PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES
Fourth Series

Volume 59, Supplement I, No. 8, pp. 117–137, 9 figs. September 30, 2008

Scientific Exploration in the Mediterranean Region
Biodiversity of the Mediterranean Opisthobranch Gastropod Fauna: Historical and Phylogenetic Perspectives

Terrence M. Gosliner[1], Juan Lucas Cervera[2], and Michael T. Ghiselin[1]

[1] *Department of Invertebrate Zoology & Geology, California Academy of Sciences, 875 Howard Street, San Francisco, California, USA; Email: tgosliner@calacademy.org; Email: mghiselin@calacademy.org;*

[2] *Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Polígono del Río San Pedro s/n, Apdo. 40, 11510 Puerto Real (Cádiz), Spain; Email:lucas.cervera@uca.es*

Opisthobranch gastropods are marine animals that differ from most other mollusks in having a reduced shell. The systematics, therefore, is based largely on the study of the soft parts, and this attracts a distinct group of specialists. Explorers of the Mediterranean opisthobranch fauna include a substantial number of persons who traveled in the area such as August Krohn (1803–1891) and Amandus Philippi (1808–1904). More substantial contributions were made by scientists who had academic positions that were located at appropriate places near the shore. Naples was a particularly active center of investigation, all the more so after the founding of the Zoological Station by Anton Dohrn. A major specialist on the group, Salvatore Trinchese (1836–1897) was influential in both research and teaching. Both he and his students occupied "tables" at the Station. French scientists did not work at the Station, but they had their own institutions. A good example is Albert Vayssière (1854–1942), who held academic positions at the University of Marseille and was active in research there for many years.

In recent years, scientists of many nationalities have been involved in studying the opisthobranch fauna, and the Portuguese and Spanish provide an instructive example. The Portuguese and Spanish tradition in opisthobranch taxonomy began in the latter part of the 19th century, but then languished for many decades during the Spanish Civil War and Franco era. The study of Iberian opisthobranchs underwent a renaissance in the 1970s and has come into full flower in the last decade. Resident workers are actively working on the fauna, training students, and developing an enduring tradition of systematic and phylogenetic study that is international in scope and impact.

The result of many years of study has been the establishment of a well-documented inventory of the opisthobranchs of the Mediterranean. On the basis of such lists, it is possible to document many trends in the investigation of the fauna and better to understand the results. The number of names introduced provides an index of such phenomena as the amount of research effort. The number of synonyms provides one way of assessing the quality of systematic work. In addition, it is possible to document changes in the composition of the fauna due to such phenomena as introduction of alien elements. Today, opisthobranchs play an increasing important role in studies of physiology, ecology, and evolution.

In traditional classifications, the gastropod mollusks have been divided into three subclasses: Prosobranchia, Opisthobranchia, and Pulmonata. The names derive from the respiratory apparatus:

prosobranchs have their gills in front, opisthobranchs have gills displaced toward the rear, and pulmonates have lungs. As a general rule, prosobranchs and opisthobranchs are marine animals, whereas pulmonates are largely freshwater and terrestrial. Only the latter two groups have been shown to represent probably monophyletic, natural groups, whereas the prosobranchs are an amalgamation of members of several distinct clades and are paraphyletic. All three groups include both snails, with well-developed shells, and slugs, in which the shell is reduced or absent, at least in the adults. But the large and beautiful marine shells that are so attractive to shell collectors are almost all "prosobranchs." Opisthobranchs are mostly slugs, and when shells are present they are either-not very conspicuous or, more often, are internal. This has two important consequences: the majority of opisthobranchs are not of much interest to shell collectors, and the systematics is based almost entirely on the anatomy of soft parts. Opisthobranchs are often colorful, have considerable aesthetic appeal, and receive much attention from underwater photographers and scuba diving enthusiasts. Opisthobranchs tend to be studied by people who specialize in the group, using different approaches, techniques, and methodologies than those employed by taxonomists who focus on shelled mollusks. Among those who do study opisthobranchs, there is a similar division between those scientists who work on the half-dozen benthic orders and those who work on the two pelagic ones ("pteropods"). Additionally, the taxonomy of many of the opisthobranchs with external shells is less precise because variation in conchological features is often not consistent with well-studied anatomical variation and is often studied by different practitioners.

Much of the traditional systematics of opisthobranchs has been studied from preserved material in collections. If more comprehensive faunistic work is to be undertaken, however, the material needs to be collected systematically and, preferably, by a specialist who is collecting and studying material that was documented while alive. This means spending extended periods of time in the field, something that is easier for those who work at an institution near to where the animals occur and where it is relatively easy to keep them alive long enough to study them. From a European perspective, the Mediterranean opisthobranch fauna is a good sample of warm-water marine opisthobranchs in general, and naturalists seeking new species and higher taxa have often made excursions there.

For biology in general, opisthobranchs have become important study organisms for two quite different reasons. First, some have nervous systems that make them excellent subjects for experimental neurophysiology. Beginning in the 1960s, members of the genus *Aplysia* in the order Anaspidea became a "model organism" (Kandel 1979). Second, many opisthobranchs contain chemicals that are thought to defend them from predators. The toxicity of some of these animals was known to the ancients. For instance, Romans used them to kill people (Caprotti 1977). However, modern interest in the secondary metabolites of opisthobranchs, stimulated in part by the search for "drugs from the sea," only dates from around 1960. Work on the evolution of chemical defense in opisthobranchs developed somewhat later (Faulkner and Ghiselin 1983). The Mediterranean fauna has played a large role in these endeavors, partly due to its proximity to important laboratories and scientists, and partly because it has a good representative sample of the group.

Our discussion of research on opisthobranchs consists of three major parts. First, we consider a few scientists who made major contributions to the study of the systematics of the group mainly in the 19th century but continuing into the early part of the 20th century. Second, we take a close look at more recent developments, focusing primarily on Portuguese and Spanish contributions. Lastly, we present a quantitative analysis of the development of our knowledge of the group, based on the literature. Obviously, such a treatment does not provide a thorough, much less complete, coverage. Our aim, however, is to provide a representative sample and some interesting case studies.

Part I. The Early Investigators

Itinerant Investigators

Much of the 19th century investigation of the world fauna of opisthobranchs was carried out as part of expeditions that brought back specimens that were deposited in museums and described by specialists. There were also travelers who worked mainly on shore. The Mediterranean was a popular place for shore-based zoological explorations (Groeben 1996, 2008). It was fairly easy to get to and usually contained a rich assemblage of warm-water animals that were largely undescribed or at best little known. Two such "scientific tourists," both of whom spent long periods in the Mediterranean, partly for health benefits, were August David Krohn (1803–1891) and Amandus Philippi (1808–1904) (Groeben 1996). Both published on a wide variety of marine animals, and both described just a few species of opisthobranchs (Krohn 1847; Philippi 1839, 1841). Krohn also worked on pteropod development and on the shell and larvae of *Gastropteron* and the abberrant nudibranch *Mnestra*. Philippi, who was born in Charlottenburg, near Berlin (McLellan 1927), after finishing his doctorate in medicine in 1830, went on his first excursion to Italy. For his first major publication, *Enumeratio Molluscorum Siciliae* (Philippi 1836), he was awarded a gold medal by Fredrich Willhelm II of Prussia. He became a professor at Cassel, but was forced out for political reasons and immigrated to Chile where he became a professor and director of the National Museum.

Resident Investigators

Scientists who resided at or near the shore had the advantage of various amenities, including laboratories, museums, and libraries. In Naples, for instance, there exists a long tradition of research on marine animals, including opisthobranch gastropods. The father of this tradition was Giuseppe Saverio Poli (1746–1825). Poli was born at Molfetta and had his university education in medicine and natural sciences at Padova. He soon gave up medical practice and traveled extensively, finally settling in Napoli. He occupied the chair of physics at the Royal Military Academy beginning in 1776, then, after a period abroad, occupied various academic posts, including that of tutor to the future Francis I. He was well connected and fostered patronage of the sciences. Although he was an eminent physicist and the author of works on various scientific topics, the work of greatest interest us in this study is his *Testacea utriusque Siciliae eorumque anathome tabulis aeneis*. This work, to which he devoted about a dozen years of research, was not complete at the time of his death. The latter parts came out posthumously, edited and supplemented by Stephano delle Chiaje (1794–1860). The work is remarkable for its beautiful and accurate anatomical drawings. Although largely on bivalves, it does treat some opisthobranchs, including pteropods and a few cephalaspideans.

Academic chairs at Napoli continued Poli's tradition. There was a zoology chair associated with a *Museo Zoologico*, established in 1813, and a chair of comparative anatomy associated with a *Museo di Anatomia Comparata* was established in 1861. Oronzo Gabriele Costa (1775–1849) occupied the zoology chair from 1832 to 1839 and his son Achille Costa (1823–1867) occupied it from 1860 to 1898. The elder Costa was author of a catalog of "testacea" of the kingdom (O. Costa 1829) (Battaglini 1991). The younger Costa described a number of pteropods, nudibranchs and sacoglossans (A. Costa 1865, 1869).

The chair of comparative anatomy was first occupied by Paolo Pancieri (1833–1877) from 1861 to 1877 (see Gasco 1878; Borelli 1991). Although Pancieri was more of a comparative anatomist than a descriptive systematist and did little work on opisthobranchs, he is noteworthy for having discovered that these and other gastropods secrete sulfuric acid (Panceri 1869).

Panceri died on 11 March 1877 and was succeeded by Salvatore Trinchese (1836–1897), who began teaching in 1880 and continued to occupy the chair until 1897. There is an excellent anthology of Trinchese's malacological works with authoritative commentary (Cimino 1989 and chapters therein by Stomeo, Cimino, and Cattaneo-Vietti) from which much of our information is drawn. Born at Martano, in the province of Lecce on 4 April 1836, Trinchese graduated in medicine at Pisa in 1860. He was then awarded a fellowship to study abroad. At Paris, he was associated with Émile Blanchard, Claude Bernard, and Henri Milne-Edwards. He became an accomplished microscopist and began publishing on molluscan nervous systems. In 1865, he was invited to Genova, where he remained until 1871, when he relocated to Bologna. While at Genova, he continued his work on molluscan nervous systems. He produced magnificent descriptions of opisthobranchs, notably eolid nudibranchs, and provided valuable contributions to their anatomy and embryology. For his work on the aeolids of the port of Genova, he was awarded a prize by the Accademia dei Lincei in 1879. In 1880, he was called to Naples where he continued his researches on opisthobranchs and became a very influential teacher. At the time of his arrival in Naples, the Zoological Station, founded by Anton Dohrn around 1872, was already flourishing. It provided excellent opportunities for young Italian zoologists, many of whom later became quite eminent (Groeben and Ghiselin 2001). These included students of Trinchese and Costa. The Italian and Neapolitan governments funded quite a number of "tables" — in effect grants in support of investigators — and these were used by many of the local students. Trinchese himself occupied a table at the Station most of the time from 12 August 1886 to 31 December 1896.

One of Trinchese's students, Giuseppe Mazzarelli (1870–1946), became a important authority on the systematics, evolution, and general biology of opisthobranchs. Even in his youth, he was an enthusiastic evolutionist and published philosophical papers while still in his teens. Not surprisingly, therefore, he tended to focus on problems of comparative anatomy, especially those of organisms of particular interest to phylogenetics, that is those thought to have primitive characters or to be of problematic position. He emphasized one group, the Anaspidea or "sea-hares," and produced a large monograph on them. This was not, however, a part of the official monograph series of the Zoological Station. Mazzarelli began occupying tables while still a student and was closely associated with the Station thereafter, even when he was a professor at Milan and Palermo. After his retirement, he returned to Naples, where he died shortly after the Second World War.

Quite a number of scientists who spent time at the Zoological Station before the First World War contributed to various aspects of the biology of opisthobranchs. However, their interests were almost exclusively in comparative anatomy, comparative embryology, and functional anatomy, as was fashionable at the time. Few worked on the systematics of opisthobranchs, but there was one important exception. This was [Ludwig Sophius] Rudolph Bergh (1824–1909) of Copenhagen, a physician, who worked at a hospital there but found time to do an enormous amount of opisthobranch systematics, based largely on expedition material from all over the world. He also was in Naples in May of 1880 and May of 1883, and although he published in the Station's house organ, he did not occupy a table during these earlier stays (Bergh 1893). Indeed, it was not until 1898, from February 8 to May 4, that he finally occupied a table at the Station. Irrespective of the matter of occupying a table, his visits to the Station allowed him to supplement his work on preserved material with observations of the living organisms. According to Vayssière (1910), Bergh traveled extensively in Europe and visited Dohrn almost every year.

Although the Zoological Station was intended to be an international laboratory, it was not utilized by French scientists prior to the First World War largely because of bitterness about the Franco-Prussian War. French investigators founded their own laboratories. Actually, their traditions were well established by that time. Antoine Risso (1777–1845) was a professor at the Lycée in

Nice. He was inspired by the work of Cuvier and included a substantial amount of material on opisthobranchs in his four volume *Histoire Naturelle des Principales Productions de L'Europe Méridionale et Particulièrement de celles des Environs de Nice et des Alpes Maritimes* (Risso 1826). He also did some descriptive taxonomy (Risso 1818).

Among French zoologists who studied opisthobranchs during the late nineteenth and early twentieth centuries, the most distinguished was Albert Vayssière (1854–1942), a student of Antoine Fortuné Marion. Vayssière's son, Paul, wrote a brief biography that has been the major source of information for this essay (P. Vayssière 1975). Albert Vayssière was born at Avignon on July 8, 1854. He spent his academic career at Marseille, where he died on January 13, 1942. Although his main interest was malacology, he was also an entomologist. His doctoral thesis was on insects (Vayssière 1882), and he was involved in agricultural entomology. He became a preparatory assistant in the zoological laboratory at the University of Marseille in 1873 and subsequently was advanced to higher-level academic positions. These included the directorship of the Laboratoire d'Endoume. Vayssière's research focused on opisthobranchs, mainly on the local fauna in the Gulf of Marseille and the surrounding area. He often collected at Cary-le-Rouet, some twenty kilometers from Marseille. The local fishermen brought him material brought up in their nets, and he put it to good scientific use. One of these uses was the investigation of the functional and comparative anatomy of a wide range of opisthobranchs, leading to a better understanding of their general biology and phylogenetic relationships. Of course, he also did a considerable amount of descriptive work. Another outcome of his studies was a better understanding of the biogeography and ecological distribution of opisthobranchs and other invertebrates. He compared the French Atlantic and Mediterranean faunas (Vayssière 1900). The Atlantic organisms were mostly northern forms, and these tended to be abundant farther to the north. The Mediterranean forms were southern animals, more common in the Gulf of Naples and the coasts of Sicily and Algeria than along the French Atlantic coast. Detailed analysis of his collection data from Marseille allowed him to document local assemblages and to explain the differences among them in terms of such influences as currents and larval dispersal (Vayssière 1920).

The Second Half of the 20th Century

One of the most important contributors to the knowledge of the Mediterranean opisthobranchs during the second half of the 20th century has been Luise R. Schmekel (b. 1935). She began working at the Naples Zoological Station in 1963. In 1976, she moved to the University of Münster (Germany) as professor of Zoology. She visited the Laboratoire Arago in Banyuls-sur-mer (France, Mediterranean) several times as well as the Zoological Station to collect opisthobranchs, focusing on the Sacoglossa and Nudibranchia. From 1965 to the present, Schmekel described two new genera of aeolid nudibranchs, 11 new species of aeolid and dendronotid nudibranchs and, most recently, nine new species of the cephalaspidean genus *Runcina*. Her most significant contribution to the Mediterranean opisthobranch fauna is the book *Opisthobranchia des Mittelmeeres: Nudibranchia und Saccoglossa* (1982), in collaboration with Adolf Portmann. This volume, which is based on sacoglossans and nudibranchs from the Gulf of Naples, provides valuable information on the external and internal anatomy and ecology of many Mediterranean species. Moreover, Schmekel studied many nudibranchs species from the histological point of view. In fact, she was the first to use transmission electron microscopy extentsively to investigate opisthobranchs in order to describe and understand the arrangement and function of their reproductive systems. She was also the advisor of Heike Wägele's doctoral thesis (1987). And, although she retired in 2000, she continues to study opisthobranchs (Schmekel and Cappellato 2001, 2002).

Part II: The Study of the Opisthobranchs from the Iberian Peninsula: The Amazing Case of Spain and Portugal.

The first published reference of an opisthobranch species from Spain was the work of Henri de Lacaze-Duthiers (1859), with a monograph about "le pleurobranch orangé" (as *Pleurobranchus aurantiacus*), based on specimens collected from the Balearic Islands. No additional records were published until 45 years later when some shelled opisthobranchs were reported from the northeastern Spanish coast (i.e., Bucquoy et al. 1886; Carus 1889–1893; Vayssière 1898, 1901, 1913; Pruvot 1901; Maluquer 1904–1916; Chia 1911–1913; Sama 1916). Together these records added 10 to 15 species to the known fauna.

In Portugal, at the end of the 19th century, Paulino d'Oliveira (1837–1899) published the first account of opisthobranchs from mainland Portugal (1895), reporting on 14 species, including the description of one new species, *Doriopsilla pelseneeri*.

Joaquín González-Hidalgo y Rodríguez (M.D.) (1839–1923), the most important Spanish malacologist during the last third of the 19th and first quarter of the 20th centuries, provided the first significant account of molluscs (land, freshwater and marine) from the Iberian Peninsula and Balearic Islands. His most important contribution in relation to the Ibero-Balearic region is included in the second part (1890–1913) of his large malacological series *Obras Malacologicas de J.G. Hidalgo*. The results of his studies concerning the marine molluscs of this region are summarized, but then updated in his subsequent *Fauna Malacológica de España, Portugal y las Baleares. Moluscos Testaceos Marinos* (1917). Nevertheless, his contribution to the knowledge of the opisthobranch molluscs from the Ibero-Balearic region was not very important because it was limited to conchological description of shelled species. We note that in his 1917 contribution, Hidalgo recorded 54 species of opisthobranchs along the Mediterranean coasts of the Iberian Peninsula and the Balearic Islands, but he did not describe any new species. Furthermore, 28 unshelled opisthobranchs species from the northern Iberian coasts, that were not included in his 1917 paper, were recorded by him in a shorter publication, which appeared a year earlier, in 1916.

With respect to the Portuguese opisthobranch fauna, Hidalgo's papers of 1916 and 1917 added 23 species to Oliveira's contribution (1895). Two decades later, the Portuguese malacologist Augusto Nobre (1865–1946) published two papers (1936, 1938–40) dealing with the marine molluscs from mainland Portugal, that included seven additional species beyond those previously recorded by Hidalgo. Scattered records of additional species from the Portuguese coasts were published during the following 50 years, until publication of a paper by García-Gómez et al. (1991) that dealt with the opisthobranchs collected during a field expedition organized by the Museum National d'Historire Naturelle of Paris in 1988 along the southern mainland Portugal coasts.

During the first half of the 1970s, the study of the opisthobranchs from the Ibero-Balearic region (mainly from Spain) underwent a fundamental transformation. Siro de Fez's (M.D.) research, based on material he collected between 1943 and 1947 from Valencia Harbour, was published in 1974, almost seven years after his death, in his book titled *Ascoglosos y Nudibranquios de España y Portugal*. Also during the early 1970s, Joandomenèc Ros started his doctoral research. His thesis, *Opistobranquios (Gastropoda, Euthyneura) del Litoral ibérico. Estudio faunístico y ecológico*, was defended at the University of Barcelona at the end of 1973. Most of the results of this thesis were then published in 1975. In 1976, Ros published the first checklist of the opisthobranchs from the Iberian coasts (but including Balearic and Canary Islands). Although no new species were described, 258 species were cited. Other contributions by Ros included several papers about the role of color in opisthobranchs (Ros 1976a, 1984) and on the development and bionomic strategies of the opisthobranchs (Ros 1981).

What led Ros to study the opisthobranchs? According to him, the reason was simple. It lay in the beauty and the shapes that he saw while diving in 1965. Later, he discovered that nobody had yet studied them in Spain (Fez's book was published after the defence of Ros' doctoral thesis). He noted that such beautiful colors were a manifestation of complicated defensive systems. For this reason, in addition to the faunistic study, ecological and ethological studies were added. Much earlier, his supevisor, Ramón Margalef, had imprinted on his doctorate students that doctoral theses should have a double objective: a faunistic/taxonomic study and an ecological one (Ros, pers. comm.).

Other Spanish malacologists followed Ros' lead in the mid- and late 1970s. Their doctoral theses focused almost exclusively on opisthobranchs. Thus, in a period of five years, Jesús Angel Ortea (University of Oviedo, 1977), Manuel Ballesteros (University of Barcelona, 1980) and Victoriano Urgorri (University of Santiago, 1981) defended their doctoral theses. The geographical area covered by Ortea and Urgorri, respectively, was the Asturian and Galician coasts (north-northwestern Iberian Peninsula, Atlantic), whereas Ballesteros focused on the Catalonian and Balearic coasts (both Mediterranean). Beyond the many records of known species of opisthobranchs, these authors have also described several new valid species from their "early" research: Ortea (6), Ortea + Bouchet (1), Ortea + Ballesteros (2), Ortea + Llera (1), Ortea + Urgorri (4) and Urgorri + Cobo + Besteiro (1). After completing their respective theses, the three authors have continued doing research on opisthobranchs, with Ortea being the most prolific student of opisthobranch systematics, while Ballesteros and Urgorri focused on problems in other areas such as benthic ecology. In the early 1980s, Ortea expanded the geographical focus of his opisthobranch research to the Canary Islands, and later to the Cape Verde Archipelago, then Cuba and the Caribbean coast of Costa Rica, becoming a prolific author of the opisthobranchs of all of these regions. Moreover, Ortea collaborated with Guido Cimino and Cimino's team from the Istituto per la Chimica di Molecole di Interesse Biologico, now renamed as Istituto di Chimica Biomolecolare in Pozzuoli (Naples, Italy). On the other hand, Ballesteros has continued with different contributions to the opisthobranch fauna from the northeastern coast of the Iberian Peninsula and the Balearic Islands, as well as his collaboration for more than 15 years with Guido Cimino and his team. This collaboration has been extended to the Antarctic opisthobranchs as well.

Urgorri had to set aside his opisthobranch studies in the mid-1980s, but he took them up again in the late 1990s in collaboration with several young Portuguese malacologists.

In the early 1980s, more young Spanish Ph.D. students, also malacologists and colleagues of Ortea, Ballesteros, and Urgorri, defending their doctoral theses in the first half of the decade: José Templado (University Complutense of Madrid, 1982), Ángel Antonio Luque (University Complutense of Madrid, 1984) and José Carlos García-Gómez (University of Seville, 1984). The first two of these doctoral theses did not involve opisthobranchs exclusively but included other gastropods. Templado's thesis focused on the southeastern coast of the Iberian Peninsula (Mediterranean) whereas Luque dealt with part of the southern Iberian Peninsula coast (mainly Granada and Malaga Provinces). García-Gómez's thesis focused largely on the Strait of Gibraltar, although it also included some sampling from along the southwestern Iberian Peninsula (Atlantic). Templado's thesis did not add new taxa, whereas Luque added one new species of opisthobranch and García-Gómez's added four more. In the meantime, the beautiful photographs of sea slugs taken by García-Gómez caused three other students from the University of Seville to "fall in love" with opisthobranchs, and they decided to do their doctoral theses on them as well. Their theses were defended during the second half of the 1980s: Antonio Medina (1986), Francisco José García (1987), and Juan Lucas Cervera (1988), leading to the establishment of the University of Seville as one of the stronger centers for opisthobranch research in Europe. Nevertheless, only Cervera's thesis focused

on faunistics and taxonomy of opisthobranchs. The other two dealt with, respectively, the histology of the gonads and gametogenesis of one species of nudibranch and the functional anatomy of three other species. The geographic area covered by the Cervera's thesis was southwestern Andalucia (Atlantic) and the Strait of Gibraltar and added six new valid species of opisthobranchs. In 1989, Juan Lucas Cervera moved to a temporary position at the University of Cadiz; two years later, the position became permanent. In September 2007, Francisco Jose Garcia was advanced to full Professor at the University Pablo de Olavide, which, like the University of Seville, is also in Seville.

Meanwhile, in 1981, Joandomenèc Ros was appointed Aggregate Professor at the University of Murcia (southeastern Iberian Peninsula). Although he returned to a full professorship at the University of Barcelona in 1986, he advised the doctoral thesis of Arnaldo Marín at the University of Murcia. In 1988, Marín defended his thesis, which focused on the "symbiosis" of the chloroplasts in Sacoglossa and the association of zooxanthellae with several nudibranch species, adding information about the diversity of opisthobranchs along the southeastern coasts of the Iberian Peninsula. However, he did not describe any new taxa in his thesis. Marín now has a permanent position at Murcia. He has continued doing research in this field, but currently most of his current research is not related to opisthobranchs. On the other hand, he served as co-advisor of Claudia Muniain's Ph.D. thesis as well as advisor of those of Francisca Giménez-Casalduero and Francisco Aguado (see below), all of which were concerned with opisthobranchs.

In May of 1987, during the second Meeting of the Italian Malacological Society held in Sorrento (Italy), Ros, Ortea, Ballesteros, García-Gómez, Templado, García, Cervera, and Marín met Guido Cimino**,** the leader of the team of organic chemists and biologists at the Istituto per la Chimica di Molecole di Interesse Biologico in Arco Felice (Naples) who were studying natural products from marine invertebrates. This meeting was both important and productive because it led to the collaboration between Spanish biologists and malacologists and the Italian chemists. This cooperation offered the opportunity for studying opisthobranchs from a different point of view, namely the chemical ecology of opisthobranchs, and resulted in several Ph.D. theses done in Spain during the 1990s (see Conxita Ávila, Luis Ángel Álvarez-Orive, Eugenia Martínez, Francisca Giménez-Casalduero, Francisco Aguado). Indeed, Cimino became one of the supervisors of Avila, Alvarez-Orive, and Martinez' Ph.D. theses. The collaboration continues to the present day.

The additions to the knowledge of the Iberian opisthobranch fauna by most of the above Spanish researchers led to the compilation of an updated checklist of the opisthobranchs of this geographical area, which included the Canary Islands and the African side of the Strait of Gibraltar, thus replacing Ros' checklist of 1976 . Because the new checklist includes taxonomic remarks, this revision was more useful than the earlier list. Also, the new list, which was completed by Cervera et al. in 1988 (*Iberus*, supl. 1:1–84), includes 389 opisthobranchs species, in contrast to the 258 species of the Ros' checklist (N.B. some taxa included in the 1988 checklist are now considered synonyms or of dubious status).

A change of focus with respect to the study of the opisthobranchs occurred in Spain during the 1990s. Thus, a new generation of young Ph.D. students focused on the systematics of opisthobranch higher taxa without restriction to the Iberian littoral: Eugenia Martínez (1995, Anaspidea of the NE Atlantic, including a section on their chemical ecology; no new taxa described) and Ángel Valdés (1996, Atlantic Porostomata nudibranchs; five new species and two new subspecies). Both were students of Ortea at the University of Oviedo. Other aspects of comparative biology were studied, such as the chemical ecology of opisthobranchs: Conxita Ávila (1993, University of Barcelona) and Luis Ángel Álvarez-Orive (1994, University of Seville), and feeding and defensive ecology in opisthobranchs by Francisca Giménez-Casalduero (1997, University of Murcia), Fran-

cisco Aguado (2000, University of Murcia), and César Megina (2000, University of Cádiz), now Ph.D. assistant at the University of Seville. During the first years of the 21st century, the trend that started in the 1990s has continued, although some doctoral theses were more traditional, such as that of Luis Sánchez Tocino (2003, University of Granada) on the Doridoidea from the coasts of Granada (southern Iberian Peninsula, western Mediterranean; some unidentified species are probably new) and Manuel Caballer Gutiérrez (2007, University of Cantabria) on the opisthobranchs from the Bay of Santander, with a review of several genera of sacoglossans and aeolids. Thus, research for doctoral theses focused on the molecular phylogeny of opisthobranchs (Cristina Grande, 2004, Museo Nacional de Ciencias Naturales of Madrid-CSIC), reproductive biology of several species of nudibranchs (Inés Martínez-Pita 2005, University of Seville), and the systematics of a dorid subfamily (Marta Pola, 2006, University of Cádiz, who described 11 new species from outside the Iberian Peninsula).

Additionally, Jesús S. Troncoso arrived from Brazil at the University of Santiago in 1985. He carried out his doctoral thesis research under the supervision of Victoriano Urgorri. His thesis (1990) was not concerned with opisthobranchs but focused on the faunistics and ecology of benthic molluscs from part of the Galician littoral. However, during the 1990s, he joined Francisco J. García, José Carlos García-Gómez, and Juan Lucas Cervera and commenced a study of the Antarctic opisthobranchs that had been collected by several Spanish benthic expeditions to Antarctica. At the end of the 1990s, together with Francisco J. García, Troncoso instituted a series of expeditions to Brazil to collect opisthobranchs at several localities in the states of Noronha, Pernambuco, Bahia, Rio de Janeiro, São Paulo, and Santa Catarina. Troncoso also participated in an expedition to the Pacific coast of Panama. Some of the results these efforts have been published during the last seven years (García and Troncoso 1999, 2001). In 1995, Troncoso moved from the University of Santiago to the University of Vigo, both in northwestern Spain. And, in 2007, Marta Domínguez (University of Vigo) defended her doctoral thesis, a faunistic study of opisthobranchs from Brazil, which was done under the supervision of Troncoso and F.J. García.

Not only Troncoso, but also several others moved from their original universities some time after they received their Ph.D. degrees. Thus, in 1996, Ángel Valdés went to the Muséum National d'Histoire Naturelle in Paris as *Chercheur Invité*, and the next year he relocated to the California Academy of Sciences (San Francisco) as postdoctoral fellow. In 2001, he accepted a position of Assistant Curator at the Natural History Museum of Los Angeles County and more recently a position as Associate Professor in the Department of Biology at California State Polytechnic University in Pomona, California.

Following the defense of her doctoral thesis, Conxita Avila held a two-year postdoctoral fellowship at Woods Hole (Massachusetts, USA) before returning to Spain as a "Ramón and Cajal" Researcher in Centro de Estudios Avanzados (CSIC) of Blanes (Gerona, Catalonia, Spain). Avila also spent short periods at the Marine Laboratory of the University of Guam (Micronesia, USA) and the Alfred-Wegener Institute for Polar and Marine Research (Bremerhaven, Germany). In January 2007, she joined the staff of University of Barcelona (Spain). Currently, her research focuses on chemical ecology of marine benthic invertebrates, not just opisthobranchs.

Luis Angel Álvarez-Orive left the University of Seville and ceased doing research in 1997 after being hired by an environmental monitoring company. Francisca Giménez Casalduero moved to the University of Alicante at the end of the 1990s, where she now holds a permanent position. Cristina Grande received a postdoctoral fellowship in 2005 at the University of California, Berkeley (California, USA) to conduct research on lower heterobranchs. Finally, Marta Pola is currently at the California Academy of Sciences (San Francisco) on a postdoctoral fellowship to work on systematics of nudibranchs as part of Terry Gosliner's research team.

Only scattered records of additional species from the Portuguese coasts were published by different authors during 50 years after Nobre's contribution, in May-June 1988.

Finally, in 1988, during the months of May–June, the Muséum National d'Histoire Naturelle of Paris organized a field trip that ventured along the southern coast of mainland Portugal. Although some new or uncommon opisthobranch taxa were described from materials collected during this trip in the early 1990s, the important contribution was the paper by García-Gómez et al. (1991) in which they reported on 84 species of opisthobranchs of which 53 were new additions to the Portuguese marine fauna. These data show how poorly known the Portuguese opisthobranch fauna was.

During the early 1990s, two young undergraduate Portuguese malacologists, Gonçalo P. Calado and Manuel Antonio E. Malaquias, expressed an interest in opisthobranchs. Thus, they contacted known Spanish specialists, namely Victoriano Urgorri and Juan Lucas Cervera, hoping to learn more about these animals. As a result of these contacts, especially during the latter half of the 1990s, Calado decided to attend the University of Santiago to undertake his doctoral thesis, which he defended in 2001, on the taxonomy and biology of the poorly known aeolid genus *Calma*. A new and cryptic species of this genus was described from this thesis (Calado and Urgorri 2002).

Malaquias defended his M.Sc. thesis on the taxonomy and ecology of *Haminoea* in Portugal at the University of Coimbra, in 2003. He since has completed his Ph.D. thesis on the systematics of the genus *Bulla* at the Natural History Museum of London (NHM) through the University of London (Queen Mary's College), held a Postdoctoral Fellowship at the NHM and was a Postdoctoral Fellow in the Museu Nacional de História Natural da Universidade de Lisboa. Currently, he holds the position ofProfessor of Invertebrate Systematics at the Bergen Museum, University of Bergen (Norway). The above cooperation has permitted the increase of the knowledge of the opisthobranch fauna in Portugal and resulted in the publication of several papers over the last seven years.

After the many contributions and additions to the opisthobranch fauna of Spain and Portugal during the 1990s and early 2000s, several Spanish and Portuguese authors considered it desirable to publish a new, updated, annotated checklist of the opisthobranchs from Spain and Portugal, including the Balearic and Canary Islands, as well as Madeira, Selvagens, and Azorean Archipelagos. This checklist, which was published by Cervera et al. (2006 [2004]), includes 523 species. This is a revised version of a checklist originally published in 1988, and many of the new additions to the 2006 list were due to the extension of the study to Madeira and the Azores, as well as to the large number of contributions concerning the Canary Islands. With respect to the Canary Islands, the number of species known from this archipelago increased from 93 to 252. Also remarkable is the increase of the species recorded from mainland Portugal, from 91 to 213 in the most recent checklist. From 1974 to date, Spanish opisthobranch workers have described one genus and 89 valid species of opisthobranchs for the Ibero-Macaronesian area, but only nine are known only for the Mediterranean. The remaining ones are known both for the Atlantic and Mediterranean coasts or have been recorded in Atlantic waters only.

Finally, the of richness of the opisthobranch fauna from Spain and Portugal in comparison with the whole European coasts can be seen when one compares the 523 species considered by Cervera et al. (2006) with of the 664 species included in the *European Marine Register of Species* (Costello et al. 2001).

There is also a remarkable recent trend in the Opisthobranch "Spanish School." This is in its participation in the education and training of several international malacologists who have come to Spain to study opisthobranchs. As mentioned above, several young Portuguese biologists have studied opisthobranch mollusks under the guidance of established Spanish researchers. Thus,

Urgorri was one of the supervisors of Calado's doctoral thesis and Cervera was one of the advisors of the Malaquias' Master's thesis. However, such interactions have crossed the Atlantic reaching Argentina and Chile, two countries without active experts on opisthobranchs. In 1993, two young postgraduate students, one Argentinian, Claudia Muniain, and one Chilean, María Angélica Fischer, arrived at the University of Oviedo to carry out their doctoral studies on opisthobranchs that occur in their respective countries. Claudia Muniain defended her doctoral thesis in 1997, based on research done under the supervision of Ortea and Marín and in collaboration with Cimino's lab in Naples. Muniain returned to Argentina and in 2004 received a permanent position as researcher of CONICET at the Museo de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires. María Angélica Fischer (born Muñoz Jiménez) moved from Oviedo to Germany in 1996. In 2000, Cervera became her supervisor. Her meeting with researchers from the University of Nijmegen (Netherlands) in 2003 provided additional focus and facilitated the defense of her doctoral thesis in 2006.

Can We Explain Why the Study of the Opisthobranchs Started so Late in Spain and Portugal?

To try to reply to this question, there are some circumstances to be considered:

1) Most of the opisthobranchs are small and most lack a shell or have one that is reduced. One finds new opisthobranchs on sandy beaches. Usually, they are collected by scuba or snorkelling, although they can be found intertidally as well.

2) Scuba-diving was developed during the second half of the 20th century. Moreover, during the earlier stages of development scuba was considered only as a tool for marine engineering or geology.

3) Both in Spain and Portugal, scuba-diving facilities were developing for tourism, mainly in those areas in which the sea conditions or the access from the shore permitted easy diving. This happened during the 1970s and earlier 1980s.

4) Malacology has had strong support by shell collectors but not professional researchers. Therefore opisthobranchs were largely overlooked by conchologists. This has led that to the fact that opisthobranchs have been studied largely within an academic setting, although more recently they have attracted the interest of diving photographers and other amateurs.

5). In 1871, the Real Sociedad Española de Historia Natural (RSEHN) was founded, but it was not until the second half of the 1970's when a group of mollusc lovers, undergraduate students in biology, other Spanish malacologists (professionals or shell collectors), decided to create a working group on Malacology within the RSEHN (1977). This working group started to enlarge and would become the core of the Spanish Malacological Society that would be founded in 1980, after the split from the RSEHN. During the last 27 years, one of the objectives of the new society has been the promotion and encouragement of malacological studies in Spain. The headquaters of the Spanish Malacological Society is the Museo Nacional de Ciencias Naturales (CSIC) in Madrid.

6) So-called "natural history" had its explosion during the second half of the XVIIIth and the XIXth centuries due to the growing interest in various subdisciplines, including malacology, that spread among the higher and cultured social classes of many European countries. Thus, many academies and research institutions were founded in this period, even in Spain and Portugal. For example, in 1772 the King of Spain, Carlos III, founded the Museo Nacional de Ciencias Naturales in Madrid (MNCN) (formerly called Real Gabinete de Historia Natural) which started with excellent collections and library, as well as many pieces of porcelain and paintings mainly from southern America. The history of this museum can lead us to understand the troubles of natural history and taxonomy/systematics during the last 234 years in Spain.

Thus, this museum suffered unfortunate and dramatic historical events. It was closed during the French invasion of Spain (1808–1813) and sacked in 1813 during the French occupation. It reopended in 1814, partly with objects taken by the French army that were later returned and the activities were increased. Once again, a new dark period (1867–1900) brought to the museum essential dismemberement and destruction. In this period, Spain faced several revolutionary events, suffered several coups d'etat and changes of political regimes and finally the wars that lead to the end of the Spanish empire, the loss of Cuba and Philippines in 1898. Obviously, during this period, the politicians and society did not show much interest and financial support for natural history. In fact, in 1895 the museum was evicted, with the accumulated collections spread among two other museums. From this point, the researchers of the MNCN continued under very difficult conditions the arduous work of inventorying of all the accumulated collections and library.

From 1901, the Spanish government gained a clear understanding of the value and usefulness of a Museum of Natural Sciences. Thus, step by step, the MNCN was emerging again. A new period (1901–1936) of investment and new collections and material were acquired, to develop a national institution dedicated to preserving and documenting natural history specimens and bibliography related to the nature conservation, to the progress of knowledge by means research, and the spreading of this knowledge through exhibitions and courses. This positive change was integrated in a new wider philosophy about science and culture that brought about the creation of the "Junta para la Ampliación de Estudios e Investigaciones Científicas (JAE)" in 1907.

With this new institution, the government hoped to end the Spanish isolation and to link Spain with European science and culture, and moreover to train the staff to carry out the necessary reforms in science, culture, and education. Thus, the effort to reform and regenerate the country was considered a national matter, independent of political swings, where intellectuals of different ideologies were involved. The JAE from the beginning was presided over by Santiago Ramón y Cajal, one of the two Spanish scientists awarded the Nobel Prize (1906). Its scientific and cultural program constituted the most innovative project in Spain from 1907 to 1939, with the creation of laboratories, research centers, fellowships to study in foreign countries, etc., as well as, helping to link Spanish scientists and intellectuals with those of other countries. Together with other research centers and institutions, the MNCN was involved within the JAE. Joaquín González Hidalgo's collections of molluscs, as well as those of other malacologists, were housed in the museum during this period.

In the meantime, in 1914 the Instituto Español de Oceanografía (IEO) was founded after the integration of the marine laboratories of Santander (1886, dependent on University of Valladolid) and Porto Pi (Majorca) (1906, dependent on the University of Barcelona) into one institution. The institute was created to explore the sea and to carry out marine research at a national level, mainly to advise the Government about assessment of the marine biological resources and fisheries. At present, the IEO is addressing the multidisciplinary study of the sea, especially problems resulting from the exploitation of resources and pollution. Thus, the IEO tends to direct its efforts to applied marine sciences, and to give concrete advice to the public administration referring to the sea, with emphasis on sustainable exploitation and conservation. The IEO represents the Spanish Government on oceanographic commissions and organizations of international scope, and participates as a scientific advisor during international negotiations on fishing agreements. Therefore, the study of the opisthobranchs is outside the scope of the institute's work.

In 1936, the Spanish civil war exploded and in 1938 the JAE was eliminated together with the closure of many laboratories and research institutions, including the MNCN. Many Spanish researchers exiled themselves and continued their research out of Spain, for example in Mexico (Fig. 1).

In 1939, Franco's regime erected the Consejo Superior de Investigaciones Científicas (CSIC), which incorporated the laboratories and research center of the JAE, including the MNCN. The period of 1936–1984 was a very dark period for the museum that largely coincides with the period of Franco's regime (1939–1975). Thus, with some exceptions there were no new research positions, with few vacancies being filled. The Museum suffered grave disorder, deterioration and losses of collections.


CIENCIA

Revista hispano-americana de Ciencias puras y aplicadas

PUBLICACIONES DE

EDITORIAL ATLANTE S. A.

INSTITUTO DE GEOFÍSICA BIBLIOTECA

SUMARIO

FIGURE 1. *Revista hispano-americana de Ciencias puras y aplicadas*. Edited in Mexico from 1940 for the Spanish scientists exiled in Mexico.

At this point, we should mention Prof. Ramón Margalef (1919–2004), the most renowned Spanish ecologist and one of the world's most outstanding limnologists. He was the strongest promoter of Spanish biological oceanography. He was lucky to meet after the 2nd World War a talent finder from an American university who offered him an unlimited opportunity to visit several research institutions in the USA and other countries. He obtained a research position at the Instituto de Investigaciones Pesqueras (CSIC) from Barcelona (now, Instituto de Ciencias del Mar) in 1950. Years later he became the Director of this center (1966–1967) providing decisive impetus towards promotion of biological oceanography, transforming it from an applied fisheries research center into a true reference center. He also provided very strong input to the journal *Investigaciones Pesqueras* (now, *Scientia Marina*) that permitted the spread of the marine science undertaken in Spain. For many years he was the most cited Spanish scientist, and together with Santiago Ramón y Cajal and Severo Ochoa (both Nobel Prize recipients) was one of the three most relevant Spanish biological scientists, among a list of ninety-five from all around the world. He was awarded by the first the Huntsman Prize (considered as the Nobel Prize of the Sea). He was the first Full Professor of Ecology of Spain (1967) at the University of Barcelona. Margalef was indirectly related to the study of opisthobranch molluscs as he was the supervisor of Joandomenèc Ros' doctoral thesis (1973).

In 1984, the Direction of the CSIC embarked upon a profound restructuring of the MNCN. New fields of research were opened and new research and technical positions were provided. In general, a major effort was made to open the Museum to the general public, as well as to supply facilities and improvement to turn the Museum into the authority for natural history in Spain. This effort implies significant financial investment. Curiously, all this effort happened simultaneously with the definitive support from the Science and Research by the Spanish and Regional Governments. In fact, the large Fauna Ibérica project to describe the Iberian fauna and lead by the MNCN began in 1987, involving Spanish and non Spanish experts in many taxonomic groups. Even if the financial support had not been all that scientists wanted, monographs on all the studied groups are being successively published. One of these groups is the opisthobranchs. These works will be divided in several volumes.

Why Did No One Study Opisthobranchs in Portugal After Paulino d'Oliverira (1895)?

To reply to this question we should refer to the four circumstances quoted in the previous section concerning Spain, i.e., most lack a shell and are small in size, the main supporters of Portuguese malacology have been shell collectors, land or freshwater malacologists, or applied malacologists (Tropical Medicine Center), scuba-diving facilities were developed by tourism and, of

course, no strong financial support was given for natural history or taxonomic/systematics studies. Some taxonomic groups have been or are being studied by Spanish experts or by Portuguese in collaboration with Spanish experts within the project "Fauna Ibérica", opisthobranchs being one of these cases.

Part III: Historical Trends in the Study of Mediterranean Opisthobranchs

The marine biota of the Mediterranean Sea is one of the most extensively studied of any region in the world. Linnaeus' earliest systematic works (1758) include many Mediterraean species. With the publication of the recent checklist of opisthobranchs from the Iberian Peninsula (Cervera et al. 2006), it is possible to combine these data with data from other recent literature to gain a quantitative picture of the opisthobranch diversity of the Mediterranean and how that diversity has been understood from Linnaean times to the present.

In compiling the quantitative list of Mediterranean opisthobranchs, only currently recognized taxa are included. Taxa with multiple synonyms, of which there are many, are indicative of the amount of systematic study that has occurred within the Mediterranean, but an historical analysis of synonyms is beyond the scope of the present analysis. Excluded from the quantitative analysis are taxa that are known to have been introduced to the Mediterranean. We, however, do address the impact of anthropogenic changes in the Mediterranean. Thus, for the purposes of this study, 537 species of opisthobranchs are recognized as naturally occurring within the Mediterranean Sea, approximately the same number as were collected in a much smaller area in northern New Guinea (536) and considerably more than were known from Hawaii (244) (Ghiselin 1993). Because the Mediterranean list represents a larger geographical area and bathymetric range, the New Guinea fauna is richer than the figures suggest.

These species are not evenly distributed within the major opisthobranch taxa (Fig. 2). There are at least three plausible explanations for the uneveness of diversity within major taxa. First and foremost, the major taxa do not represent equivalent evolutionary units. They are not all sister taxa of each other. While in traditional ranked classification they are all considered orders, they do not represent branches that diverged from a common ancestor at the same time. The older lineages have had more time to diversify. Secondly, it appears that these taxa species have evolved at different rates. Some clades have speciated far more rapidly than others. And thirdly, there may have been differences in the rates of invasion from outside the area and in extinction within it.

The Cephalaspidea, which are relatively diverse, represent one of the most basal taxa of opsithobranchs. Their morphological and ecological diversity is very high. Included within this taxon are representatives with a well developed shell, intermediates that have a reduced shell and others that have a greatly reduced internal shell. Traditionally, those with an external shell have been studied by general conchologists while those with an internal shell have been studied by specialists who have worked only with opisthobranchs. When we compare the diversity of shelled forms that were described during different periods of time (Fig. 3), it is evident that the greater percentage of externally-shelled forms were described prior to 1900, while the majority of the internally-shelled taxa have been described much more recently, particularly in the last 50+ years.

The Anaspidea are a realtively morphologically uniform group of opisthobranchs with relatively low diversity and few trophic specialists. Thirteen species are known to be native to the Mediterranean. The vast majority of species have been described prior to 1850 (Fig. 4), with only three taxa described in the last 156 years. Despite the fact that they lack external shells, most species are at least seasonally common and are large and conspicuous. Thus they have been relatively well studied for a longer period.

The Sacoglossa represent a diverse assembledge of morphological forms from shelled to entirely shelless taxa. They are well represented in the Mediterranean with 46 native species. Most are small and cryptic in their appearance. Almost all species are specialized herbivores, feeding on diverse algal prey. This diversity of prey allows for a high diversity of sacoglossans to coexist without competitive exclusion. Within the Mediterranean fauna species have been described over the entire span of systematic history and continue to be named in large numbers (Fig. 5).

Whereas most major groups of opisthobranchs are benthic organisms for the vast majority of their lifespan, two major groups are holoplanktonic, spending their entire lives as members of the plankton community. The Thecosomata are shelled and are suspension feeders. On the other hand, the Gymnosomata lack a shell and are predatory, often feeding on members of the Thecosomata. The thecosomes have a higher species diversity within the Mediterranean than do the gymnosomes (Fig. 6). Also thecosomes continue to be described in high numbers whereas few gymnosomes have been named within the last 50 years. This attests to the relatively early focus and continued interest in plankton communities within the Mediterranean by resident and visiting oceanographers.

The vast majority of opisthobranch species are members of the Nudibranchia and this is certainly the case within the Mediterranean, where more than half of the opisthobranchs are nudibranchs. They are highly specialized as to prey preferences. Within the Nudibranchia, the group with the largest number of species is the Doridina, followed by the Aeolidina, Dendronotina, and Arminina (Fig. 7).

Within the Doridina, the most diverse group of nudibranchs, two groups have traditionally been recognized, the Cryptobranchia and the Phanerobranchia. Recent phylogenetic studies suggest that Cryptobranchia is likely monophyletic while Phanerobranchia is paraphyletic (Valdés 2002; Fahey and Gosliner 2004;

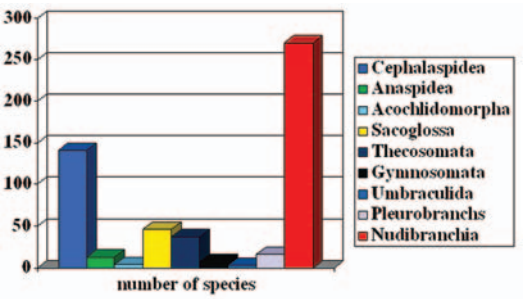

FIGURE 2. Species diversity of various opisthobranch clades found in the Mediterraean.

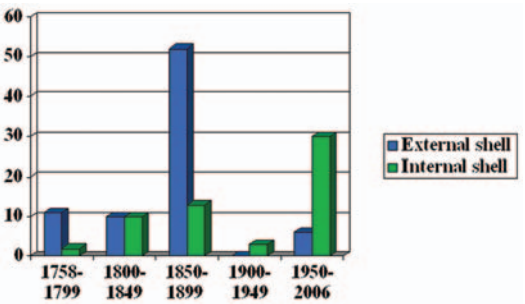

FIGURE 3. Historical differences in species description of externally-shelled versus internally shelled Cephalaspidea.

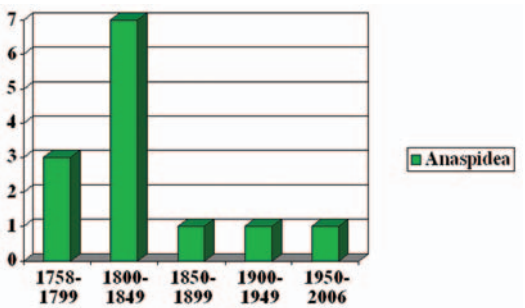

FIGURE 4. Historical descriptions of Mediterrean Anaspidea.

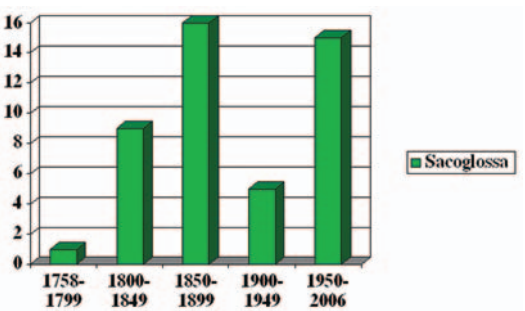

FIGURE 5. Historical descriptions of Mediterranean Sacoglossa.

Pola et al. 2007). Within the Mediterranean cryptobranchs, which are largely predators on sponges, are more diverse than "phanerobranchs" which are specialists on bryozoans and ascidians. Large numbers of species of both groups have been described in the last fifty plus years (Fig. 8). This is most likely due to the advent of scuba diving collection of species that were never encountered by intertidal collecting and trawling methods.

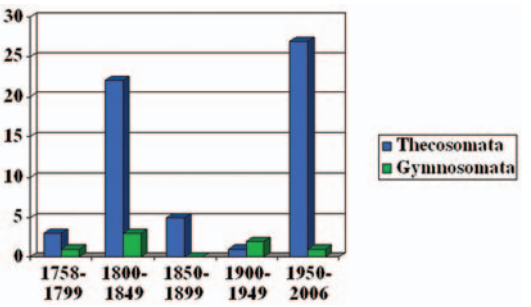

FIGURE 6. Historical descriptions of Mediterranean Thecosomata and Gymnosomata.

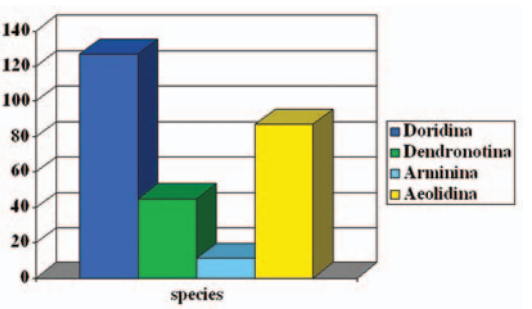

FIGURE 7. Species diversity of various nudibranch clades found in the Mediterraean.

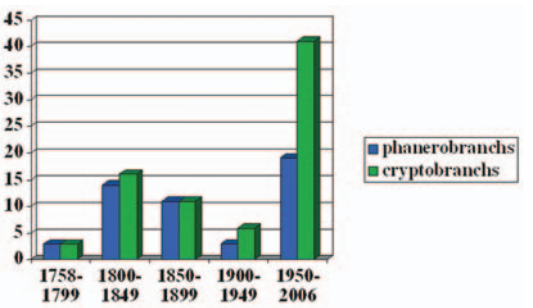

FIGURE 8. Historical descriptions of Mediterranean Cryptobranchia and "phanerobranchs"

While the above historical patterns differ significantly between different opisthobranch taxa, with the greatest number of species being described at different periods, several general patterns emerge. In almost all cases, description of new taxa continues today and is often progressing at the highest rate since the Linnean era. Our understanding of Mediterranean opisthobranch diversity continues to grow and new taxa continue to be discovered. Another pattern that is consistent within all groups of opisthobranchs is that the period when the fewest number of species was described was between 1900–1949 (Figs. 3–6, 8). It is evident that the era including the two great World Wars took a heavy toll on systematic and biodiversity research. To personalize this point, included in this paper is a reproduction of a letter written by the French opisthobranch systematist Alice Pruvot-Fol to Dr. Frank MacFarland. MacFarland was a Professor of Biology at Stanford University and President of the Calfornia Academy of Sciences. The letter (Fig. 9), part of the MacFarland archives at the California Academy of Sciences, dated in August 1945, not only clearly states the hardships endured by Pruvot-Fol but describes the adverse impact on her scientific productivity. As a result of not being able find a seat on a train, she was unable to return to her work at the marine laboratory and was forced to conduct literature reviews rather than examine specimens and describe new taxa. It should be noted that of the 15 species of Mediterranean opisthobranchs described by Pruvot-Fol, one was described in 1937 and the balance between 1948 and 1957. Clearly, World War II profoundly impacted not only her work but all research on the Mediterranean biota.

Description of the opisthobranch diversity of the Mediterrean has spanned a long period and is far from complete, as evidenced by the many new taxa that continue to be described. Over the almost 250-year history of discovery, many systematists have contributed to our knowledge of the opisthobranch fauna of the region. The 537 species have been described by 150 distinct senior authors. Not all of these authors have contributed equally to our understanding of the Mediterranean

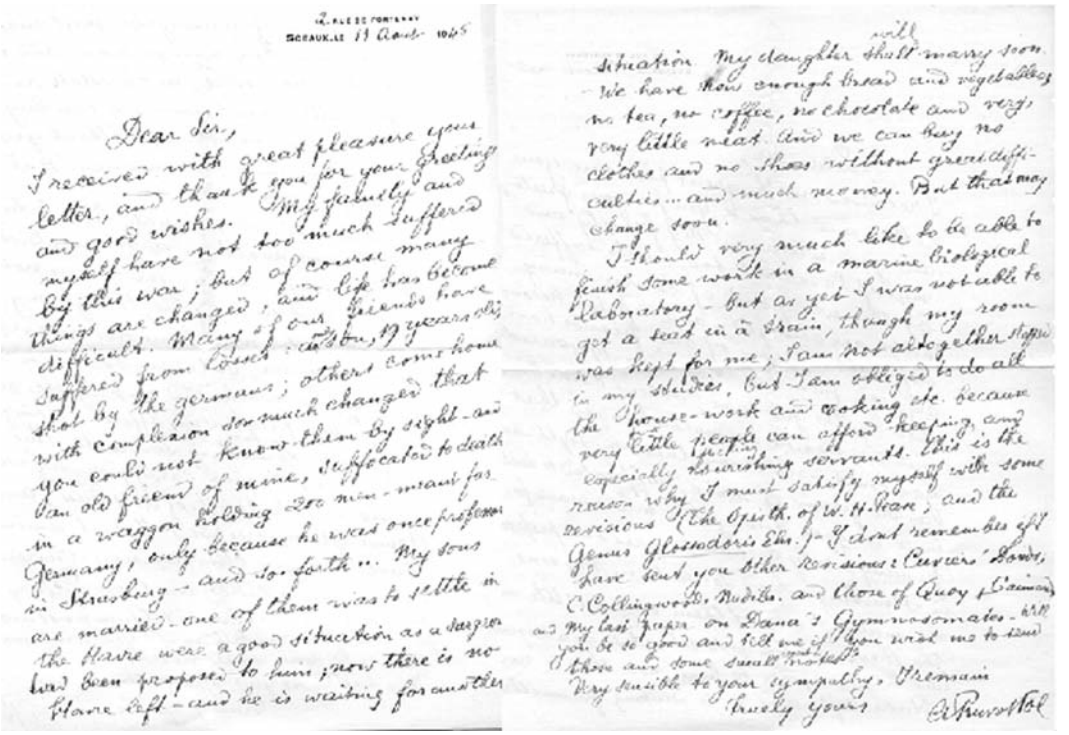

FIGURE 9. Letter from Alice Pruvot-Fol to Frank MacFarland, August 11, 1945.

opisthobranch fauna. Ten authors have described a disproportionate number of the species. These individuals and the number of species they described are shown in Figure 10. Collectively, they described 193 of the 537 Mediterranean opisthobranchs or 36% of the known fauna. Four of them published most of their systematic work in the last half of the 20th century and three continue to publish to the present. This again reinforces the point that much of our current knowledge of Mediterranean opisthobranchs has been developed only recently. A combination of new collecting techniques (especially scuba and various underwater vacuuming tools) and exploration of new geographical areas such as the Canary Islands, Madeira, the coast of mainland Portugal and the northern coast of Africa have contributed to this recent and continuing discovery of novel Mediterranean opisthobranchs.

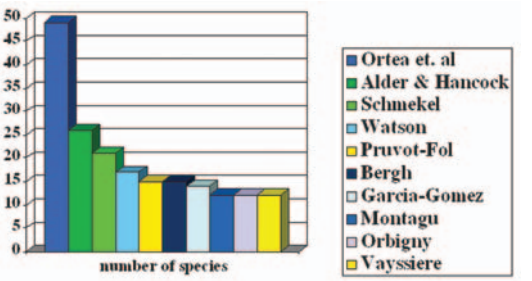

FIGURE 10. Top ten authors who have described the most Mediterranean opisthobranch species.

In addition to the 537 presumed native species of opisthobranchs found in the Mediterranean Sea, 21 species appear to have been introduced by human activities such as shipping and culturing of non-native species for food. Of the twenty-one species known to be introduced to the Mediterranen, 18 are known to have been allowed entry by the contruction of the Suez Canal, resulting in what is called Lessepsian migration from the Red Sea into the Mediterranean (Gofas and Zenetos 2003). Of the three remaining introduced species, one each has likely been introduced from California, Japan and South Africa. The Californian and South African species were likely introduced

by discharge of balast water while the Japanese species was most likely transported together with introduced shellfisheries from Japan.

In conclusion, the above data document historical patterns of study within the Mediterranean region. Taxonomic differences in the timing of study of different opisthobranch groups reflect different systematists studying shelled and unshelled opisthobranchs. Also evident is the difference in timing and greater apparent completeness of knowledge of common and conspicuous groups versus those that are smaller, more cryptic or inhabiting areas that require scuba diving. While introduction of non-indigenous species has added to the known biodiversity of Mediterranean opisthobranchs, clearly indigenous taxa are also continuing to be discovered, especially within the internally-shelled Cephalaspidea, Sacoglossa and Nudibranchia. This incompleteness of inventory of species of opisthobranchs found in the Mediterranean Sea, one of the best known marine regions in the world, has profound implications as to the even greater incompleteness in the knowledge of the constituent fauna of other lesser known regions. These data reinforce previous studies (Gosliner and Draheim 1996), suggesting that probably half of the world's opisthobranch taxa remain unknown. These studies of biodiversity that are largely conventional will be further impacted by forthcoming genetic studies that are likely to reveal more cryptic species. We are a long way from being able to produce comprehensive lists of opisthobranch taxa in the better known portions of the ocean, let alone in areas that are less explored.

Acknowledgments

This paper was benefited by the project CGL2006-05182 (JLC), supported by the Spanish Ministry of Education and Science and the Fauna Iberica Project (REN 2001-1956-C17-021GLO). Angel Luque and José Templado helped to find some important data and information and José Luis Carballo provided information used in Figure 1. This work was also supported by a National Science Foundation PEET grant DEB 9978155 Phylogenetic systematics of dorid nudibranchs and DEB 0329054 Phylogeny of the Nudibranchia to T. Gosliner and Á. Valdés.

Literature Cited

Battaglini. P. 1991. Il contributo de Oronzio Gabriele Costa nella ricerca scientifica naturalistica italiana dell '800. *Bollettino della Società dei Naturalisti in Napoli* 98/99:171–191.

Bergh, R. 1893. Die Gruppe der Doridiiden. *Mittheilungen aus der Zopologischen Station zu Neapel* 11:107–135, Taf. 8.

Borelli, A.1991. Paolo Panceri nella Napoli del secondo ottocento. *Fridericiana* 1:93–113.

Bucquoy, E., P. Dautzenberg, and G. Dollfus. 1886. *Les mollusques marins du Roussillon. Tome I. Gastropodes*. Fascicule 13. J.B. Baillière & fils., Paris, France. 487–570 pp., pls. 61–66.

Calado, G., and V. Urgorri. 2002. A new species of *Calma* Alder & Hancock, 1855 (Gastropoda: Nudibranchia) with a review of the genus. *Journal of Molluscan Studies* 68:311–317.

Capriotti, E. 1977. Molluschi e medicina nel Io secolo d. C. (studi di malacologia perinascimantale, II). *Conchiglie* 13:137–144.

Carus, J.V. 1889–1893. *Prodomus Faunae Mediterraneae. Sive Descriptio Animalium Maris Mediterranei Incolarum quam comparata Silva Rerum quatenus innotuit adectis Locis et Nominibus Vulgaribus. Vol. II. Branchiostomata. Molluska. Tunicata. Vertebrata*. Schweizerbartsche, Stuttgart, Germany. ix + 854 pp.

Cervera, J.L., G. Calado, C. Gavaia, M.A.E. Malaquias, J. Templado, M. Ballesteros, J.C. García-Gómez, C. Megina. (2004) 2006. An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletín del Instituto Español de Oceanografía* 20(1–4):1–122.

Cervera, J.L., J. Templado, J.C. García-Gómez, M. Ballesteros, J. Ortea, F.J. García., J. Ros, and A.A.

Luque. 1988. Catálogo actualizado y comentado de los Opistobranquios (Mollusca, Gastropoda) de la Península Ibérica, Baleares y Canarias, con algunas referencias a Ceuta y la Isla de Alborán. *Iberus,* suplemento 1:1–84.

Costa, A. 1865. *Di una nuova specie mediterranea di molluschi pteropodi del genere* Spiralis. *Rendiconti dell' Accademia delle Scienze Fisiche e Matematiche di Napoli* (4):1–4.

Costa, A. 1869. Illustrazione di due generi di molluschi nudibranchi. *Atti della Reale Accadmia delle Szienze Fisiche e Matematiche di Napoli* 3(19):1–6, Tav. I.

Costa, O.G. 1829. *Catalogo sistematico e ragionato de' testacei dele Due Sicilie*. Tipografia della Minerva, Napoli, Italy. 8 + cxxxii pp., Tav. I–II.

Costello, M., L.C. Emblow, and R. White, eds. 2001. *European Register of Marine Species. A check-list of marine species in Europe and bibliography of guides to their identification*. (Patrimonies Naturels) 50. Museum National d'Histoire Naturelle. Paris, France. 463 pp.

Chía, M. de. 1911–13. Aplec de notícies sobre els mol.luscs de Catalunya i catáleg provisional dels mateixos. *Bulletì de l'Istituciò Catalana d'Historia Natural*, 2ª época, 11:12–16, 28–33, 58–63, 66–72, 108–112, 127–128, 139–141; 12:11–13, 18–24, 103–107, 126–128, 157–159, 189–191; 13:109–111; 14:58–68.

Cimino, G. 1989. *Salvatore Trinchese: Opera*. Edizioni Theoria, Roma, Italia. 326 pp.

Fahey, S.J., and T. Gosliner. 2004. A phylogenetic analysis of the Aegiridae Fischer, 1883 (Mollusca, Nudibranchia, Phanerobranchia) with descriptions of eight new species and reassessment of phanerobranch relationships. *Proceedings of the California Academy of Sciences*, ser. 4, 55(34):613–689.

Faulkner, D.J., and M.T. Ghiselin. 1983. Chemical defense and the evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. *Marine Ecology—Progress Series* 13:295–301.

Fez, S. de. 1974. *Ascoglosos y Nudibranquios de España y Portugal*. CSIC, Valencia, Spain. 325 pp.

García, J., and J. Troncoso. 1999. Description of a new species of *Phidiana* Gray, 1850 (Nudibranchia: Facelinidae) from Pacific Ocean waters of Panama. *The Veliger* 42(2):190–193.

García, J., and J. Troncoso. 2001. *Favorinus elenalexiae*, a new species (Opisthobranchia: Aeolidiidae) from the estern Pacific Ocean. *Nautilus* 115(2):55–61.

García-Gómez, J.C., J.L. Cervera., F.J. García, J., S.F. García-Martín, A. Medina, and L.P. Burnay. 1991. Resultados de la campaña internacional de biología marina "Algarve 88": moluscos opistobranquios. *Bollettino Malacologico* 27(5–9):125–138.

Gasco, F. 1878. *Paolo Panceri*. Cav. G. de Angelis e Figlio, Napoli, Italia. 36 pp.

Ghiselin, M.T. 1993. How well known is the opisthobranch gastropod fauna of Madang, Papua New Guinea? *Proceedings of the Seventh International Coral Reef Symposium, Guam, 1992,* 2:697–701.

Gosliner, T., and R. Draheim. 1996. Indo-Pacific opisthobranch gastropod biogeography: how do we know what we don't know. *American Malacological Bulletin* 12(1/2):37–43.

Groeben, C. 1996. *Naturalisti a Napoli nella prima metà dell '800.* Pages 76–84 *in* F. Cacciapuoti, C. Groeben, and J. Massarese, eds., *Il sogno mediterraneo: tedeschi a Napoli al tempo di Goethe e di Leopardi*. Gaetano Macchiaroli Editore, Napoli, Italia.

Groeben, C. 2008. Tourists in science: 19th century research trips to the Mediterranean. *Proceedings of the California Academy of Sciences*, ser. 4, 59(9):139–154 [this volume].

Groeben, C., and M.T. Ghiselin. 2001. The Zoological Station at Naples and its impact on Italian zoology. Pages 321–347 *in* A. Minelli and S. Casellato, eds., *Giovanni Canestrini, Zoologist and Darwinist*. Istituto Veneto di Scienze, Lettere ed Arti, Venecia, Italia.

Hidalgo, J.C. 1916. Datos para la fauna española (Moluscos y Braquiópodos). *Boletín de la Real Sociedad Española de Historia Natural* 16:235–246.

Hidalgo, J.C. 1917. Fauna malacológica de España, Portugal y las Baleares. *Trabajos del Museo Nacional de Ciencias Naturales,* Serie Zoología, 30. Madrid, Spain. 752 pp.

Kandel, E. 1979. *Behavioral biology of* Aplysia *:a contribution to the comparative study of opisthobranch molluscs*. W. H. Freeman and Company, San Francisco, California, USA. xiii + 463 pp.

Krohn, A. 1847. Observations sur deux nouveaux genres de gastéropodes (*Lobiger* et *Lophocercus*). *Annales des Sciences Naturelles, Zoologie* (3)7:52–60, pl. 2.

Lacaze-Duthiers, H. 1859. Histoire anatomique et physiologique du pleurobranche orangé. *Annales des Sciences Naturelles, Zoologie* 11:201–202, pls. 6–12.

MALUQUER, J. 1904. Contribució a la fauna malacológica de Catalunya, III. Alguns molluscs marins del Masnou. *Boletín del Instituto Catalán de Historia Natural*, 2ª época, 1:69–74.

MALUQUER, J. 1907. Molluscs marins de Catalunya. *Boletín del Instituto catalán de Historia Natural*, 2ª época, 7:19–21.

MALUQUER, M. 1906–1909. Molluscs marins de Catalunya. *Trabajos del Museo de Ciencias Naturales de Barcelona* 1906–1907:14, 27, 42 and 103.

MALUQUER, M. 1912. Contribució a la fauna malacologica de Catalunya. *Boletín del Instituto Catalán de Historia Natural,* 2ª época, 12:50.

MALUQUER, M. 1915. Mollusc de la costa de l'Empordá. *Boletín del Instituto Catalán de Historia Natural,* 2ª época, 15:87–88.

MALUQUER, M. 1916. Treballs oceanografics de la costa de l'Epordá. *Annuari—Junta de Ciènces Naturals,* Barcelona: 221–261.

MCLELLAN, M.E. 1927. Dr. Rudolph Amandus Philippi. *The Auk* 44:158–159.

NOBRE, A. 1936. *Moluscos marinhos de Portugal*. Porto, Portugal 2:1–378.

NOBRE, A. 1938–1940. *Fauna malacológica de Portugal I. Moluscos marinhos e das águas salobras*. Companhia Editora do Minho, Porto, Portugal. 806 pp.

PANCERI, P. 1869. Gli organi e la secrezione dell'acido solforico nei gasteropodi, con un'appendice relativa ad altri glandolari dei medisimi. *Atti della Reale Accademia delle Scienze Fisiche e Matematiche di Napoli*, 4(10):1–56.

PHILIPPI, R.A. 1836. *Enumeratio molluscorum siciliae cum viventum in tellure tertaria fossilium quae in itinere suo observavit*. S. Schropp, Berlin, Germany. xiv + 267 pp.

PHILIPPI, R.A. 1839. Einige zoologische Notizen. 1. Zwei neue Arten von *Euplocamus*. *Archiv für Naturgeschichte* 5:111–134, Taf. I–IV.

PHILIPPI, R.A. 1841. Zoologische Bemerkungen. *Archiv für Naturgeschichte* 7:42–59.

POLA, M., J.L CERVERA, AND T.M. GOSLINER. 2007. Phylogenetic relationships of Nembrothinae (Mollusca: Doridacea: Polyceridae) inferred from morphology and mitochondrial DNA. *Molecular Phylogenetics and Evolution* 43:726–742.

PRUVOT, G. 1901. Le "Roland" et sa première croisiére sur la côte de Catalogne en juillet-aout 1900. *Archives de Zoologie Experimentale et Generale* 9:1–42.

RISSO, A. 1818. Sur quelques Gastéropodes nouveaux, Nudibranches et Tectibranches observées dans la mer de nice. *Journal de Physique* 87:368–377.

RISSO, A. 1826. *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice*. F.-G. Levrault, Paris, France. 5 vols.

ROS, J. 1975. Opistobranquios (Gastropoda: Euthyneura) del litoral ibérico. *Investigación Pesquera* 39(2):269–372.

ROS, J. 1976. Catálogo provisional de los opistobranquios (Gastropoda: Euthyneura) de las costas ibéricas. *Miscelánea Zoologica* 3(5):21–51.

ROS, J. 1976a. Sistemas de defensa en los Opistobranquios. *Oecologia aquatica* 2:41–77.

ROS, J. 1981. Desarrollo y estrategias binómicas en los opistobranquios. *Oecologia aquatica* 5:147–183.

ROS, J. 1984. Les nudibranches en tant que sémaphores: messages vrais et messages faux daris la communication visuelle d'un groupe de mollusques benthiques. Pages 325–335 in A. de Haro and X. Espadaler, eds., *Processus d'acquisition precoce. Les communication*. (*Publ. Universitat Autónoma de Barcelona et la Societè Française pour l'ètude du comportement animal*).

SAMA, A. DE. 1916. Mollusca marina in littora Calafell et Villanova s Antoni de Samà lecta. et nunc in Museo Barcinonense Scienciarum Naturalium servata. *Annuari — Junta de Ciènces Naturals,* Barcelona, 1916: 47–62.

SCHMEKEL, L., AND D. CAPPELLATO. 2001. Contributions to the Runcinidae. I. Six new species of the genus *Runcina* (Opisthobranchia Cephalaspidea) in the Mediterranean. *Vie et Milieu* 51(3):141–160.

SCHMEKEL, L., AND D. CAPPELLATO. 2002. Contributions to the Runcinidae. II. Three new species and comparative studies on five established species of *Runcina* (Opisthobranchia Cephalaspidea) in the Mediterranean. *Vie et Milieu* 52(2–3):85–102.

SCHMEKEL, L., AND A. PORTMANN. 1982. *Opisthobranchia des Mittelmeeres*. Springer Verlag, Berlin, Germany. 410 pp.

VALDÉS, Á. A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zoological Journal of the Linnean Society* 136:535–636.

VAYSSIÈRE, A. 1898. Monographie de la famille des pleurobranchidés. I. *Annales des Sciences Naturelles, Zoologie* 8(8):209–402.

VAYSSIÈRE, A. 1900. Considérations sur les différences qui existent entre la faune des Opisthobranches des côtes océaniques de la France et celles des nos côtes Méditerranéennes. *Comptes Rendus de l'Académie des Sciences de Paris* 130:926–927.

VAYSSIÈRE, A. 1901. Monographie de la familie des Pleurobranchidés (Deuxiéme et dernière partie). *Annles des Sciences Naturelles, Zoologie* 12:1–85, pls. 1–6.

VAYSSIÈRE, A. 1910. Nécrologie (Rudolph Bergh 1824–1909). *Journal de Conchyliologie* 58:1190–119.

VAYSSIÈRE, A. 1913. *Mollusques de la France et des regions voisines.* I. Encyclopedie Scientifique, G. Doin et Cie Edit. Paris, France. 420 pp.

VAYSSIÈRE, A. 1920. Sur la faune marine de la côte occidentale du golfe de Marseille. *Comptes Rendus de l'Académie des Sciences de Paris* 170:914–916.

VAYSSIÈRE, P. 1975. Albert Vayssière (1854–1942), entomologiste et malacologiste: sa vie, ses publications, ses taxa. *Tethys* 7:321–338.

Page intentionally left blank