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Ludwig Döderlein's Pioneering Research on Echinoderms, Ecology and Evolution: A brief historical review*

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Abstract

The German zoologist and paleontologist Ludwig Heinrich Philip Döderlein (1855–1936) was one of the foremost echinoderm researchers of his time. Self-taught in many subjects of natural science, he rose from provincial obscurity to international fame. We present some aspects of: a) his life history; b) his echinoderm research; c) his contributions to ecology and 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, being second only to the Zoological Museum of Strasbourg in the diversity of Döderlein specimens that survived the perils of two world wars.

Key words: history of sciences, Ludwig Döderlein, biography, Germany, Strasbourg

Biographical Introduction

Döderlein was born on March 1855 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 (1870–1871), Döderlein became a school teacher in the Alsace town of Mühlhausen (Mulhouse), where he met Kenji Oosawa (1852–1927), a Japanese student of medicine and physiology who was enrolled at the University of Straßburg (today Strasbourg). Oosawa 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. He started collecting animals and plants early in 1880, immediately after his arrival in Japan (Fujita 2008; Namikawa 2009).

Döderlein was the first to recognize that Sagami Bay is exceptionally rich in marine fauna. This relatively small bay (ca. 2,700 km^2) immediately south of Tokyo is a world-famous area, for many

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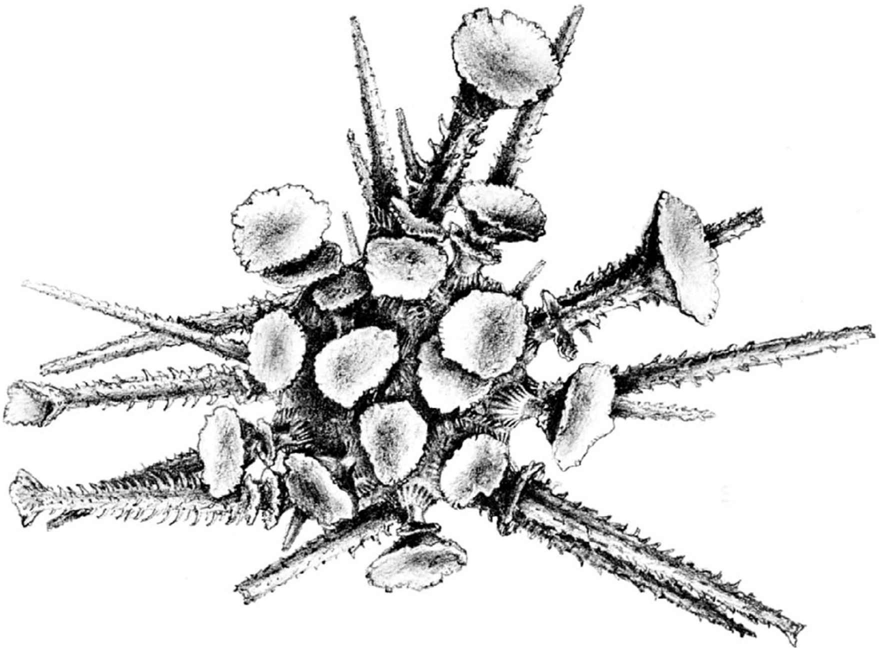

FIGURE 1. *Goniocidaris clypeata* Döderlein. Illustration of whole animal, drawn by Döderlein and Scharfenberger, Plate 6, Figure 1 of *Die Japanischen Seeigel. 1. Theil. Familie Cidaridae und Saleniidae* (1887).

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-long tradition in Sagami Bay research (Nishikawa (ed.) 1999; National Museum of Nature and Science, Tokyo (ed.) 2007; Scholz (ed.) 2009). After his return from Japan in 1881, Döderlein worked as curator and director of the zoological museum in Straßburg for almost forty years. In 1919, the Döderlein family had to leave the Alsace and move to Germany. This was in accordance with the Treaty of Versailles, as Döderlein had not been a resident in Alsace prior to 1870. He continued his scientific career in Munich (1919–1936).

Today, the importance of the Döderlein legacy in Japan 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 (ed.) 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; 1894), while fishes were described by Steindachner and Döderlein (1883a, 1883b, 1884, 1887). It was Japanese echinoderms that became Döderlein's life-long passion.

Döderlein's research on echinoderms

Over the course of 51 years, from 1885 to 1936, Döderlein published 42 papers on echinoderms (data derived from the Zoological Record), a total of approximately 1,670 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* (1917, 192 pages) and *Luidia* (1920, 101 pages), based on Siboga Expedition collections, a report on the sea urchins collected by the "Deutsche Tiefsee-Expedition" (1906, 230 pages), and a paper on Indo-Pacific basket stars (1927, 105 pages). He described 50 new genera and 374 new species and subspecies of echinoderms, the new species representing about 7%

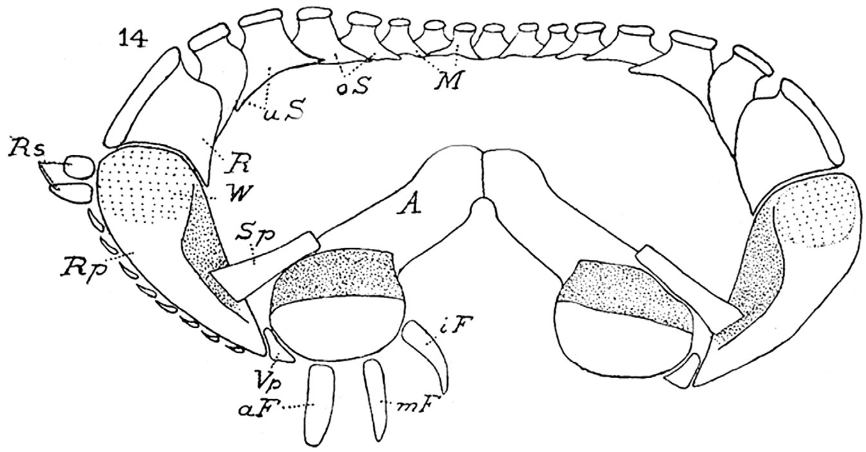

FIGURE 2. Cross-section of an arm of *Luidia brevispina,* Plate 19, Figure 14 from Döderlein's monograph of the asteroid genus *Luidia* (Döderlein 1920). The simple but informative illustration technique was followed by H.B. Fell, A.M. Clark and M.E. Downey, and others.

of the total number of echinoderm species known at the time. His "success rate"—the percentage of his new genera and new species/subspecies which are today regarded as valid ("accepted" by current online databases—World Asteroidea database, World Ophiuroidea database, World Echinoidea database), is as follows:

Crinoidea: 1 new genus, 1 (100 %) valid, 10 new species, 10 (100 %) valid.
Asteroidea: 19 new genera, 11 (58 %) valid; 137 new species and subspecies, 71 (52 %) valid.
Ophiuroidea: 19 new genera, 16 (84 %) valid; 70 new species and subspecies, 35 (50 %) valid.
Echinoidea: 12 new genera, 5 (26 %) valid; 157 new species and subspecies, 52 (33 %) valid.

For comparison, Döderlein's contemporary, René Koehler (1860–1931) at the University of Lyon, had a "success rate" of approximately 48 % in his taxonomic work on Echinoidea and Ophiuroidea. Later authorities, such as Mortensen (1868–1952, Echinoidea) and Fisher (1878–1953, Asteroidea) enjoyed a success rate of approximately 68 %.

In his echinoderm research, Döderlein 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 some of his earlier works (for example Döderlein 1887a), he apparently prepared his own line illustrations; afterwards, 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 1902, 1906), 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 1872–1874). Döderlein's macro- and microscopic photographs were of a high quality. He described the technology in detail (Döderlein 1906) and obviously produced the photographs himself.

In almost all of his taxonomic work, Döderlein presented details of morphology. He also attempted to place the species he identified in a wider context. He listed and discussed the other species known from the genus, offered summary notes on distribution and affinities of these taxa, discussed their evolutionary history, and provided a dichotomous key to the taxa. One of his first significant echino-

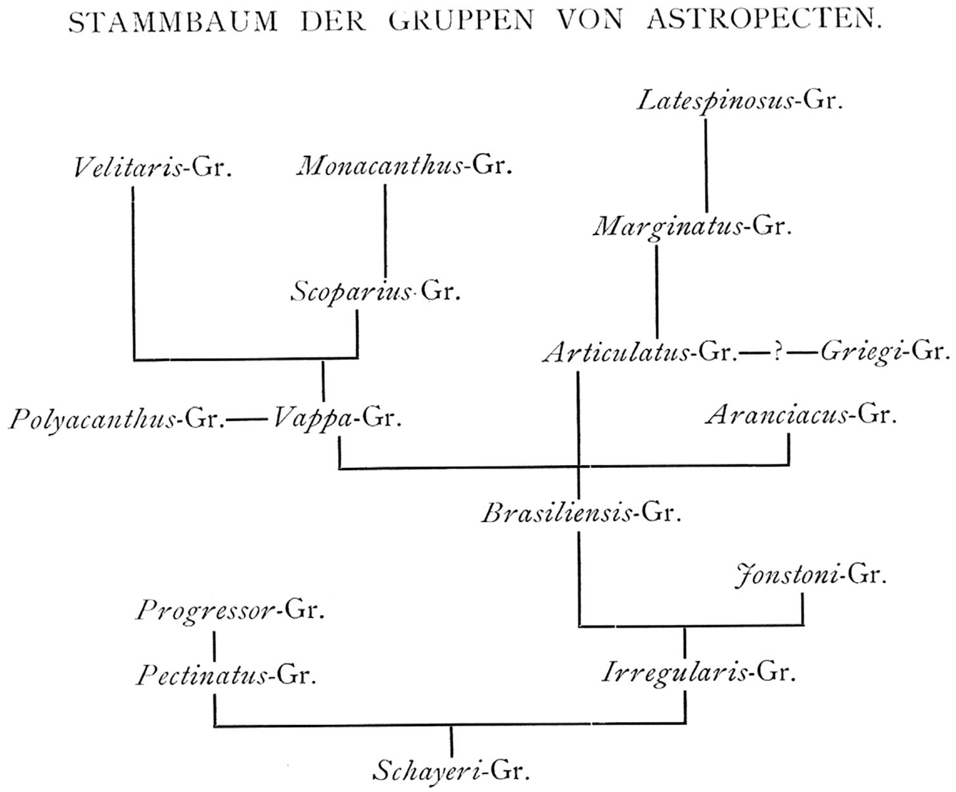

FIGURE 3. The "family tree" of species-groups of the asteroid genus *Astropecten.* In his 1917 monograph of this extraordinarily difficult genus, Döderlein clarified the status of approximately 70 species, including descriptions of 19 new species.

derm publications, on cidaroid and salenioid echinoids of Japan (1887a), is a comprehensive analysis of the taxonomy and evolution of these echinoid groups, 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 1911). 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 analyzes 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, Vol. 1, p. 43 (1928). In discussing the higher classification of the 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 (1887a). 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, René Koehler, 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 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 family's type genus. This genus has been the subject of two publications by Döderlein, an essay (1901) and a taxonomic revision (1902). He selected *Fungia* as a model taxon to determine whether forms of reef corals can be systematically arranged in natural groups consisting of subgenera, species, subspecies and varieties. Furthermore, he wanted to investigate whether such a classification can be used to discern evolutionary trends in order to determine natural relations between these groupings.

Based on his taxonomic revision of *Fungia*, Döderlein (1901, 1902) presented indeed 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 an otherwise solid corallum wall; (3) a size increase of costal spines; (4) and septal teeth. Based on these findings, Döderlein distinguished seven species groups in *Fungia* (Fig. 4).

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 evolutionary lineages of species that were based on the following trends: a reversal from a free-living to an attached mode of life, a development from a single mouth to more than one, and a trend from small to large septo-costal ornamentations. Wells (1966) followed Gardiner (1909) in using the overall growth form 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 by Döderlein (1901, 1902). These morphological differences were also treated by Vaughan & Wells (1943) and Wells (1956), but without reference to Döderlein's work. Therefore, the evolution model of the Fungiidae presented by

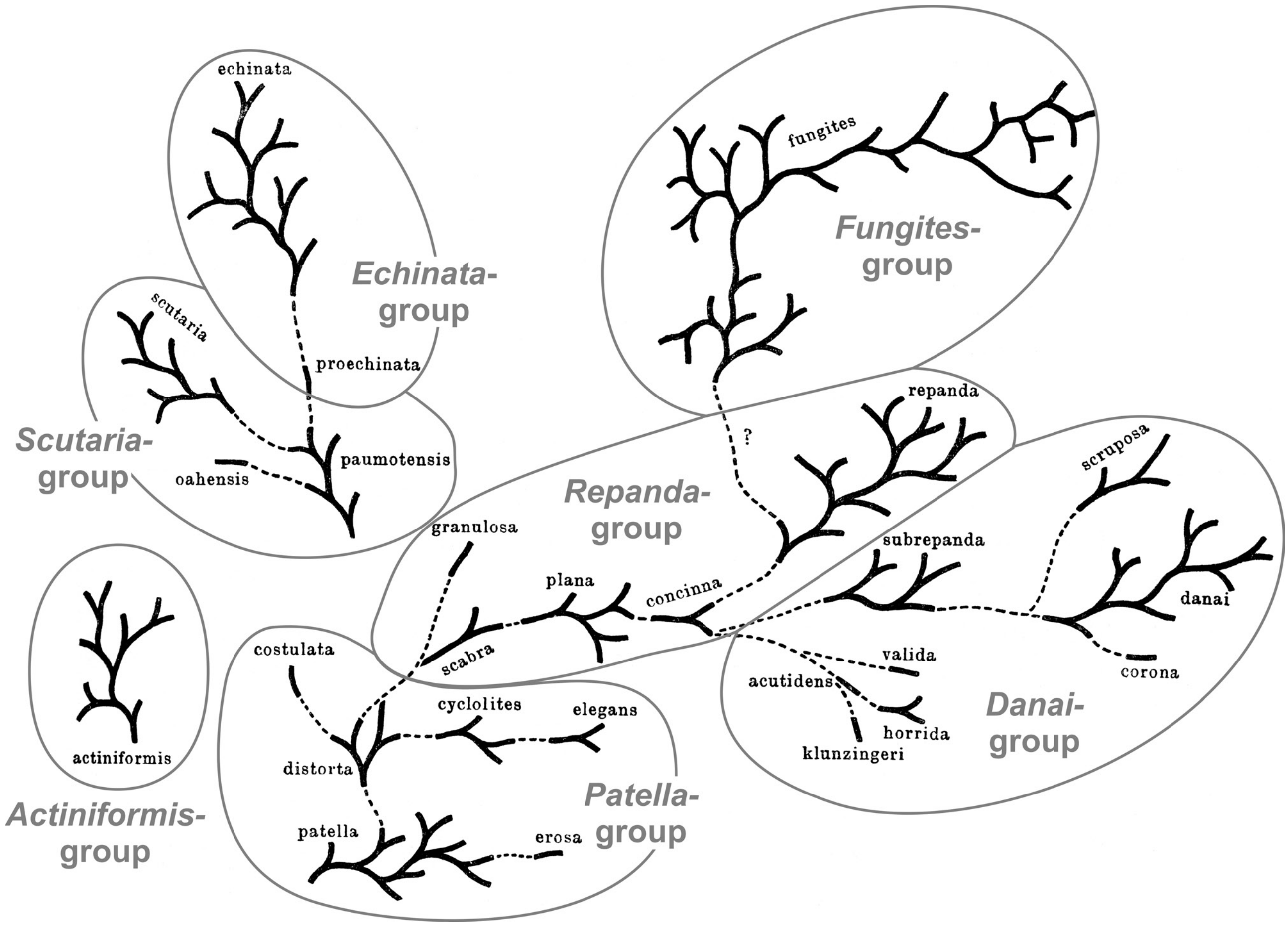

FIGURE 4. Döderlein's (1902) model of *Fungia* phylogeny based on corallum size, the absence or presence of perforations in the corallum wall, and size increases of the costal spines and the septal teeth. Outlines of *Fungia*-species groups added in grey.

Wells (1966) and other authors (Cairns 1984; Hoeksema 1989; 1991; Gittenberger *et al.* 2011; Hoeksema *et al.* 2012; Benzoni *et al.* 2012), should partly be credited to Döderlein.

With regard to the life history of fungiids, Döderlein (1901, 1902) discerned three kinds of asexual reproduction (Hoeksema 1989: Fig. 42): (1) the regeneration of new polyps (anthocaulus phase) from attachment stalks that were vacated by older corals entering the anthocyathus phase (Hoeksema & Yeemin 2011); (2) the development of attached polyps at the outside of parent animals by budding (Hoeksema 2004); (3) self-fragmentation (autotomy) by the fission of corals along radial slits (Hoeksema & Waheed 2011). The last mechanism only occurs in free-living *Cycloseris* corals showing the *Diaseris*-form (Döderlein 1902; Hoeksema 1989; Hoeksema & Waheed 2011).

Döderlein (1902) also remarked on the great instraspecific 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 several new varieties, which can actually be attributed to ecophenotypic corallum variability (Boschma 1925; Hoeksema & Moka 1989; Hoeksema 1993; Gittenberger & Hoeksema 2006).

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

Summarizing Döderlein's major scientific achievements

In total Döderlein published about one hundered papers. Taxa other than echinoderms he treated—mostly taxonomically but also with regard to faunistics—were calcareous sponges (*e.g.* Döderlein 1897) and insects (*e.g.* Döderlein 1912). Döderlein was also a widely recognized expert on vertebrates (*e.g.* Döderlein 1882a, 1882b). In his very first study, his doctoral thesis, he dealt with the anatomy of a mammalian species (Döderlein 1878). His familiarity with fossils enabled him to contribute the entire part on vertebrates for a comprehensive text book on systematic palaeontology (Steinmann & Döderlein 1890). Vertebrate studies also served as basis for theoretical considerations (*e.g.*, Döderlein 1887b: "Döderlein's law" on impact on evolution of enlargement of body portions; Döderlein 1903: conclusions related to speciation and species concepts).

In total, his publications show that the breadth 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).

Sometimes, natural history collections reveal much of the collector. A "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, this material was 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.

There is a detailed report about the distribution of Döderlein's Japanese material in European museums (Nishikawa 1999). According to Nishikawa (1999) (Table 1), by far the largest part of the samples (ca. 76 %, mainly Porifera, Mollusca, Crustacea, Bryozoa, Verterbata) remained in Strasbourg; some specimen found their way to Berlin (5 %, mainly Pisces, Ascidiacea); the The Bavarian State Collection of Zoology (ZSM) now houses approximately 20 %. Accordingly, the ZSM owns an important portion of the scientific legacy of Ludwig Döderlein. This mainly consists of invertebrate collection samples that gathered himself in Japan in 1879–1881, and partly of samples from collecting expeditions of others that were sent to him for taxonomic investigation.

The largest portion of the material that came through Döderlein to the ZSM comprises echinoderms. The portion contributed by Döderlein represents about two thirds of the 4,600 echinoderm samples. The majority of this material was collected in Japan. 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.

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 day the great breadth of his interests and capabilities was unusual. 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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