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Ludwig Döderlein (1855- 1936): Some aspects of his life, research, and legacy

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The German zoologist and palaeontologist Ludwig Heinrich Philipp Döderlein (1855–1936) was one of the foremost echinoderm researchers of his time. Self-taught in many subjects of natural science, he had risen from provincial obscurity to international fame. Thanks to the efforts of a Japanese research team, it has become apparent that Döderlein was probably the most important pioneer of marine biology research in Japan. After his 1879–81 stay at the University of Tokyo, he remained internationally well-connected throughout his professional life. Yet, in his last two decades, he looked back on his early struggles not with self-satisfaction but with bitterness. He spent much of the rest of his life trying to regain the collections he had to leave behind when he was forced to leave Strasbourg in 1919.

This article is not a comprehensive study of the life and work of Ludwig Döderlein. We present some aspects of: a) his life history; b) his echinoderm research; c) his contributions to evolutionary biology, with the coral genus *Fungia* as an example; and d) his achievements in building up and promoting biological collections. The latter is illustrated by the Bavarian State Collection of Zoology (ZSM), being second only to the Zoological Museum of Strasbourg in the diversity of Döderlein specimens that survived the perils of two world wars. This all is supplemented by the first comprehensive bibliography of studies by Döderlein.

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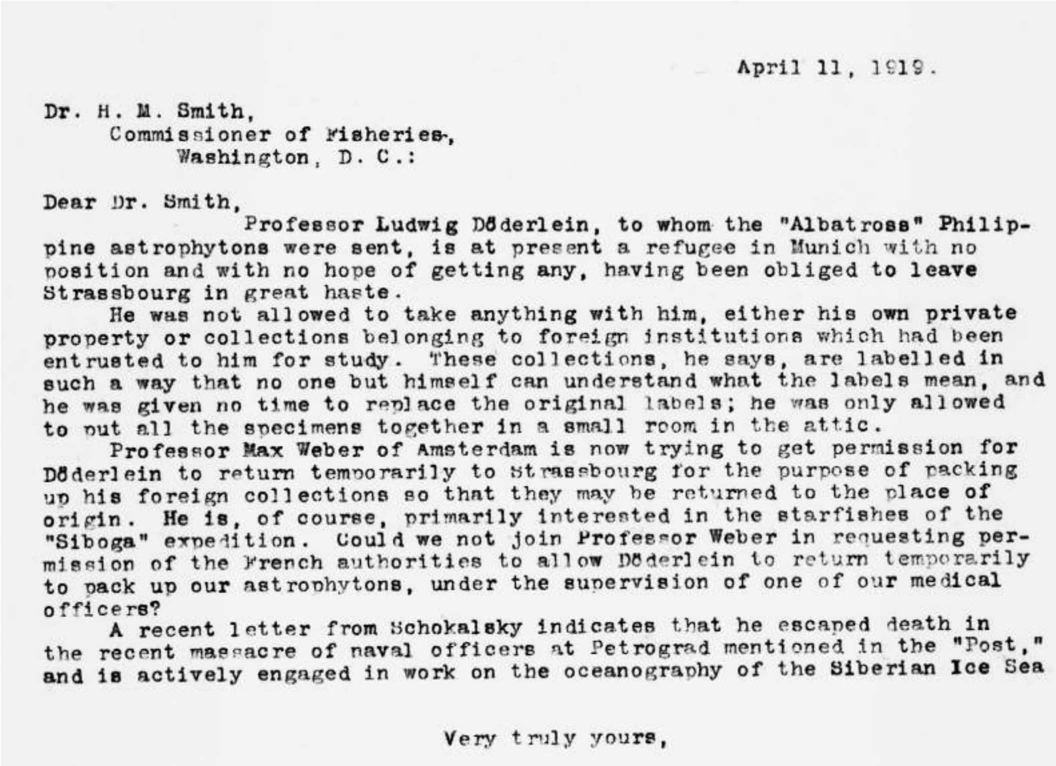
Biographical introduction

On April 20, 1922, 68-year-old Ludwig Döderlein was down on his luck. He wrote to his former staff member, Dr. Adolf Burr, in Strasbourg (April 20, 1922). “It’s a dreadful situation … prices are exploding, and people do not know any more how to survive.” (the complete letter exchange between Burr and Döderlein was published in Scholz & Lang 1999). “The bright day is done, and we are for the dark” – this was written at the same time by the English composer Edward Elgar (1857–1934, cited after Kennedy 1973) for the same reason: the Great War, friends lost in the trenches, economies in shambles. Döderlein’s prospects were felled in full flight. In 1919, the Döderlein family was deported across the Rhine into Germany. This was in accordance with the Treaty of Versailles, as Döderlein had not been a resident in Alsace prior to 1870. All of his and his family’s belongings, along with several collections of specimens, were lost. They now belonged to France, after Strasbourg changed from German to French



April 11, 1919.

Dr. H. M. Smith,
Commissioner of Fisheries,
Washington, D. C.:

Dear Dr. Smith,

Professor Ludwig Döderlein, to whom the "Albatross" Philippine astrophytons were sent, is at present a refugee in Munich with no position and with no hope of getting any, having been obliged to leave Strassbourg in great haste.

He was not allowed to take anything with him, either his own private property or collections belonging to foreign institutions which had been entrusted to him for study. These collections, he says, are labelled in such a way that no one but himself can understand what the labels mean, and he was given no time to replace the original labels; he was only allowed to put all the specimens together in a small room in the attic.

Professor Max Weber of Amsterdam is now trying to get permission for Döderlein to return temporarily to Strassbourg for the purpose of packing up his foreign collections so that they may be returned to the place of origin. He is, of course, primarily interested in the starfishes of the "Siboga" expedition. Could we not join Professor Weber in requesting permission of the French authorities to allow Döderlein to return temporarily to pack up our astrophytons, under the supervision of one of our medical officers?

A recent letter from Schokalsky indicates that he escaped death in the recent massacre of naval officers at Petrograd mentioned in the "Post," and is actively engaged in work on the oceanography of the Siberian Ice Sea

Very truly yours,

Fig. 1. Letter from Austin H. Clark, US National Museum, Smithsonian Institution, in support of Ludwig Döderlein's attempt to regain access to his collections in Strasbourg. Source: Smithsonian Archives.

administration. His subsequent attempt to visit the Zoological Museum in Strasbourg, the museum he once had headed, failed due to the Rhine becoming an impenetrable boundary. His intention was to regain his collections, an attempt that enjoyed international support e.g. from the Smithsonian Institution (Fig. 1).

Döderlein was born on March 1853 in the village of Bergzabern in the Palatinate. He went to school in Bayreuth, both places belonging at that time to the Kingdom of Bavaria. After Alsace was confiscated by Prussia in the aftermath of the Franco-Prussian war (1870–71), Döderlein became a school teacher in the Alsace town of Mulhouse, where he met Kenji Oosawa (1852–1927), a Japanese student of medicine and physiology who was enrolled at the University of Strasbourg. Evidently, Oosawa was well connected. He mediated the invitation of Ludwig Döderlein to Japan, where he became Professor of Natural History in the Medical Department of the newly founded University of Tokyo (summarized from Scholz & Nishikawa 1999, Scholz & Lang 1999, Scholz 2006). Döderlein stayed in Japan for two years as an "oyatoi (= employee) gaikokujin (= foreign)" professor (Fig. 2). He started collecting animals and plants early in 1880, immediately after his arrival in Japan (Fujita 2008, Namikawa 2009).

Fortunately, numerous historical documents from the period 1879 to 1881, and from Döderlein's later years, survived the perils of a troubled 20th century, for they were kept by the great-grandchildren of Ludwig Döderlein who live in Landau and Kaiserslautern, Germany. They kindly provided access to their family archive.

In his unpublished Japan diary, Döderlein wrote in April 1881: *"[I] bought a great number of things: … Euptectella and some other sorts of glass-sponges, … Cidaris papillata, crayfish, gorgonians, etc. I asked the people to collect these kinds of things for me as I would come back next month. I had to buy a big basket in order to take all of it with me. I collected various things on the beach and also, took with me some living specimens in big glasses … There is hardly anyone who doesn't leave that lovely island (Enoshima) without having bought a souvenir from the stalls to take it home. The zoologist can use those shops to gain best profit from them. Here*

Fig. 2. Ludwig Döderlein (front row, dark coat) as an "oyatoi" (= employee) "gaikokujin" (= foreign) professor in Tokyo, 1881 (image courtesy of the Mrs. Follenius Buessow, Landau, and Dr. Döderlein, Kaiserslautern, Germany).

he can buy what any zoological museum is lacking and ardently wishing for at a very low price …" (Döderlein 1881, transl.).

Döderlein was the first to recognize that Sagami Bay is exceptionally rich in marine fauna. This relatively small bay (ca. 2700 km^2) immediately south of Tokyo is a world-famous area, for many rare and unique marine animals have been discovered there. Döderlein's discovery was not only the point of departure for his own scientific career, but also the start of a 130 years tradition in Sagami Bay research (Nishikawa (ed.) 1999, National Museum of Nature and Science, Tokyo (ed.), 2007, Scholz (ed.) 2009). Apparently, Döderlein recommended that a marine biological station should be established in the area. This suggestion was communicated to Kakichi Mitsukuri (1858–1909), Professor of Zoology at the University of Tokyo. In 1884, Mitsukuri decided to establish a marine biological station at Misaki. The colourful history of this station is reviewed in Spencer Jones et al. (2011).

Today, the importance of the Döderlein legacy has been well established thanks to the Monbusho grant "Taxonomic and historical studies on Prof. Ludwig Döderlein's collection of Japanese animals" (1997–2003) (see Nishikawa 1999, Mawatari 2009). A wealth of information was provided by Döderlein's Sagami Bay collections. They were intensively studied by Döderlein or by his colleagues. For example, the Japanese crustaceans and bryozoans were reported by Ortmann (1890–94) (e. g. Ortmann 1890, 1893), while fishes were described by Steindachner & Döderlein (1883a,b, 1884, 1887). The Japanese echinoderms became Döderlein's life-long passion, and it was echinoderms that he was trying to recover from Strasbourg when he wrote desperate letters to Burr in 1920 to 1922.

Döderlein's research on echinoderms

Over the course of 52 years, from 1885 to 1936, Döderlein published 43 papers on echinoderms (see complete bibliography of studies by Döderlein – below),

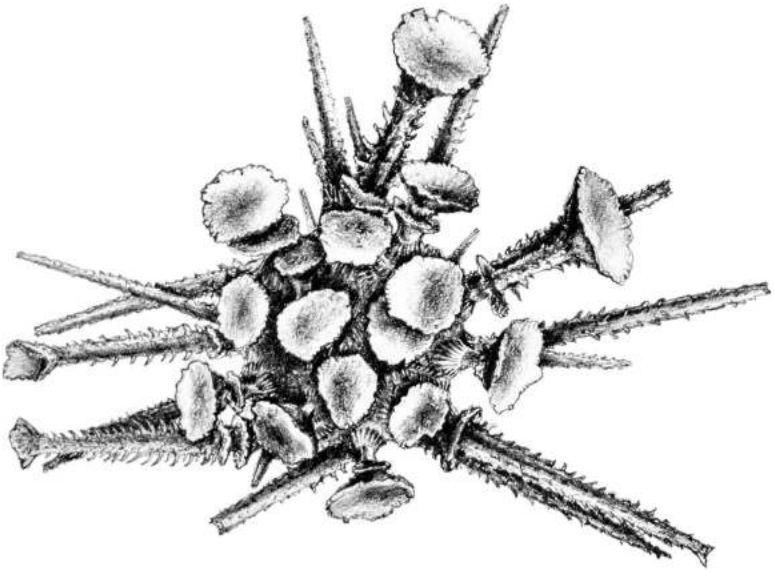


Fig. 3. *Goniocidaris clypeata* Döderlein. Illustration of whole animal, drawn by Döderlein and Scharfenberger, plate VI figure 1 of "Die Japanischen Seeigel. 1. Theil. Familie Cidaridae und Saleniidae" (Döderlein 1887c).

a total of approximately 1670 printed pages, plus hundreds of illustrations in the form of plates and text-figures. His larger works included monographic studies of the sea star genera *Astropecten* (Döderlein 1917, 192 pages) and *Luidia* (Döderlein 1920, 101 pages), based on Siboga Expedition collections, a report on the sea urchins collected by the Deutschen Tiefsee-Expedition (Döderlein 1906a, 230 pages), and a paper on Indo-Pacific basket stars (Döderlein 1927c, 105 pages). He described approximately 50 new genera and 374 new species of echinoderms, and the majority of these taxa remain valid today. In his echinoderm research he covered all groups except the Holothuroidea – a preference shared with Austin Hobart Clark (1880–1954) of the United States National Museum! Döderlein's publications reflect particular attention to detail, his descriptions of new taxa are admirably thorough and well-illustrated, and care is taken to compare and contrast new species with known congeners. In almost all of his taxonomic work, Döderlein attempted to place the species he identified in a wider context. He would list and discuss the other species known from the genus, offer summary notes on distribution and affinities of these taxa, and provide a dichotomous key to the taxa. One of his first significant echinoderm publications, on cidaroid and salenioid echinoids of Japan (Döderlein 1887c), is a comprehensive analysis of the taxonomy and evolution of these echinoid groups (Fig. 3), and it epitomizes his entire research output on echinoderms.

Space limitations prevent a detailed study of Döderlein's echinoderm publications, but one of his papers is discussed here in a little more detail; it provides a window into Döderlein's research methodology. His 1911 paper on basketstars (brittle stars with branching arms) has the unassuming title "Über Japanische und andere Euryalae", but it is in fact a superb world-wide revision of the group, with comprehensive descriptions of new and old species and genera, annotated checklists, keys, and ample illustrations (Döderlein 1911b). This 123-page paper includes 9 plates and 52 text-figures. Eight new genera are characterized, and 9 new species are described; almost all of these new taxa remain valid to this day. In the introductory sections, Döderlein discusses the history of scientific study of the group, and the current composition of the families. He then reviews and analyses in detail the relative value of the characters used in classification. The taxonomic section is then followed by a detailed synopsis of the group down to the species level, with synonymies for every species, and with detailed literature references. The illustrations are informative and of high quality. Finally, unlike some of his contemporaries, Döderlein is unfailingly polite in his discussions of the work of his predecessors and contemporaries.

For an appreciation of the overall quality of Döderlein's echinoderm research, we can do no better than quote from Theodor Mortensen's great Monograph of the Echinoidea (Mortensen 1928, p. 43). In discussing the higher classification of the

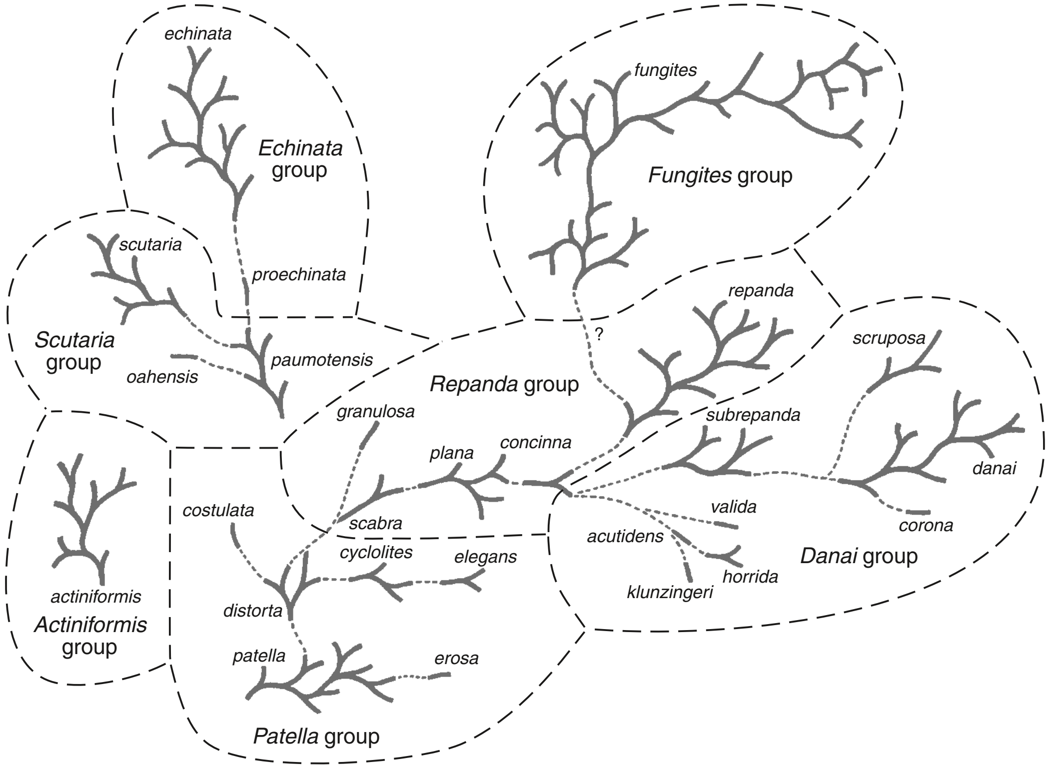


Fig. 4. Döderlein's (1902) model of *Fungia* phylogeny based on corallum size, the absence or presence of perforations in the corallum wall, and size increases of the costal spines and the septal teeth. For comparison, see cladograms presented by Gittenberger et al. 2011, Hoeksema et al. 2012.

cidaroid echinoids, Mortensen notes: "A very earnest attempt at a natural classification was then given by Döderlein in his excellent work *Die Japanischen Seeigel. I. Cidaridae u. Saleniidae (1887)*. Through his deep-going studies he reached some very important results, which ought to stand as a firm basis for all future considerations of the mutual affinities of Cidarids". This is high praise indeed from Mortensen, who could be very critical of the work of his colleagues!

Döderlein's publications grace the literature on echinoderms. His work was, and remains, highly regarded. Despite many personal and professional difficulties brought on by illness and the Great War, he came to occupy an enviable place in the pantheon of echinoderm researchers, and his name ranks with those of his great contemporaries, such as Alexander Agassiz, Hubert Ludwig, Theodor Mortensen, Hubert Clark, Austin Clark, and Walter Fisher.

Anyone who spends some time with the great collections of Ludwig Döderlein preserved in several museums in central Europe will come away with an overwhelming impression of respect for Döderlein the taxonomist. Yet, during his lifetime, Döderlein was equally well known as an evolutionary biologist. This can be perfectly well illustrated by his research on corals.

From taxonomic analysis to theories on evolution and ecology: Ludwig Döderlein's pioneering research on mushroom corals

The scleractinian family Fungiidae is a monophyletic group of reef coral species, which is widespread in the tropical Indo-Pacific (Wells 1966, Hoeksema 1989). They can occur abundantly in massive multispecies assemblages on coral reefs, from shallow reef flats down to deeper reef bases (Hoeksema 1991a, 2012, Hoeksema & Koh 2009, Hoeksema & Matthews 2011). They are commonly known as mushroom corals because of their appearance; most species are discoid, with septa typically radiating from the central mouth towards the periphery. This shape is most characteristic of species formerly classified with *Fungia* Lamarck, 1801, the type genus of the family. This genus has been the subject of two publications by Döderlein, an essay (1901a) and a taxonomic revision (1902a). He selected *Fungia* as a model taxon to determine whether many forms of reef corals could be systematically arranged in natural groups consisting of subgenera, species, subspecies and varieties. Furthermore, he wanted to investigate whether such a classification could be used to discern evolutionary trends from primitive to more advanced in order to determine natural relations between these groupings. He selected *Fungia* instead of other coral genera, because he did not consider this genus as too large and the specimens did not seem to be too fragile.

Based on his taxonomic revision of *Fungia*, Döderlein (1901a, 1902a) indeed presented an evolution model (Fig. 4). He referred to morphological developments in species lineages, while recognizing the occurrence of parallel developments: (1) an increase in corallum size; (2) the appearance of perforations in the corallum wall (from a solid wall to perforations only at the corallum periphery, to perforations over almost the whole corallum wall, including near the centre); (3) a size increase of the costal spines; and (4) a size increase of the septal teeth.

Based on these findings, Döderlein distinguished seven species groups in *Fungia*:

The *Patella* group. In some species Döderlein (1902a) distinguished a complete form (*Cycloseris*-form) and a self-fragmenting form (*Diaseris*-form). At present, this species group is still recognized, consisting of species belonging to the genus *Cycloseris* Milne Edwards and Haime, 1849 (Gittenberger et al. 2011, Benzoni et al. 2012), although it is richer in species and morphologically more diverse than the *Patella* group presented by Döderlein (1901a, 1902a). It is unfortunate that Döderlein named this the *Patella* group, because the species after which it has been named, *Madrepora patella* Ellis and Solander, 1786, does not belong to that group; it appears to be synonymous with *Fungia fungites* (Linnaeus, 1758) (see Hoeksema 1989).

The *Actiniformis* group. Originally, it consisted of a single species, *Fungia actiniformis* Quoy and Gaimard, 1833. Wells (1966) classified this group as the monospecific subgenus *Heliofungia* Wells, 1966, which at present is considered a separate genus with two species (Gittenberger et al. 2011).

The *Scutaria* group, which is represented by most species belonging to the genera *Lobactis* Verrill, 1864, and *Pleuractis* Verrill, 1864 (Gittenberger et al. 2011). *Pleuractis taiwanenis* (Hoeksema & Dai 1991), originally described as *Fungia (Pleuractis) taiwanesis* was described as the first polystomatous *Fungia* species because of its close resemblance to *P. moluccensis* (Van der Horst, 1919) and therefore deviating from the original concept of a monostomatous *Fungia* (Hoeksema & Dai 1991, Hoeksema 1993b).

The *Echinata* group, which is presently known as *Ctenactis* Verrill, 1864, consisting of three species (Hoeksema, 1989). *Ctenactis crassa* (Dana, 1846) is the only consistently polystomatous species of the genus, but Döderlein (1901a, 1902a) did not recognize it as belonging to the *Echinata* group.

The *Repanda* group. Later, this group was classified as two subgenera, i.e., *Verrillofungia* Wells, 1966, and *Wellsofungia* Hoeksema, 1989, but at present its species belong to *Lithophyllon* Rehberg, 1892 (Gittenberger et al. 2011).

The *Danai* group is presently known as *Danafungia* Wells, 1966 (Gittenberger et al. 2011).

The *Fungites* group, which is presently known as *Fungia* Lamarck, 1801, and is represented by only one species, *F. fungites* (see Gittenberger et al. 2011).

In Döderlein's (1901a, 1902a) study *Fungia* was represented by all free-living monostomatous (solitary) species that belonged to the Fungiidae. Although Döderlein's species groups of *Fungia* are more or less represented by currently valid fungiid genera (Gittenberger et al. 2011), *Fungia* is now only known by its type species, *Fungia fungites* (Linnaeus, 1758).

Since Döderlein's work, the charismatic Fungiidae have become an ideal model taxon for phylogeny reconstructions. Wells (1966) presented a generic revision of the Fungiidae, in which he distinguished various evolutionary species lineages that were based on the following trends: a reversal from free-living to attached growth forms, a development from monostomatous coralla (with only a primary centre) to polystomatous ones (with the addition of secondary centres), and a trend from small septo-costal ornamentations to coarse ones. Wells (1966) followed Gardiner (1909) in using the overall growth form of mushroom corals to distinguish genera, but he did not mention that the differences in morphology and microstructures of the septo-costal ornamentations of mushroom corals, which he used to distinguish six subgenera in *Fungia*, had already been described in much detail by Döderlein (1901a, 1902a). Actually, the characters used by Döderlein (1901a, 1902a) to distinguish species groups in *Fungia* were also used for the subgenera distinguished by Wells (1966). These morphological differences were also treated by Vaughan and Wells (1943) and Wells (1956), but they did not refer to Döderlein's work. In fact, with the exception of the *Patella*-group, which was classified as the genus *Cycloseris*, Vaughan and Wells (1943) and Wells (1956) referred to the same species groups as Döderlein (1901a, 1902a) did, but without referring to his work. The evolution model of the Fungiidae presented by Wells (1966), which served as basis for later studies (Cairns 1984, Hoeksema 1989, Gittenberger et al. 2011, Benzoni et al. 2012; Hoeksema et al. 2012), actually should partly be credited to Döderlein.

With regard to the life history of fungiids, Döderlein (1901a, 1902a) discerned three kinds of asexual reproduction (see Hoeksema 1989: fig. 42): (1) the regeneration of new attached polyps (anthocaulus phase) from attachment stalks that were vacated by detached older corals of the same genotype, the anthocyathus phase (Hoeksema & Yeemin 2011); (2) the development of new attached polyps at the outside of parent animals by budding, which may result in patches of reef surface becoming densely covered by monospecific stands of mushroom corals (Hoeksema 2004); (3) self-fragmentation (autotomy) by the fission of corals along radial slits where the coral skeleton becomes partly dissolved (Yamashiro et al. 1989, Yamashiro & Nishihira 1994; Hoeksema & Waheed 2011). The last mechanism only occurs in corals showing the *Diaseris*-form, which belong to free-living *Cycloseris* species (Döderlein 1902a, Hoeksema 1989). All segments contain a part of the mouth and develop into new coralla by regenerative growth along the breakage lines of the original fragments, after which the fragmentation is repeated again. Mushroom corals may also break and regenerate by external force if the coralla are extremely thin, which is common in some polystomatous species that show fragments containing secondary mouths. These fragments can easily grow into large clones of their parent corals (Hoeksema & Gittenberger 2010). This signifies the advantage of a tendency towards indeterminate growth in the derived polystomatous forms over the ancestral monostomatous shape of *Fungia*, in which growth is limited by the presence of only a single mouth, with the exception of corals in the *Diaseris*-form (Hoeksema 1991b).

Döderlein did not elaborate on the evolutionary developments in the life history traits of polystomatous mushroom coral species. Perhaps he did not perceive that in his species groups of *Fungia*, consisting of free-living, monostomatous mushroom corals, larger, polystomatous species also belong. Thanks to phylogenetic studies it is now recognized that polystomatous species such as *Ctenactis crassa* (Dana, 1846) and *Pleuractis taiwanensis* (Hoeksema & Dai, 1991) are close relatives to monostomatous species (Hoeksema 1989, 1993b, Gittenberger et al. 2011).

Döderlein (1902a) also remarked on the great intraspecific variation in reef corals, which he related to their sedentary mode of life and which he considered a cause for confusion in coral taxonomy. Although he synonymized various mushroom coral species, he also named some new ones and several new varieties. Some of these were used as examples of geographic races or subspecies by Mayr (1942). However, Boschma (1925) pointed out that much intraspecific variation in mushroom corals may occur at a single locality and that these varieties may reflect ecophenotypes. The importance of phenotypic corallum variability has been confirmed in later studies (Hoeksema & Moka 1989, Hoeksema 1993a, Gittenberger & Hoeksema 2006).

Döderlein published his coral studies in the German language, and therefore the ideas that he presented on the evolution and ecology of mushroom corals may be well-known but they have not been credited to him. These ideas are well accepted in modern reef coral science, probably more than generally realized.

Summarizing Döderlein's major scientific achievements

The genus *Fungia* represented one of the many animal taxa Döderlein studied apart from the Echinodermata. The latter counts for about half of his approximately one hundred publications. In the research field of stony corals there was one more paper, a systematic study on the scleractinians of the Gulf of Naples (Döderlein 1913a). Other taxa of invertebrates he treated – mostly taxonomically but also with regard to faunistics – were calcareous sponges (e. g. Döderlein, 1884) and insects (e. g. Döderlein, 1912b). However, Döderlein was also a widely recognized expert on vertebrates. Here only his studies on fish (e. g. Steindachner & Döderlein 1883a,b, 1884, 1887) were focused on systematics. In the case of tetrapods, he was mainly interested in comparative anatomy and morphology, with an evolutionary-phylogenetic focus. In his very first study, his doctoral thesis, he treated the anatomy of a mammalian species (Döderlein 1878a,b). This was followed by faunistic essays on Japanese vertebrates (snakes, birds, mammals; e. g. Döderlein 1882a,b, 1883b) and later by investigations on fossil vertebrates, mainly mammals. Thus, Döderlein was not only a zoologist but also a palaeontologist; he even left the milieu of the animal kingdom twice, with a paper on Japanese flora (Döderlein 1881a) and a field guide for mushroom collectors (Döderlein 1918). His interest in palaeontology might have been triggered by examination of fossil sites in his adopted country, the Alsace (e. g. Döderlein & Schumacher 1887). His familiarity with fossils enabled him to contribute the entire part on vertebrates for a comprehensive text book on systematic palaeontology (Steinmann & Döderlein 1890). Except for a single digression to echinoids (Döderlein 1887b) he remained with vertebrates in palaeontology. Of particular impact were Döderlein's investigations on pterosaurians in the terminal phase of his scientific career. He described soft parts, such as the throat pouch, the tail sail, and also taxonomic characters distinguishing long- and short-tailed forms (e. g. Döderlein 1929a–d).

One technical aspect is noticeable in Döderlein's systematic and morphological studies. He began to use photography early (Döderlein 1888), and he later applied it almost excessively (Döderlein 1902a, 1906a), replacing line drawings to a large extent. This presumably was facilitated by echinoderm research where, for some groups, photography became a common form of illustration very early (e. g. Agassiz 1874). Döderlein's macro- and microscopic photographs were of a high quality. He described the technology in detail (Döderlein 1906a) and obviously produced the photographs himself.

There are other remarkable topics and interests in his scientific career that are worthy of mention. Among them was his contribution to establishment of rules for zoological nomenclature. Döderlein was a member of a German team of zoologists who published (e. g. Carus et al. 1894) proposals for such rules ahead of the formation of the International Commission on Zoological Nomenclature (Melville 1995). Further, there is his impact on evolutionary hypotheses – of mainly vertebrates. This concerned the development of a terrestrial way of life (Döderlein 1912c), digestion (Döderlein 1921a), and development of aerial locomotion (Döderlein, 1901d). In the study "Phylogenetische Betrachtungen" (Döderlein 1887a) he introduced a law, later named after him as "Döderlein's law", founded upon his assumption that certain organs or parts of the body show a tendency to enlargement beyond the functional requirements, leading to eventual decline and extinction. As one of many examples, he cited the sabertooth cats. We know today, thanks to studies by Turner & Antón (1997) and many others, that the saber- or dirktooth arrangement was a very functional feature. Again, due to space constraints, we cannot dwell upon the ramifications of "Döderlein's law". Some of his thoughts, related to the so-called orthogenesis theories of evolutionary progress, are not very relevant in today's investigations of evolutionary theory.

Problems encountered during taxonomic studies are treated in the theoretical paper "Über die Beziehungen nahe verwandter 'Thierformen' zueinander" (Döderlein 1903). In this, he developed far-reaching conclusions related to speciation and species concepts. The genus *Fungia* (see above) was just one example that he discussed.

Fig. 5. Ludwig Döderlein in his final years at the ZSM in Munich.

In total, his publications show that the breadth of Ludwig Döderlein's interests extends far beyond the fields for which he is best known – taxonomy and systematics; in particular, his essays on local faunistics of the Alsace indicate that he was a passionate field observer with conservation interests. This is also reflected by another late work, an identification guide for the German fauna (Döderlein 1932).

When his complete oeuvre is considered, Ludwig Döderlein emerges as a scientist with an extremely broad spectrum of interests and expertise. From the vantage point of today – in an age of increasing specialization in science and other fields – this range of knowledge and skills appears to be enormous. Indeed, even in Döderlein's days the great breadth of his interests and capabilities was unusual.

Döderlein's collection (ZSM)

The Bavarian State Collection of Zoology (ZSM) owns an important portion of the scientific legacy of Ludwig Döderlein. This mainly consists mostly of invertebrate collection samples that he gathered himself in Japan in 1879–1881, and partly of samples from collecting expeditions of others (e. g. Sarasin in Ceylon, Semon in Amboina, Marine Station Naples, expeditions of the vessels Valdivia and Siboga) that were sent to him for taxonomic investigation. Moreover, his entire scientific library was donated to the library of the ZSM; this comprises material that he managed to transfer from the Strasbourg museum to Munich, along with material that he accumulated in his later scientific career in Munich (1919–ca. 1936) (Fig. 5).

In order to better understand Döderlein's scientific legacy, it is first necessary to look at the history of the collections. In the case of the material accumulated by him, this originally was Döderlein's property. During his professional activity in the Strasbourg museum, parts of the collections were transferred to the holdings of this museum. As has become evident from the correspondence between Döderlein and his confidant in Strasbourg (Scholz & Lang 1999), the determination of items belonging to the museum, or to Döderlein, was a matter for debate. The principles applied for this subdivision were roughly as follows: Examined material that had been handed over to the museum remained in the possession of the museum of Strasbourg; the remainder that was still in the process of examination was left to Döderlein's disposal for transport to Germany. As can be deduced from the specimens of the ZSM, however, the definition of "ongoing investigation" was interpreted fairly inaccurately by Döderlein. Some quite important specimens, whose examination had been finished years before Döderlein's deportation, were also transferred to Munich. This includes specimens collected by Döderlein, but described by others, such as the brachiopod *Rhynchonella döderleini* (Davidson, 1986), which was not considered in the 1999 report of Nishikawa et al. (Nishikawa 1999). In the case of material from other institutions, this, typically, was loaned material that had to be returned to the parent organization after completion of the investigation. However, as the existence of not inconsiderable quantities of such material on the ZSM shows, this was not generally the case. Typically, there were agreements according to which taxonomists were allowed to keep parts of the loaned material. But no records on this have survived. In some cases, collections may not have been returned to their owners; this is indicated, for example, by labels of other museums among the *Fungia* material of Döderlein. There is a detailed report about the distribution of Döderlein's Japanese material in European museums (Nishikawa 1999). In brief, according to Nishikawa (1999, table 1): by far the largest part of the samples (ca. 76 %, mainly Porifera, Mollusca, Crustacea, Bryozoa, Vertebrata) remained in Strasbourg; some specimen found their way to Berlin (5 %, mainly Pisces, Ascidiacea); the ZSM now houses approximately 20 % (mainly Echinodermata).

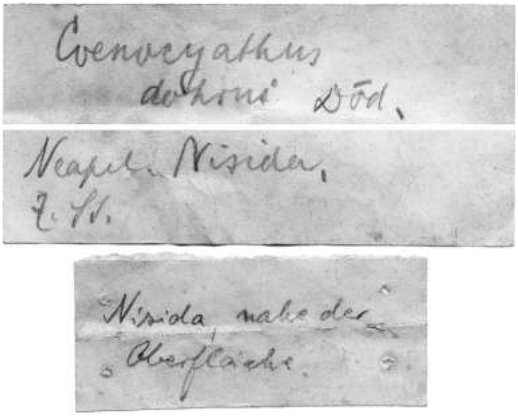


Fig. 6. Original specimen labels, prepared by Döderlein for the syntypes of *Coenocynathus dohrni* Döderlein, 1913.

In assessing the total extent of the Döderlein material, there is the following problem: for samples of ZSM invertebrates, it often is impossible to determine the precise origin, because in World War II almost all of the documentation (lists, correspondence, etc.) were lost. However, in the case of Döderlein, the samples could be identified by the characteristic labels with his typical handwriting (Fig. 6). Until a thorough survey has been conducted, it is impossible to accurately estimate the extent of the material.

In terms of systematics, the largest portion by far of the material that came through Döderlein to the ZSM comprises echinoderms; in addition there are smaller proportions of other taxa. For the echinoderm collection the portion contributed by Döderlein is about two thirds of the 4600 samples. The majority of this material is samples from Japan. It appears that most of the Japanese specimens that Döderlein had in hand have survived, and can be found in the ZSM collection. Much less material from his other echinoderm studies is in the ZSM. There are 130 samples from the Valdivia expedition, but little remains from the Siboga, the Gauss and the Semon Expedition.

The Döderlein echinoderms are characterized by the relatively high proportion of type material. According to the type catalogue of Jangoux et al. (1987) approximately 93 species (plus a number of subspecies) are represented by types. However, a brief survey for the present paper revealed that the general Döderlein echinoderms include many more types than indicated in this catalogue. Jangoux et al. (1987) apparently only included such specimens that were obvious as types from labels. Döderlein, however, hardly ever marked the type status on labels; similarly, he did not discuss the type status of material in his publications.

Apart from echinoderms, the ZSM houses smaller amounts of Döderlein material of other invertebrate taxa such as Foraminifera, Brachiopoda, and Hydrozoa. Particularly worth mentioning are the scleractinians: There is the material of Döderlein's *Fungia* studies and also the material of the Neapolitan stony corals (Döderlein 1913a), which was also "discovered" during a survey for the present publication.

Last Harvest

"In society you will not find health, but in nature"
Henry David Thoreau
(Natural History of Massachusetts, 1842)

As can be seen from the example of the Neapolitan stony corals, a detailed survey of the entire Döderlein collections in the ZSM would be a worthwhile task. Besides a considerable number of types, probably further material of scientific value would come to light. Likewise, a reassessment of what Döderlein wrote many decades ago on taxonomy and evolutionary biology, may generate considerable knowledge, as illustrated by the scleractinian family Fungiidae.

Frequently under-valued, natural history collections are unique databases giving a perspective through time and space, sometimes also bringing back to light valuable insights into the life and thinking of the collecting scientist. A true "Döderlein Renaissance" began in the field of collections when a colleague from Japan, Shunsuke F. Mawatari (Hokkaido University, Sapporo), re-discovered a large portion of Döderlein's biological collection in the Zoological Museum in Strasbourg in 1991. Previously, these specimens were considered to be lost in the wars (Mawatari 2009). In the last two decades, the "Döderlein Renaissance" has mainly been relevant for Japan, and Japanese specimens. We now have a much more realistic picture of the true importance of Döderlein in Japan than we were able to have two decades ago. Regrettably, a similar re-evaluation of the Döderlein collections from the Mediterranean is lacking, and this is the region where Döderlein made the second of his two voyages to foreign shores. Advised by his doctors, Döderlein went to Algiers in 1902, hoping to cure his pharyngeal tuberculosis. As in Japan some years before, he spent much of his time collecting as reported in the unpublished family chronicles, edited by his great-grandson (Döderlein 2000).

As a reassessment of the entire Döderlein collection aside from Japan is still lacking, the last harvest has not yet been brought in. Coming from rather diverse fields of specialization, we hope that because of our different backgrounds we have been able to convey some idea of the wealth of the biological information collected and disseminated by Döderlein, and of the treasures that remain hidden in the collection drawers of museums all over the world. As a result of our investigations, we are humbled in light of the dedication, and the achievements, of the great Ludwig Döderlein.

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