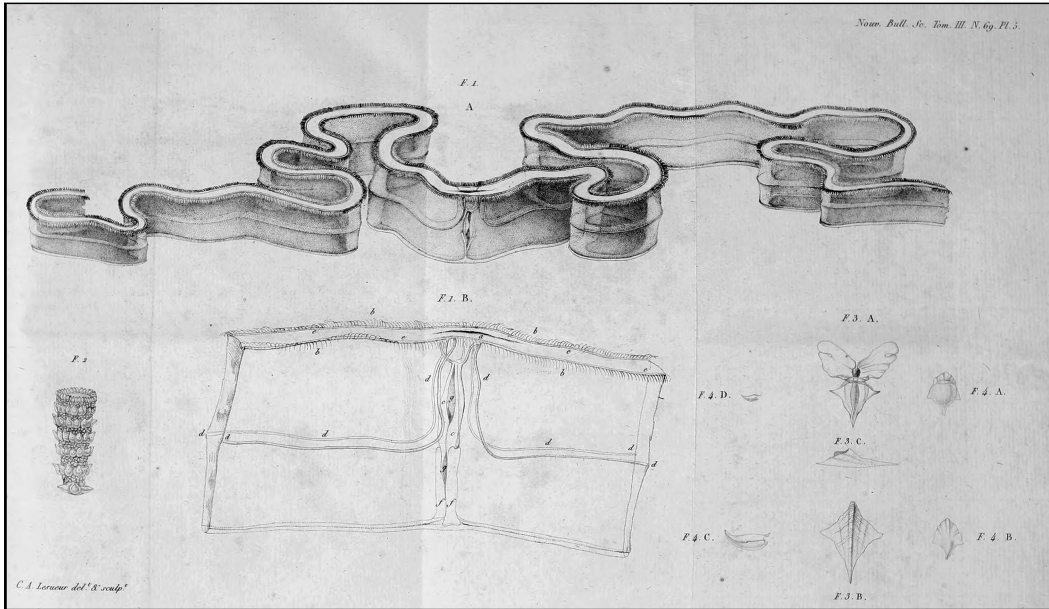
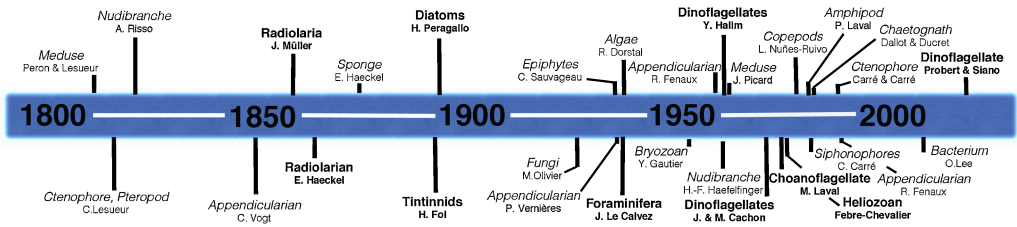
astounding variety of taxa, although clearly dominated by protists (Fig. 1). Here the history of this long biological exploration is outlined.

The Early Naturalists and Travelers

Following the explorations of Péron and Lesueur (Lesueur 1813; Péron and Lesueur 1809), the Bay was relatively ignored by biologists until the 1850's with exception of the description of two nudibranchs in 1818 by Antoine Risso of Nice, better known as an ichthyologist. Villefranche, as a site of exceptional diversity, was then ‘re-discovered’ by Karl Vogt of the University of Geneva during his stay in nearby Nice in 1851. His monographic treatise “Recherches sur les animaux inférieurs de la Méditerranée” (Vogt 1854) was based on work in a number of locales but did highlight the qualities of the Bay of Villefranche and included descriptions of a new ctenophore, an appendicularian, and a spectacular siphonophore (Fig. 1).

Vogt's text perhaps inspired the first protistological explorations, those of Johannes Müller who described several radiolarians and acantharians from the bay (e.g. Fig. 1). He recommended the site to Ernst Haeckel who later recounted (Haeckel 1893) his impressions from his visit in August–September of 1856:

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“In company with Heinrich Müller and K. Kupfer, we investigated especially the rich pelagic animal life of the beautiful bay of Villafranca. There, for the first time, I met those wonderful forms of the pelagic fauna which belong to the classes of the siphonophores, pteropods, and heteropods. I also there first saw living polycyttaria, acanthometra, and polycystina, those phantasmic forms of radiolaria, in the study of which I spent so many later years.”

Haeckel himself later published descriptions of a radiolarian (Haeckel 1860) and a sponge (Haeckel 1872) from Villefranche.

A Permanent Facility

The origins of a permanent laboratory on the Bay of Villefranche can be traced to Jules Barrois of the University of Lille and Herman Fol of the University of Geneva. Barrois worked on embryogenesis of bryozoa. Fol and Haeckel were students together and traveling companions. Fol, primarily an embryologist but with interests in everything from tintinnids (as a young man he was a student of Edouard Claparède) to aquatic optics, spent winters in Villfranche and described several species of tintinnid ciliates from the Bay (Fig. 2). Barrois and Fol together created a laboratory in an abandoned lazaret (quarantine building) on the bayside, inaugurating the “Laboratoire de Zoologie de Villefranche-sur-Mer” in 1882. Barrois petitioned the French government to allow use of the nearby former prison and hospital ‘Le Galériens’. The buildings had been leased to the Russian Navy in 1858 by the former governing power of Villefranche and Nice, the Duke of Savoy, as a coal depot but it had been unused for many years. In addition the region had since been ceded to France, not bound by the agreement with Russia. In 1884 his request was granted with the consent of the Russian Consul (Mosse 1952). The spacious facility, with a stone pier on the Bay, hosted a wide range of scientists, including Alexander Aggasiz, and Hippolyte Pergallo whose ‘Diatomées de Villefranche’ (Peragallo 1888) included several new species still considered valid today (e.g., Fig. 2).

The laboratory was modelled on the Naples Laboratory and early on Oxford had agreed to ‘rent a table’.

The Russian Period

Perhaps a victim of his own success, Barrois was soon evicted. The facility was retrieved by the Russians in 1888 at the demand of Alexis Korotneff of the University of Kiev who had frequented the laboratory in previous years and now wanted to establish a Russian research facility: The “Russian Zoological Station”. While the Russian Zoological Station was smaller than the well-established laboratories of Naples and Roscoff, it soon became none-the-less a well-known facility as attested by this mention in Anton Chekov’s novel ‘The Duel’ (1891) in the character Laevsky’s comment to the character Samoylenko:

“All the serious zoologists work at the biological station at Naples or Villefranche”

The ‘Russian Period’ lasted from 1888 to 1918. Charles Kofoid visited the laboratory in 1908 as part of his tour of European laboratories destined to help in the design and construction of what would become Scripps Institute of Oceanography in California. Kofoid (1910) stated that it was financed largely by an annual grant from the Russian Ministry of Education with the salaries of Alexis Korotneff and his assistant, Michael Davidoff paid by the University of Kiev. Unlike Naples, where visiting scientists were expected to pay bench fees, or use the tables rented by their institutions, researchers from around the world were welcomed, supplied nearly gratis not only with a room, but also “research table, the supply of living material, and the usual chemicals and reagents...”. Kofoid noted that an informal teaching component existed: “For several years a practical course in marine zoology for advanced students has been offered in March and April.... Students are expected to bring their own microscopes.” This rather extraordinary institution, difficult to imagine today, not surprisingly ran into financial troubles following the Russian Revolution. Interestingly,

Figure 1. The top panel is a time-line of the major Villefranche species descriptions (protistan taxa bolded). The middle panel is the plate from Claude Lesueur’s 1813 article containing the first depictions of new species from the Bay of Villefranche: the ctenophore *Cestum venerius* (1), the pterpod *Cavolina inflexa* (4). The lower left panel is Karl Vogt’s depiction of the spectacular siphonophore he described in 1852, from Villefranche, now known as *Halistemma rubrum*. The lower right panel is the first plate from Johannes Müller’s 1856 publication describing several new radiolarians from Villefranche including *Acanthodesmia vinculata* (4-7).

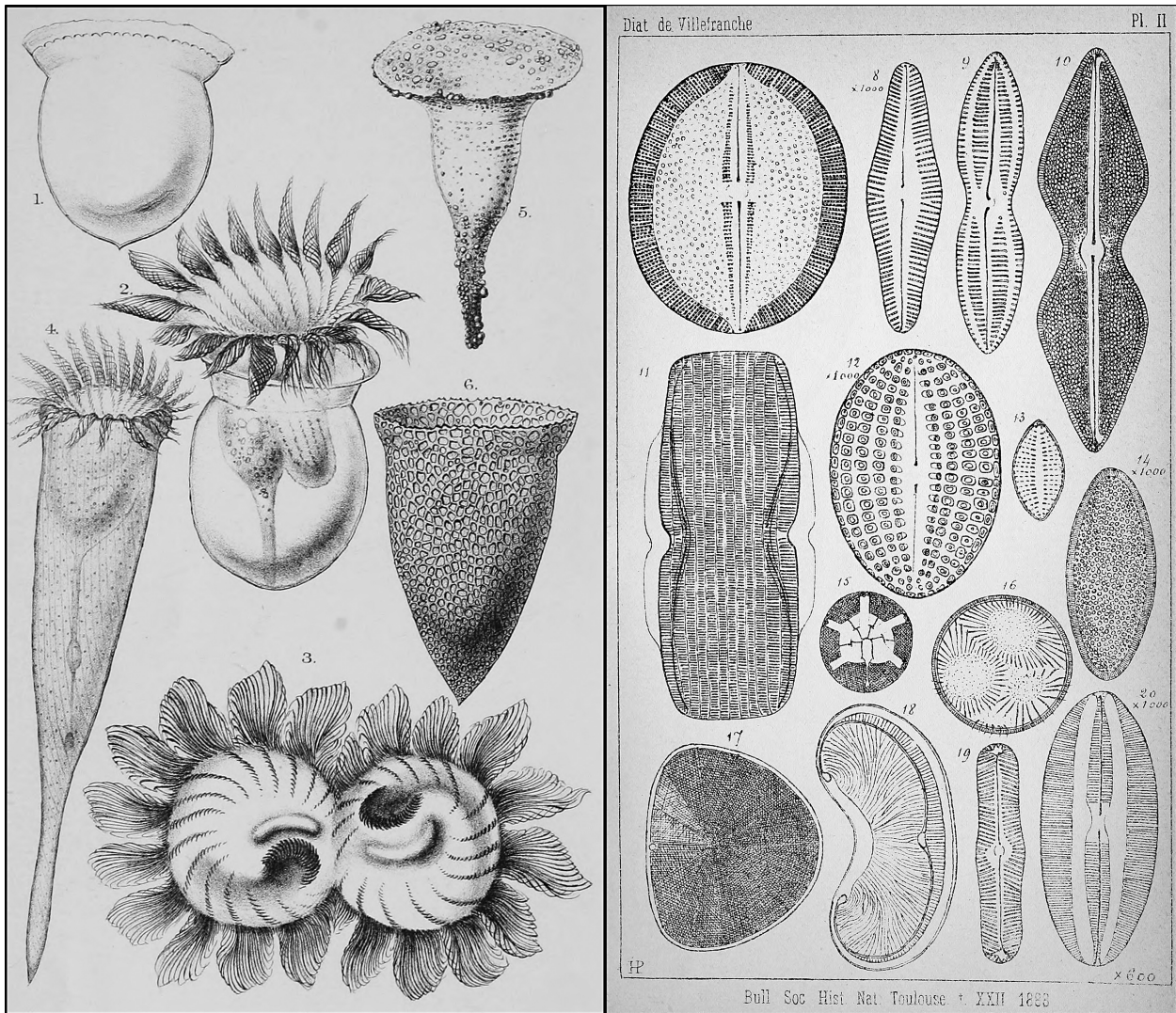


Figure 2. The left panel is from Hermann Fol's 1881 paper in which he described the species now known as *Cyttarocyclus ampulla* (1-3) and *Rhabdonella spiralis* (4) from the Bay of Villefranche. The right panel is Plate 2 from Hippolyte Pergallo's 1888 paper on the diatoms of Villefranche including several new species, among them *Amphora alata* (11).

despite their open-door policy, the Russian Period corresponds with a period in which no new species (currently recognized as valid) were described (Fig. 4)

La Station Zoologique and The University of Paris

The facility was virtually inactive from 1918 - 1931 and formerly taken over by the French Ministry of Education in 1932. It was re-established as the "Station Zoologique", a satellite station of the Banyuls Arago Laboratory in Banyuls-sur-Mer. The

University of Paris ran the Banyuls laboratory and Station Biologique de Roscoff as field campuses. Consequently the Station Zoologique became a facility of the University of Paris. A strong protistological connection remained. The Villefranche laboratory was administratively under the direction of Edouard Chatton, as head of the Banyuls facility from 1937 until his death in 1947. In contrast to the early days, from the 1920's to the 1950's most of the new forms described were benthic. A new macrophyte was described (Dorstal 1929) and Sauvageau found new epiphytes (Sauvageau 1933, 1936). With regard to protists, most of the new species described were benthic foraminifera

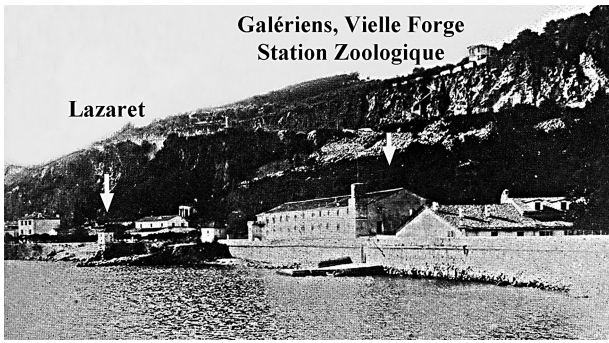


Figure 3. The Russian Zoological Station in 1908, photographed by Michael Davidoff, scanned from Kofoid 1910. Labels were added to show the old lazaret used by Jules Barrois and Herman Fol and the buildings of the Station Zoologique.

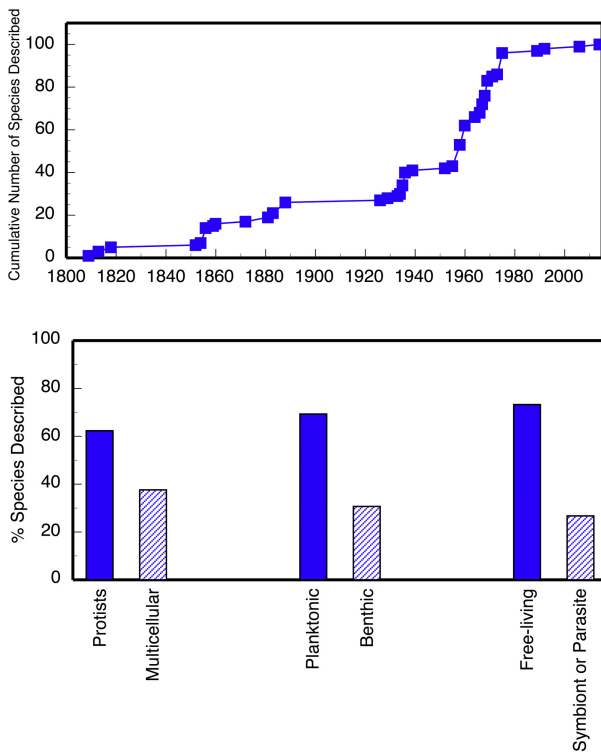


Figure 4. Accumulation of numbers of new species as a function of time based on the data given in Table 1. Note the remarkable increase during the relatively short-lived “period of protistology” from the mid 1960’s to the late 1970’s. Overall, protists account for a majority of the new forms described from the Bay of Villefranche.

(Le Calvez 1935, 1939; Le Calvez and Le Calvez 1958).

In the 1950’s there began a shift in focus at the Station Zoologique, as in many institutions, away

Table 1. Species described from the Bay of Villefranche grouped by taxa.

PROTISTS

Apicomplexan parasite on Foraminifera

Trophosphaera planorbulinae Le Calvez 1939

Foraminifera

Adelosina mediterraneanensis Le Calvez & Le Calvez 1958

Astrorhiza vermiculata Le Calvez 1935

Bathysiphon humilis Le Calvez 1935

Biloculinella wiesneri Le Calvez & Le Calvez 1958

Cycloforina villafranca Le Calvez & Le Calvez 1958

Quinqueloculina laticollis Le Calvez & Le Calvez 1958

Quinqueloculina viennensis Le Calvez & Le Calvez 1958

Quinqueloculina williamsoni Le Calvez & Le Calvez 1958

Rhabdammina inaequalis Le Calvez, 1935

Saccamina fragilis Le Calvez 1935

Siphonaperta oscinclinatum Le Calvez & Le Calvez 1958

Triloculina ornata Le Calvez & Le Calvez 1958

Heliozoan

Hedraiophrys hovassei Febvre-Chevalier 1973

Choanoflagellate

Salpingoeca pelagica Laval 1971

Diatom

Amphora alata Pergallo 1888

Amphora valida Pergallo 1888

Leptocylindrus mediterraneus Peragallo 1888

Rhizosolenia formosa Pergallo 1888

Rhizosolenia tempere Pergallo 1888

Gregarian parasites

Cephaloidophora vibiliae Théodoridès & Desportes 1975

Aggregata maxima Théodoridès & Desportes 1975
Cephaloidophora alii Théodoridès & Desportes 1975

Cephaloidophora apsteini Théodoridès & Desportes 1975

Cephaloidophora phrosinae Théodoridès & Desportes 1975

Cephaloidophora tregouboffi Théodoridès & Desportes 1975

Cephaloidophora vivieri Théodoridès & Desportes 1975

Lateroprotomeritus conicus Théodoridès & Desportes 1975

Paraophiodina eucopiae Théodoridès & Desportes 1975

Paraophiodina korotneffi Théodoridès & Desportes 1975

Thalicola filiformis Théodoridès & Desportes 1975

Table 1 (Continued)

Dinoflagellate

- Brandtodinium nutricula* Probert & Siano 2014
Cachonodinium caudatum Cachon & Cachon 1969
Cymbodinium elegans Cachon & Cachon 1967a
Filodinium hovassei Cachon & Cachon 1968
Gloeodinium marinum Bouquaheux 1971
Greuetodinium cylindricum Greuet 1968
Histioneis elegans Halim 1960
Histioneis faouzii Halim 1960
Histioneis imbricata Halim 1960
Histioneis rampii Halim 1960
Histioneis villafranca Halim 1960
Kofoidinium pavillardii Cachon & Cachon 1967b
Kofoidinium splendens Cachon & Cachon 1967b
Leptophyllus dasypus Cachon & Cachon-Enjumet 1964
Leptospathium navicula Cachon & Cachon-Enjumet 1964
Myxodinium pipiens Cachon, Cachon & Bouquaheux, 1969
Petalodinium porcelio Cachon & Cachon 1969
Pomatodinium impatiens Cachon & Cachon-Enjumet 1966
Protoperidinium tregouboffii Halim 1955
- Radiolaria**
Acanthodesmia vinculata Müller 1858
Acanthometra alata Müller 1856
Acanthometra dichotoma Müller 1856
Amphilonche elongata Müller 1856
Cladococcus arborescens Müller 1856
Collosphaera ligurina Müller 1856
Plectagonidium deflandrei Cachon & Cachon 1969
Sphaerzoum spinulosum Müller 1856
Spongospaera streptacantha Haeckel, 1860
Thalassicolla morum Müller 1856
- Ciliates**
Condonaria cistellula Fol 1883
Cyttarocyllis ampulla Fol 1881
Phryodendron hollandaei Batisse 1969
Rhabdonella spiralis Fol 1881
Tintinnopsis nucla Fol 1883
- BRYOZOA**
Hagiosynodos tregouboffi Gautier 1952
- PORIFERA**
Leucandra crambessa Haeckel 1872
- APPENDICULARIA**
Appendicularia tregouboffi Fenaux 1960
Mesoikopleura haranti Vernières 1934
Oikopleura longicauda Vogt 1854
Desmophyes villafrancae Carré 1969
Prayola tottoni Carré 1969
- SIPHONOPHORE**
Halistemma rubrum Vogt 1852
Sphaeronectes bougisi Carré 1968
Sphaeronectes fragilis Carré 1968
Sphaeronectes gamulini Carré 1966

Table 1 (Continued)

CHAETOGNATHE

- Parasagitta megalophthalma* Dallot & Ducret 1969

CNIDARIA

- Koellikerina fasciculata* Péron & Lesueur 1809
Merga tregoubovii Picard 1960
Tregoubovia atentaculata Picard 1958

CTENOPHORE

- Cestum veneris* Lesueur 1813
Ctenella aurantia Carré & Carré 1993a
Minictena luteola Carré & Carré 1993b
Haeckelia bimaculata Carré & Carré 1989

CRUSTACEANS

- Copepod (parasites on deep-sea fish)
Clavella porogadi Nuñez-Ruivo 1964
Clavella hardingi Nuñez-Ruivo 1964
 Amphipod (parasitic)
Bougisia ornata Laval 1966

PTEROPODS

- Cavolinia inflexa* Lesueur 1813

NUDIBRANCHES

- Elysia timida* Risso 1818
Felimare villafranca Risso 1818
Limenandra nodosa Haefelfinger & Stamm 1958
Trapania lineata Haefelfinger 1960
Trapania maculata Haefelfinger 1960

MACROALGAE

- Caulerpa ollivieri* Dorstal 1929

ALGAL Epiphytes

- Cladosiphon lubricus* Sauvageau 1936
Climacosorus mediterraneus Sauvageau 1933
Myriactula elongata Sauvageau 1936
Myriactula oxalifera Sauvageau 1936
Myriactula rigida Sauvageau 1936
Myrionema hemisphericum Sauvageau 1936
Myrionema siliquosum Sauvageau 1936

FUNGI

- Thalassoascus tregoubovi* Ollivier 1926

EUBACTERIA

- Shewanella irciniae* Lee et al. 2006

from descriptive zoology. Ecology on the one hand and cell biology on the other were to be developed. Despite the shifts in institutional focus away from biological exploration, a large number of new taxa were described in the 1960's and 1970's. The new taxa were primarily protists from the plankton. This 'protistological period' reflected the fact that several protistologists of reknown were based at Station Zoologique: Jean and Monique Cachon (dinoflagellates), Youssef Halim (dinoflagellates), Michéle Laval (choanoflagellates and tintinnid ciliates), Jean Febvre and Collete Febvre-Chevalier (acantharia and heliozoa). Species discoveries were dominated by descriptions of dinoflagellates, both

free-living and parasitic forms (Cachon and Cachon 1967, 1969a; Halim 1955, 1960) as well several gregarine parasites (Théodoridès and Desportes 1975).

In 1974 the three laboratories of Villefranche (Station Zoologique, the Laboratory of Marine Chemistry and Physics, and the Geodynamics Laboratory) were grouped to form a single campus and in 1989 the campus was given the status of Oceanographic Observatory. Along with these administrative changes was the separation of the researchers in the Zoological Station into two research groups, one focusing on biological oceanography, today known as the Laboratoire Océanographique de Villefranche-sur-Mer, the other on developmental biology, today known as the Laboratoire de Biologie du Développement.

From the end of the protistology period in the mid-1970's to the present, the discovery rate appears to have declined to nearly zero (Fig. 3). This reflects the re-focusing of the biological research groups in Villefranche away from descriptive biology. However, the burgeoning use of molecular approaches by both groups may open the door again to the discovery of new taxa. Probert et al.'s description of the radiolarian symbiont, previously thought to be a *Symbolinium*, as a new taxon is an excellent example. The authors of the study are interested primarily in the general questions of symbiosis. However, examining questions of function, form and cellular regulation with modern molecular tools can lead to the obligation to describe new taxa when it turns out that your research subjects were not who everyone thought they were. There appears hope then that although classical taxonomy has nearly disappeared from investigations in the Bay of Villefranche, the use of molecular techniques may continue to reveal new forms. In addition, the Villefranche laboratory remains a site which welcomes visiting researchers. In recent years visitors who have continued protistological exploration of the Bay of Villefranche include Sabine Agatha, Tsvetan Bachvaroff, Charles Bachy, Tristan Biard, D. Wayne Coats, Johan Decelle, Fernando Gomez, Laure Guillou, Sergey Karpov, Puri López-García

David Moreira, Fabrice Not, Ian Probert, and Noritoshi Suzuki. While they haven't described new species, most have not given up hope!

It is perhaps worth noting in closing that the protistological investigations using material from the Bay have yielded not only increases in species lists but some declines as well. Michèle Laval's laboratory work showed conclusively that the tintinnid previously known as *Coxiella annulata* was not a distinct species but actually nothing

more than morphological variant of *Favella ehrenbergii* (Laval-Peuto 1981). Likewise cultures of the dinoflagellate *Ceratium ranipes* with its distinctive 'fingers' showed that the 'fingerless form' *C. palmatum* was the nighttime morph of *C. ranipes* who grows its fingers every morning and absorbs them at sunset (Pizay et al. 2009). Sequencing of single cells revealed that several heretofore distinct tintinnid species of different families were but one and the same (Bachy et al. 2012). All in all then it is perhaps hazardous to state unequivocally that exploration of the Bay of Villefranche using molecular methods in the Bay of Villefranche will surely yield significant increases in new species!

Methods

Assembling the list of species described began with combing the annual volumes of the collected reprints, the official production of the laboratory (1927 - 1992). Listings of the more recent works (1993 - present) are available on the laboratory websites. Next, papers which were cited in the articles 'written from Villefranche', as well as the papers citing these Villefranche papers, were examined. Species listings of the World Registry of Marine Species (<http://www.marinespecies.org>) and Algae-Base (<http://www.algaebase.org>) were searched for species names including the letter sequences which appeared common in names of species described: "villfran" "korotr", "tregoub". For each species, the current validity of the species names was determined by consulting World Registry of Marine Species, AlgaeBase and the Encyclopedia of Life (<http://eol.org>). Approximately 1 out of 2 of the species described from the Bay of Villefranche are currently considered to be junior synonyms. Thus, about 200 species have been described but only 101 are currently recognized as valid (Table 1).

Acknowledgements

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