



Taxonomy and nomenclature in the widespread and well-known sea anemone *Metridium* de Blainville, 1824

Marymegan Daly¹ · Heather Glon^{1,2} · Yang Li³

Received: 4 December 2023 / Revised: 22 February 2024 / Accepted: 29 February 2024 / Published online: 26 March 2024
© The Author(s) 2024

Abstract

Metridium senile (Linnaeus, 1761) is simultaneously one of the most familiar sea anemones in temperate shallow water and a species embroiled in taxonomic and nomenclatural confusion. Their large body size, characteristic ruff of tentacles, and ability to thrive on artificial and natural substrates make these animals conspicuous and common on rocky ledges, pilings, wharfs, shipwrecks, and bivalve reefs. Their reported range encompasses all temperate habitats in the northern hemisphere plus a handful of locales in the temperate southern hemisphere that have typically been characterized as anthropogenic introductions. Understanding the range of *M. senile* has been confounded by confusion about its circumscription relative to its congeners and inconsistency in the names used. Here, we summarize the taxonomy of the genus and clarify the status of *M. senile*. Based on results of recent phylogenetic studies, we consider *Metridium* to have two valid species: *M. farcimen* (Brandt, 1835) and *M. senile*. We recognize *M. senile* as the valid, appropriate name for all populations of *Metridium* in the Atlantic and for some of the populations in the Pacific. We consider *M. dianthus* (Ellis, 1767), *M. exile* Hand 1955, *M. huanghaiense* Pei, 1998, and *M. sinensis* Pei, 1998 to be junior synonyms of *M. senile*. We clarify the differences between *M. senile* and *M. farcimen*, and comment on the status of *M. canum* Stuckey, 1914.

Keywords Cnidaria · Actiniaria · Invasive species · Plumose anemone

Introduction

Sea anemones of the genus *Metridium* de Blainville, 1824, are common and abundant in habitats accessed by humans, including docks and piers, shipwrecks, and rocky habitats in the intertidal and subtidal. Their relatively large body size and their fringe of many short tentacles on an undulating oral disc make them both conspicuous and distinctive (Fig. 1). The traits that makes them recognizable in their native habitat have been an advantage in tracking the occurrence of *Metridium* in new habitats (Riemann-Zürneck 1975, 1986; Griffiths et al.

1996; Häussermann and Försterra 2005; Carlton 2011; Martin et al. 2015; Laird and Griffiths 2016; Glon et al. 2020; Teng et al. 2021; Yan et al. 2021; Häussermann et al. 2022; Molinet et al. 2023; Gimenez et al. 2023).

The current synthesis of taxonomy for *Metridium* identifies five species within the genus (Rodríguez et al. 2023): *Metridium canum* Stuckey, 1914; *Metridium dianthus* (Ellis, 1767); *Metridium exile* Hand, 1955; *Metridium farcimen* (Brandt, 1835); and *Metridium senile* (Linnaeus, 1761). Two species previously listed within the genus (see Fautin 2016), *Metridium huanghaiense* Pei, 1998 and *Metridium sinensis* Pei, 1998, have been synonymized with *M. senile* (see Li and Xu 2020 and below). All species of *Metridium* have a smooth, muscular column and a wide oral disc fringed with numerous, short tentacles. Within species, there may be diversity in color, tentacle length, and polyp size (Hand 1955; Fautin et al. 1989). Differences among species include overall body size and reproductive biology, but high intraspecific variation and plasticity causes confusion about species boundaries.

Confusion in the systematics of *Metridium* is remarkably long standing and durable. These problems have two

Communicated by B. W. Hoeksema

✉ Marymegan Daly
daly.66@osu.edu

¹ Department of Evolution, Ecology & Organismal Biology, The Ohio State University, Columbus, OH 43215, USA

² Maine Department of Natural Resources, Boothbay Harbor, ME 04575, USA

³ Laboratory of Marine Organism Taxonomy and Phylogeny, Chinese Academy of Sciences, Qingdao, China

Fig. 1 A clonal group of *Metridium senile* in the public aquarium, Newport, OR. Note the thin, undulating oral disc of the largest specimen and the numerous, strongly tapering tentacles



components. One is identity: how many species are there, and what are the boundaries and diagnoses of those species? The second is nomenclature. Because of the taxonomic confusion and geographic range of this group of anemones, names have proliferated. A genome-scale phylogeny for *Metridium* (Glon et al. 2023) has clarified circumscription of the lineages within the genus, finding two well-supported lineages (Fig. 2). While convincingly answering the question of identity for the Atlantic and Eastern Pacific representatives of *Metridium*, this does not resolve the question of nomenclature, or remedy

the long-standing issues surrounding usage and circumscription. Here, we explicate the rationale for considering the valid species of *Metridium* to be *M. senile* and *M. farcimen*, taking a historical and geographic approach in discussing the taxonomy of the group. Our goal is to acknowledge and address the evidence and context for prior taxonomies and to make clear how these relate to our current understanding of diversity in the genus. We highlight key studies that use *Metridium* and connect these to the systematic framework to support the application and interpretation of those works.

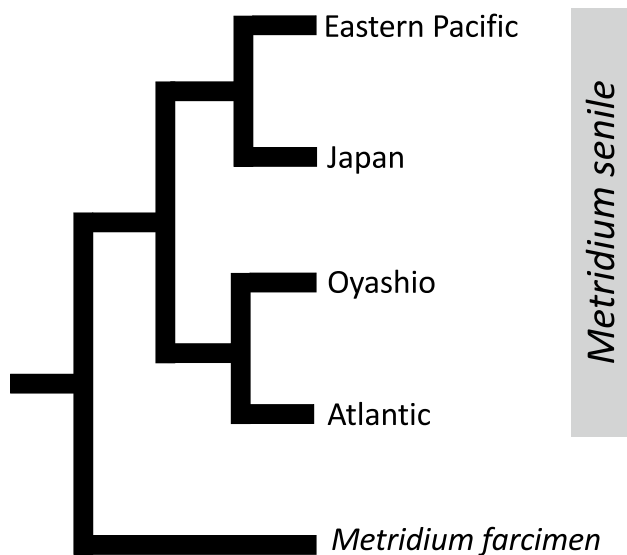


Fig. 2 Simplified phylogenetic tree for *Metridium*, based on target enrichment sites from across the genome (see Glon et al. 2023 for original trees and methods). For *Metridium senile*, names at the end of branches refer to clade names from Glon et al. 2023 and refer broadly to the geographic location from which the samples were collected

How many species are there in *Metridium*?

Because members of *Metridium* show high variation in size and color and lack discrete diagnostic features, genetics were hailed for their potential for evaluating diversity within this group. Following Hoffmann's (1976, 1981) pioneering work on genetics of Northeastern Atlantic populations of *M. senile*, Bucklin and Hedgecock (1982) evaluated differences between large-bodied forms from the Pacific, smaller bodied forms from the Pacific, and smaller bodied forms from the Northwest Atlantic and recommended recognizing those as three species. Bucklin (1985) followed that work with a closer look at the smaller bodied, clonal forms in the Atlantic. The enzyme loci she used failed to distinguish between populations in the British Isles that were identified as *M. senile dianthus* and *M. s. pallidum* but were able to distinguish populations from the Eastern (British Isles) and Western (MA, USA) North Atlantic (Bucklin 1985).

Contemporary sequence-based analyses of genomic data (Glon et al. 2021, 2023) detect a distinct population in the Northwest Pacific, consistent with the finding of Bucklin and Hedgecock (1982). Contrary to early allozyme studies, genomic analyses find a single, wide-spread population in the North Atlantic, with shared haplotypes between the Eastern (Ireland, Norway) and Western (New Brunswick, Canada, and ME, USA) North Atlantic (Fig. 2). These findings are robust in terms of method and type of genomic data and affirm the conclusion of McMurrich (1911) and Stephenson

(1935), who argued for a single species in the Atlantic. Local differences within Atlantic populations noted by Bucklin (1985) and Hoffmann (1976) are not incompatible with the broader interpretation of gene flow and connectivity between Atlantic populations, suggesting some local differentiation, either through sexual or asexual means.

More unexpectedly, genome-scale genetic analysis also finds that the Atlantic populations of *Metridium* are not segregated from some of the Pacific populations of *Metridium*. Aquaculture practices may explain the connection between, e.g., French and Japanese populations, since oyster farming in France in the mid-twentieth century included culture material from Japan (Grizel and Heral 1991). Less recent exchanges through the Arctic are also possible (see Glon et al. 2023). Although Atlantic populations are not genetically segregated from all Pacific populations, some Pacific populations are distinct from the mixed Atlantic and Pacific population. Members in the mixed Pacific and Atlantic group are highly variable in size and color and often occur in aggregations of multiple individuals. Individuals in the distinct Pacific group are typically larger bodied and solitary.

The large, solitary *Metridium*

The distinctiveness of the large-bodied species within *Metridium* has been recognized since at least 1934, when Carlgren (1934) noted that a large specimen from Alaska of what was called *Metridium fimbriatum* Verrill, 1865 differed in the size and relative occurrence of cnidae, compared to *M. dianthus* from Europe. Carlgren (1934) mentioned that these differences were not consistent across specimens, which he interpreted as a difference in development, with specimens of *M. dianthus* losing some types of cnidae as they matured.

Using electrophoretic data, Bucklin and Hedgecock (1982) distinguished large bodied, solitary individuals within Pacific populations of what they called *M. senile*, and subsequently described these large-bodied forms as *M. giganteum* (Fautin, Bucklin, & Hand, 1989). The new name was justified by the imprecision of the usage of the name *M. fimbriatum*, which Verrill (1865) erected for *Metridium* in the Northeast Pacific but which had not applied exclusively to large and solitary polyps. Nomenclatural and archival research by Fautin subsequently uncovered older names for the large, solitary polyps: Tilesius (1809), following an epithet used by locals in Kamchatka, called large polyps "*Actinia priapus*" and Brandt (1835) described large, solitary polyps from Kamchatka as *Actinia Polystephanus farcimen*, but neither of those authors provided illustrations and type specimens were neither mentioned in the original description nor subsequently found (see Fautin and Hand 2000; Fautin 2016). The connection between *Actinia priapus* Tilesius 1809 and *Actinia farcimen* of Brandt (1835)

was suggested by McMurrich, although he was uncertain (McMurrich 1901: 13 “may also be a synonym”). There is greater certainty for the description given by Brandt (1835), which can only be this species, given the large size, smooth column, and numerous tentacles, leading Fautin and Hand (2000) to synonymize *M. giganteum* with *Actinia farcimen*, calling the species *Metridium farcimen* (Brandt, 1835). They also include specimens originally described as *Isometridium rickettsi* Carlgren 1951 within *M. farcimen* (see Fautin and Hand 2000).

Undisputedly, the largest bodied species in the genus, *M. farcimen* reaches heights of up to a meter, and is distributed from at least the tip of Kamchatka, Russia, through the Aleutian Islands to the Gulf of California, occurring at depths of greater depth at lower latitudes (Fautin and Hand 2000). Type specimens are unknown for *M. farcimen* but have been deposited for its junior synonyms *Metridium giganteum* Fautin, Bucklin & Hand, 1990 and *Isometridium rickettsi* (see Fautin and Hand 2000).

The smaller, often clonal *Metridium*

The very broad range and phenotypic variability of the smaller bodied, often clonal species within *Metridium* has led to confusion about its circumscription and to an abundance of names. At present, the clonally reproducing members of *Metridium* in North America and Europe are generally called *Metridium senile* or *Metridium dianthus*. The pattern of usage is difficult to parse, but in general, *Metridium senile* is applied to populations in North America and to smaller and shallower populations in Europe. *Metridium dianthus* is used primarily for European populations, and typically applied to larger animals with more numerous tentacles found in deeper water. The European names seem to align with what Bucklin (1985) and Stephenson (1935) before her referred to as varieties *dianthus* (larger body, more numerous tentacles) and *pallidum* (smaller body, fewer tentacles, typically shallower), respectively, but the distinctions are not clear, and usage is inconsistent (Manuel 1988). Genetic analysis does not find distinction between the Eastern and Western Atlantic populations, or between these and the smaller-bodied form of *Metridium* in the Pacific.

The history of names and their use is complex and warrants thorough discussion to eliminate the confusion that has hampered assessment of diversity in the genus. Andres (1883: 139) encapsulates the problem very well (translation ours): “the synonymy is complicated because the species was described independently by various authors and because the compilers [of biodiversity and taxonomy] gradually accepted all names without noticing their identical characters.”

We recognize *Metridium senile* (Linnaeus, 1761) as the appropriate valid name for the single species of *Metridium*

in the North Atlantic and for some populations of *Metridium* from the Pacific. The epithet “senile” is the oldest species epithet for this taxon (Daly et al. 2007), in continuous use since its description, with the combination *Metridium senile* first published by Haddon (1889: 323). Haddon’s (1889) use of this combination is made within the discussion of *Paraphellia expansa* Haddon, 1886, rather than as part of an entry focused on *Metridium* and has not been previously credited in key treatments of this species (e.g., Stephenson 1935; Fautin 2016). Although it is the junior subjective synonym of *M. senile*, *Metridium dianthus* remains the type species of *Metridium* by monotypy (Dunn and Hulseman 1979; Fautin 2016, and references therein).

Priapus senilis was described by Linnaeus (1761) from Sweden and was included in the twelfth edition of *Systema Naturae* as *Actinia senilis*, reflecting Linnaeus’s creation of the genus *Actinia* for what are now recognized as actinarians (Linnaeus 1767). Like many early descriptions, neither of Linnaeus’ (1761, 1767) written treatments contained much diagnostic power. Contemporary with this generic re-assignment by Linnaeus (1767), Ellis described *Actinia dianthus* Ellis, 1768 with a written description that is brief but accompanied by a diagram that shows an anemone with a stout column and a strongly lobed disc fringed with numerous, short tentacles (Fig. 3a). Notably (and contra the locality information given in Fautin 2016), the name *Actinia dianthus* is used explicitly in reference to animals found in Sussex (Ellis 1768: 436), although the manuscript in which it is described refers in its title to “newly ceded islands” and includes accounts of diversity in the West Indies. Perhaps because the image so effectively captured the distinctive features of this anemone, the name *Actinia dianthus* was quickly adopted and widely used for the European member of *Metridium*, albeit under multiple generic assignments (Ellis and Solander 1786; Oken 1815; de Blainville 1830; Johnston 1838; Couch 1844; Dalyell 1848; Gosse 1855, 1860; Tugwell 1856; Milne Edwards 1857; Stephenson Wright 1859; Andres 1883; Pennington 1885; Carlgren 1893, 1934; Nordgaard 1905; Walton 1908; Nafilyan 1912; Gemmill 1920; Elmhirst 1925).

An additional name used for this species comes from a mention by Müller (1776) of “*Actinia plumosa*” in his monograph of Danish and Norwegian animals. This was interpreted as a proposal of a new name, *Actinia plumosa* Muller, 1776 by some workers (e.g., Gmelin 1788; Rapp 1829; de Blainville 1830; Ehrenberg 1834; see Fig. 3b). However, because “*Actinia*” was also used as a common name for sea anemones, it is plausible that Müller (1776) was using this phrase descriptively to mean “the plumose anemone,” a common name that remains applied to *Metridium senile* and an interpretation underscored by the absence of a description or diagnosis along with the name. de Blainville (1824: 470) used the phrase in this way, noting that the *M. dianthus* of

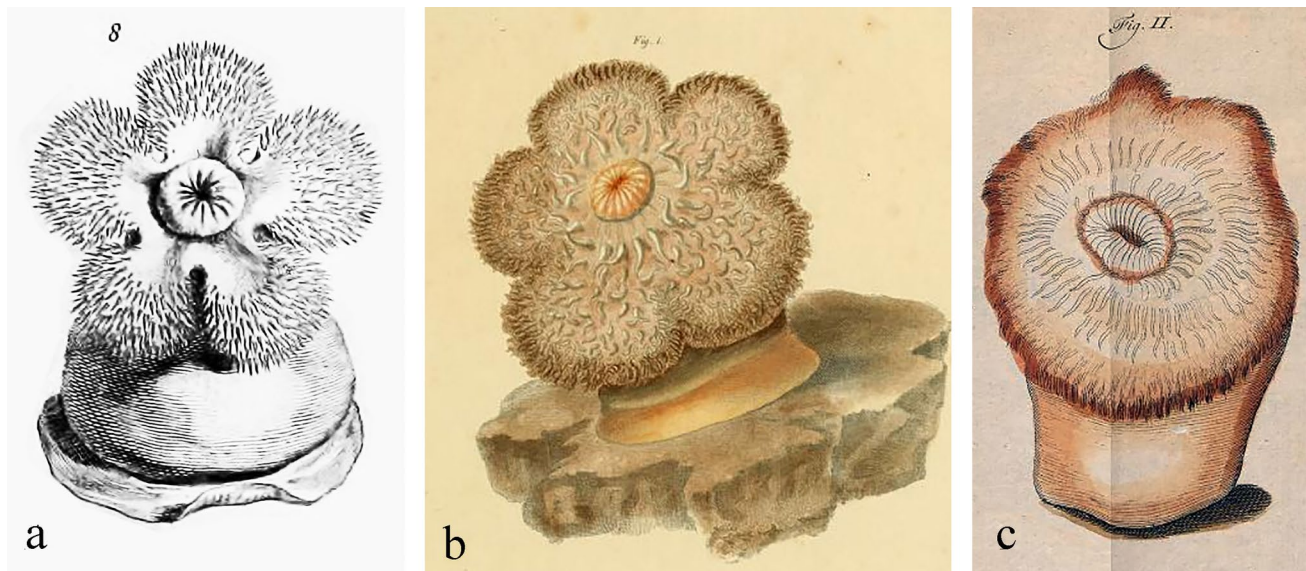


Fig. 3 Key depictions of *Metridium senile* in historical literature. **a** Drawing included by Ellis (1768) in his description of *Actinia dianthus*; **b** Drawing of *Actinia dianthus* included by Rapp (1829) in his monograph of sea anemones; **c** Drawing of *Actinia dianthus* included

in Baster (1759). This figure was referenced by Linnaeus (1761) in his re-classification of *Priapus senilis* as *Actinia senile*. All images provided through Biodiversity Heritage Library

Oken (1815) was “l’actinia plumosa” of Linnaeus, with use of an article and the lack of capitalization differentiating the common French name “l’actinia” from the genus “*Actinia*.” Gmelin (1788) treated *Actinia plumosa* as a name and considered it a synonym of *Actinia senilis*, citing “Syst nat XII. 2, p. 1088 n.3” and the Latin description Linnaeus gave in that reference under his entry for *Actinia plumosa*; despite making this connection, Gmelin elected to use the junior epithet “plumosa” rather than the senior “senilis.” Despite these early citations of the synonymy between *A. plumosa* and *P. senile* and the association of these two with *Actinia dianthus* by de Blainville (1824), after the mid-nineteenth century, most accounts listed this species as *Metridium dianthus*, (e.g., Milne Edwards 1857; Wright 1859; Hertwig 1882; Andres 1883; Pennington 1885; Carlgren 1893, 1933; Dixon and Dixon 1891; Duerden 1898; Nordgaard 1905; Walton 1908; Nafilyan 1912; Gemmill 1920; Gravier 1920; Pax 1920, 1928; Stephenson 1920; Verrill 1922; Elmhirst 1925; Stephenson 1925).

The precedence of *A. dianthus* over *P. senilis* was not universally recognized. Adams (1800) attributed specimens from Wales to *Actinia senilis*, noting the “soft hairy appearance arising from the slender form and number of tentacles.” Although Adams’ (1800) concept aligns with that figured by Ellis (1768) and is from the British Isles rather than Scandinavia, he applied Linnaeus’ name *P. senilis* to the specimens rather than Ellis’ (1768) name *A. dianthus*. Andres (1883: 138) indicated that the *Actinia senilis* of Adams (1800) and of Pennant (1812) was a synonym of *Actinia dianthus*, but also indicated that he did not consider these wholly identical

with Linnaeus’ (1761) concept of *P. senilis*. Haddon (1889: 323), in a discussion of problems with *Sagartia* Gosse, 1860, noted that the appropriate name for *Actinia dianthus* (at that time called *Actinoloba dianthus*) was *Metridium senile*. McMurrich (1911, 1914) explicitly synonymized *Actinia dianthus* with *Priapus senile* because populations identified under those names overlap in size, color, and internal anatomy. He further argued that, despite the imprecision of Linnaeus’ (1761) original description, subsequent treatment by Linnaeus and others makes the name *P. senilis* applicable, which reinforced Haddon’s (1889) argument that *P. senile* has priority over *A. dianthus* (see McMurrich 1911). Even Verrill’s (1914) argument for use of the epithet *dianthus* over *senilis* acknowledged identity between the concepts of the names and the priority of *senilis*; Verrill preferred *dianthus* on the basis of quality of the description and the “obscurity” of the Linnaean name, not precision or priority. Despite McMurrich’s (1914) reiteration of the importance of priority and the clarity of intent with this specific Linnaean name, given its connection to local vernacular names and the citation by Linnaeus of images from e.g., Baster (1759: Tab XII, see Fig. 3c) that provide diagnostic features, prominent experts like Verrill (1922), Pax (1922, 1928), and Carlgren (1928, 1933), continued to use *Metridium dianthus* over *Metridium senile*. This promoted confusion because it implied that there were differences between *M. dianthus* and *M. senile*.

The confusion over names was intensified by the discovery of similar animals in the Northwestern Atlantic. Le Sueur (1817) proposed the name *A. marginata* Le Sueur, 1817, for

specimens from Boston Bay with a wide, lobed oral disc and numerous short tentacles. This name was used a handful of times (e.g., Milne Edwards 1857; Verrill 1864; Parker 1900), but not exclusively: Couthouy (1839) identified specimens from Massachusetts under the European names *A. plumosa* and *A. senilis* and Stimpson (1853) reported *A. dianthus* and *A. marginata* from Grand Manan, citing *A. dianthus* as a questionable identification and giving Johnston, 1838, as its authority (Johnston cites Ellis as authority for the species). Andres (1883) synonymized *Metridium marginata* with *M. dianthus* in his catalog of Actiniaria without much explanation, but McMurrich (1901) elaborated on this, noting that the anatomical attributes of *M. dianthus* reported by Carlgren (1893) from the Eastern North Atlantic were identical to what he observed in *Metridium* from the Western North Atlantic.

Stephenson (1935) synthesized life history, anatomy, and cnidae from various European populations and found no consistent anatomical or life history features to differentiate them, concurring with McMurrich (1901, 1911), and citing *M. dianthus* and *M. marginatum* among the junior

synonyms of *M. senile*. To account for the extensive variation in this species, Stephenson (1935) recognized varieties, distinguishing variety *M. senile dianthus* as the larger-bodied forms and variety as *M. senile pallidum* the smaller-bodied forms but noting that there are no easily quantifiable features differentiating these and that “it is extremely difficult to say where *pallidum* ends and *dianthus* begins” (Stephenson 1935: 221).

In his revision, Stephenson listed five confirmed synonyms and four questionable synonyms (Table 1), with the ambiguity lack of detail in the descriptions of those taxa. The otherwise comprehensive list provided by Stephenson (1935) includes a few errors and points for clarification. Stephenson (1935: 214) lists McMurrich (1911) as the first use of the combination *Metridium senile*, omitting the earlier combination by Haddon (1889). The name *Actinia pallida*, created by Holdsworth (1855), has been interpreted as *M. senile* (see Stephenson 1935), but the description is broad enough to include other species (e.g., *Diadumene cincta*). Stephenson (1935) cites Dalyell (1848) as coining the name *Actinia dianthus-plumosa*, but this seems to be

Table 1 Nominal species that are in full, partial, or questionable synonymy with *Metridium senile*. Species are listed in order of their original description

Original binomen	Author	Source for synonymy	Notes
<i>Priapus senilis</i>	Linnaeus, 1761		Haddon (1889) is the author of the combination <i>Metridium senile</i>
<i>Priapus judaicus</i>	Linnaeus, 1761	Stephenson 1935	Species insufficiently described and epithet not widely used. Synonymy was with <i>A. dianthus</i> and listed as questionable
<i>Actinia dianthus</i>	Ellis, 1768	Haddon 1889	
<i>Actinia candida</i>	Müller, 1776	Stephenson 1935	Species insufficiently described and epithet not widely used. Synonymy was with <i>A. dianthus</i>
<i>Actinia plumosa</i>	Müller, 1776	Andres 1883	Synonymy was with <i>A. dianthus</i>
<i>Actinia rufa</i>	Müller, 1776	Stephenson 1935	Species insufficiently described and epithet not widely used
<i>Actinia pentapetala</i>	Pennant, 1777	Andres 1883	Synonymy was with <i>A. dianthus</i>
<i>Actinia varians</i>	Müller, 1806	Carlgren 1928	Species insufficiently described and epithet not widely used
<i>Actinia marginata</i>	Le Sueur, 1817	McMurrich 1901	Synonymy was with <i>A. dianthus</i>
<i>Actinia dianthus-plumosa</i>	Dalyell, 1848	Stephenson 1935	Stephenson misinterpreted a section heading as a name. This combination has never been used
<i>Actinia pallida</i>	Holdsworth, 1855	Stephenson 1935	
<i>Actinia aurantiaca</i>	Jordan, 1855	Stephenson 1935	Listed as a questionable or pro parte synonym. Name is a homonym of <i>Actinia aurantiaca</i> Delle Chiaje 1825
<i>Actinia pellucida</i>	Alder, 1858	Stephenson 1935	Listed as a questionable or pro parte synonym. Name is a homonym of <i>Actinia pellucida</i> Hollard 1848
<i>Sagartia pura</i>	Alder in Gosse, 1860	Stephenson 1935	Species insufficiently described and epithet not widely used
<i>Metridium fimbriatum</i>	Verrill, 1865	Andres 1883	Also pro parte synonym of <i>M. farcimen</i>
<i>Metridium exile</i>	Hand, 1955	Reimann-Zürneck 1975	
<i>Paraisometridium pehuense</i>	Zamponi, 1978	den Hartog and Ates 2011	
<i>Metridium huanghaiense</i>	Pei, 1998	Li and Xu 2020	Li (2013) is the first instance of the synonymy, but this thesis does not meet Article 8 of the ICZN
<i>Metridium sinense</i>	Pei, 1998	Li and Xu 2020	Li (2013) is the first instance of the synonymy, but this thesis does not meet Article 8 of the ICZN. Species epithet modified here to correct Latin

a misinterpretation by Stephenson of the formatting convention of that section of Dalyell's book: although joined by a dash in the header, the epithets are treated as distinct names in the text, rather than as a single, hyphenated epithet. Two of the names recognized as synonyms of *M. senile* by Stephenson (1935), *Actinia aurantiaca* Jordan, 1855 and *Actinia pellucida* Alder, 1858, are homonyms of *Actinia aurantiaca* Delle Chiaje, 1825 (now *Condylactis aurantiaca*) and *Actinia pellucida* Hollard, 1848 (now *Aiptasiogeton hyalinus* (Delle Chiaje, 1822) (see Fautin 2016).

Stephenson's (1935) discussion of anatomy and variation emphasizes North Atlantic populations, but he includes *Metridium fimbriatum* Verrill, 1865 among the junior synonyms of *M. senile*. Verrill (1865) described *Metridium fimbriatum* from San Francisco, noting its high similarity to *M. marginatum* of the Northwest Atlantic. Verrill claimed that *M. fimbriatum* had more numerous and slender tentacles than *M. marginatum* but provided no specific information about tentacle number or length. In his description of *M. fimbriatum*, Verrill (1865) hypothesized that *M. marginatum*, *M. fimbriatum*, and *M. dianthus* will "eventually be found to belong to one variable and widely diffused species." Torrey (1898) acknowledged that the primary difference between these was geographic. McMurrich (1901) explicitly regarded *M. fimbriatum* as a synonym of the Atlantic species *M. marginatum* and *M. dianthus*, noting that the broad range of variation in color and size within each of the recognized species overlapped, and that anatomical differences related largely to size and irregularities of asexual reproduction. Torrey's (1902) landmark treatment of variation in *Metridium* underscores McMurrich's (1901) conclusion.

Although *Metridium fimbriatum* was initially used for small, bodied, clonal forms, it came to apply also to the large-bodied polyps from Alaska and the Pacific Northwest of the USA and Canada. McMurrich (1901: 13) was equivocal on the connection between smaller bodied, highly variable forms and the larger bodied forms described by Tilesius (1809). Carlgren (1933) identified differences that corresponded to size and geography among *M. fimbriatum*, presaging the differentiation between *M. farcimen* and *M. senile*.

Hand (1955) re-evaluated the variation among Pacific populations of *Metridium* and compared these explicitly to samples and accounts of Atlantic populations. Based on anatomy and cnidom, Hand (1955) recognized two forms in the Pacific. He did not recognize *M. senile* as an appropriate name for small bodied *Metridium* occurring in the eastern Pacific. Hand (1955) called the large bodied, generally northern form *Metridium senile fimbriatum*, noting that this combination was suggested in a footnote by Carlgren (1934) and used by Uchida (1938) for a population in Japan, but failing to acknowledge that the name was created for small-bodied forms. Hand described *Metridium exilis* Hand, 1955 (correctly rendered as *M. exile*: see Fautin 2016), for

small-bodied specimens from the intertidal of open coast and bays of California. Contra the synonymies by McMurrich (1901) and Stephenson (1935), Hand recommended that the name *M. senile* be reserved for Atlantic populations, citing the perceived absence of catch tentacles in populations in the Pacific as a distinguishing feature; Hand (1955) was incorrect in his interpretation of these as absent in the smaller bodied, asexually reproducing *Metridium* of the Pacific (see Purcell 1977) or in the *Metridium* of the North Atlantic (see Williams 1975).

Despite Hand's (1955) recommendation that the small-bodied, clonal *Metridium* of the Northwestern Pacific be identified as *M. exile* rather than *M. senile*, most authors continued to use the name *M. senile* (Purcell 1977; Sebens 1981; Walsh 1981; Walsh and Somero 1981; Bucklin 1982; Greene and Schoener 1982; Purcell and Kitting 1982; Chadwick 1987; Francis 1988; Harris 1991; Lissner et al. 1991; Parker and Tunnicliffe 1994; Masuda and Stone 2003; Kramer and Francis 2004; Goddard and Love 2010; Nelson and Craig 2011; but see Kostina 1988; Harris 1991). The lack of use in reference to specimens or living populations and a proposal of synonymy by Riemann-Zürneck (1975) notwithstanding, *M. exile* was treated as a valid name (e.g., Östman et al. 2010; den Hartog and Ates 2011). Allozyme (Bucklin and Hedgecock 1982), and life history (Bucklin 1980, 1987) data were interpreted to support distinction between the Atlantic *M. senile* and the Pacific *M. exile*, but this has not been replicated with sequence-based genetic analyses (see Glon et al. 2021, 2023) or any detailed and repeatable analyses of behavior or anatomy. We reject Hand's (1955) distinction between Atlantic and Pacific populations of the smaller-bodied, asexually reproducing *Metridium* and affirm Stephenson's (1935) contention that both Atlantic and Pacific populations belong to *Metridium senile* (Linnaeus, 1761). This makes *M. exile* a junior subjective synonym of *M. senile*, as initially proposed by Riemann-Zürneck (1975).

Two additional names have been applied to populations of *Metridium* in the Pacific Ocean. *Metridium huanghaiense* Pei, 1998 (originally *huanghaiensis*: see Fautin 2016) and *Metridium sinense* (previously rendered as *sinensis*) were first described in Pei (1998) from the Yellow Sea. Although a key accompanies the description that purports to differentiate these species from *M. senile fimbriatum*, the text of the description does not distinguish them (Fautin and Hand 2000) and does not provide comparable or descriptive information about the new species, describing *M. sinense* as not undergoing asexual reproduction and *M. huanghaiense* as having an opaque body wall and tentacles that are not in a ruffle. The citation of Verrill (1865) and Carlgren (1934) as the references for *M. senile fimbriatum* furthers the confusion: Verrill's (1865) description was clearly what is now *M. senile*, as it is small-bodied, clonal, and abundant in the midcoast of California, whereas Carlgren (1934) applied the

name to animals now considered *M. farcimen*. The key in Pei (1998) cites the body of *M. senile fimbriatum* as large but also allows for asexual reproduction, a trait further elaborated upon in the text (Pei 1998: 134), which suggests that Verrill's (1865) sense of the taxon is intended, rather than Carlgren's (1934). Based on an examination of type and other specimens from Pei's (1998) descriptions, Li (2013) and Li and Xu (2020) considered *M. huanghuaense* and *M. sinense* both junior synonyms of *Metridium senile*.

Sea anemones described as similar to *M. senile* have been documented from South America under two names. Riemann-Zürneck (1975) identified a population of large-bodied animals with an undulating oral disc and numerous short tentacles as *Metridium senile lobatum* (Carlgren, 1899). Zamponi (1978) erected a new genus and species, *Paraisometridium pehuense* Zamponi, 1978 (correctly rendered as *P. pehuense*; see Fautin 2016) for a population of anemones from Pehuenco, Buenos Aires, Argentina. Zamponi's (1978) description underscored the similarity of *P. pehuense* with *M. senile* and assigned the new genus to Metridiidae. Subsequently, populations inferred to represent introduced *M. senile* have been documented in Argentina (reviewed in Gimenez et al. 2023), Chile (reviewed in Häussermann and Försterra 2005; Häussermann et al. 2022), and South Africa (Griffiths et al. 1996). Recognizing the anatomical similarity between *P. pehuense* and *M. senile* and the potential of *M. senile* to be introduced, den Hartog and Ates (2011) synonymized *P. pehuense* with *M. senile*; Gimenez et al. (2023) concurred with this interpretation, but noted that the type material for *P. pehuense* is poorly preserved making the synonymy somewhat difficult to affirm. Likewise, based on anatomical study, ecological modeling, and biogeographic evidence, Häussermann et al. (2022) and Gimenez et al. (2023) argue that Riemann-Zürneck's "*M. senile lobatum*" are more appropriately identified as *M. senile* and likely represent an introduction to South America, an interpretation that seems to align with Riemann-Zürneck's interpretation of the material (see e.g., Riemann-Zürneck 1986). However, Fautin and colleagues (1989) argued that *M. senile lobatum* was a synonym of *Actinothoe lobata* (Carlgren, 1899). Genetic evaluation of populations of putative *M. senile* from Argentina and Chile confirmed identity of these with Northern Hemisphere populations (see Gimenez et al. 2023; Glon et al. 2023). At present, *P. pehuense* seems appropriately categorized as a junior synonym of *M. senile*, and *M. senile lobatum* is a pro parte synonym of both *A. lobata* and of *M. senile*. Records and accounts of *Actinothoe lobata* likely encompass some records more appropriately designated *M. senile*, but disentangling these and revising that species is outside of the scope of the present work.

The concept of *Metridium senile* proposed here encompasses populations that span the temperate North Atlantic and Pacific Oceans. The original description of *Priapus*

senile was based on specimens from the Baltic Sea but did not designate a type specimen; type material also is not known for *Actinia dianthus* (see Fautin 2016). Based on records from the literature and museum specimens, we consider *M. senile* to be generally sub-Arctic, but populations may occur at or near the Arctic Circle (Rodríguez et al. 2023). Populations in the Southern Hemisphere are inferred to be anthropogenically introduced, but cold-water connections via the Pacific Ocean are possible (Glon et al. 2021, 2023). In temperate regions, *M. senile* ranges from the intertidal to approximately 200 m; at lower latitudes, they may occur only subtidally. *Metridium senile* is highly variable in color and size, with the largest specimens approximating *M. farcimen* in size and the smallest being orders of magnitude smaller. Generally capable of asexual reproduction, clonal aggregations of *M. senile* may dominate in suitable habitat.

A dubious species of *Metridium*

Metridium canum is a composite species for which the identity of the constituent species is unclear. Hand (1961) re-described specimens of *M. canum* from Otago Harbor (New Zealand) as *Mimetridium cryptum* Hand, 1961, a member of family Actinophoridae Carlgren 1938. Hand (1961: 83) equivocated on whether the Otago specimens were the same as the Kermadec (now Rangitāhua) Island material originally described as *M. canum*, given the differences in habitat between temperate Otago and subtropical Rangitāhua, difference in reported size (Otago material is at least an order of magnitude larger in body size), and differences in natural history (under stones in Rangitāhua vs. in sediment in Otago Harbor). He left it as a partial synonymy, with the detailed accounts by Parry (1951) and Batham (1956) of *Metridium canum* interpreted to be *Mi. cryptum* (see Hand 1961; Batham 1965). Thus, the sole report of specimens of *M. canum* other than those attributable to *Mi. cryptum* is the original description by Stuckey (1914), which was not accompanied by the deposition of specimens, included no figure of the material observed, and failed to describe attributes that would substantiate its inclusion in *Metridium*. The appropriateness of the genus designation of *M. canum* was questioned by Stephenson (1920: 528), who questioned whether it might be a juvenile, or misattributed to the genus. The small size and location reported for *M. canum* in Rangitāhua is out of line with what is known of *Metridium*, whose members are generally larger than 1 cm in diameter as adults, and which are temperate rather than subtropical. The animals described by Stuckey (1914) have approximately two times as many tentacles as mesenteries: with 200 tentacles, the smaller than 1 cm diameter column would bear five cycles of mesenteries; given that Stuckey (1914) reports 45 pairs mesenteries (inferred to be four cycles, with

the last incomplete) the final cycle is likely to be microcyclic. These attributes are consistent with multiple taxa that occur in the region, including members of Diadumenidae Stephenson, 1920, Haliactinidae Carlgren, 1949, and Sagaritidae Gosse 1858 in addition to *Metridium*. The information provided by Stuckey (1914) is insufficient to identify new specimens or affiliate his description with a described taxon. Thus, we consider *Metridium canum* a *nomen dubium*.

Differentiating species of *Metridium* in the field

Although our concept for *M. senile* simplifies identification of the smaller bodied form, difficulty remains in differentiating a large specimen of *M. senile* from a member of *M. farcimen*. Their ranges overlap in the Northwestern Pacific Ocean, and, for specimens of comparable size, no diagnostic anatomical differences have been reported. Although length of nematocysts capsules differentiate *M. farcimen* from *M. senile*, the range of capsule sizes overlap and only the size of capsules in the acontia are significantly different in animals of equivalent size (Kramer and Francis 2004), with ecological differences (flow regime, depth: see Anthony 1997) important in the attainment of very large size in *M. senile*. Genetic differences are likewise not absolute, with some individuals of apparent hybrid origin being detected through genome sequencing (see Glon et al. 2023). In the shared range of *M. farcimen* and *M. senile*, large animals can only be identified definitively through microscopic or genetic analysis.

Family-level taxonomic implications

Three genera have been assigned to family Metridiidae: *Metridium* de Blainville, 1824, *Isometridium* Carlgren, 1951, and *Parisometridium* Zamponi, 1978. Both *Isometridium* and *Paraisometridium* are monotypic and are now recognized to be junior synonyms of *Metridium*: *Isometridium rickettsi* is a junior subjective synonym of *M. farcimen*, and *P. pehuense* is a junior subjective synonym of *M. senile*. Thus, in our view, Metridiidae has only one valid, accepted genus, *Metridium*, and two valid accepted species, *Metridium senile* (Linnaeus, 1761) and *Metridium farcimen* (Brandt, 1835).

Acknowledgements Our understanding of the diversity and taxonomy of *Metridium* benefited from conversations with Ron Ates, Daphne Fautin, Bernard Picton, and Estefania Rodriguez. We acknowledge the staff of the World Register of Marine Species and the Biodiversity Heritage Library, whose efforts to make nomenclatural information available were invaluable to this project. Comments from Karen Sanamyan, Bert Hoeksema, and two anonymous reviewers improved this manuscript.

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No animal testing was performed during this study.

Sampling and field studies The study does not contain sampling material or data from field studies.

Data availability This study did not generate new data. All sequence data referenced in this work are available through GenBank, with accession information in the referenced papers.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by all authors. The first draft of the manuscript was written by MD. All authors commented on previous versions of the manuscript and read and approved the final manuscript.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adams J (1800) Description of some marine animals found on the coast of Wales. *Trans Linn Soc* 5(7–13):1.2
- Alder J (1858) A catalogue of the zoophytes of Northumberland and Durham. *Trans Tyneside Natu' Field Club* 3:93–161
- Andres A (1883) *Le Attinie* (Monografia). Volume 1 (Bibliografia, introduzione e specigrafia). *Coi Tipi der Salviucci, Rome*
- Anthony KR (1997) Prey capture by the sea anemone *Metridium senile* (L.): effects of body size, flow regime, and upstream neighbors. *Biol Bull* 192:73–86
- Baster J (1759) *Opuscula subseciva. Observationes miscellaneas de animalculis et plantis quibusdam marinis, eorumque ovariiis et seminibus continentia*. Volume 1. J. Bosch, Harlem
- Batham EJ (1956) Ecology of southern New Zealand sheltered rocky shore. *Trans Roy Soc NZ* 84:447–465
- Batham EJ (1965) Rocky shore ecology of a southern New Zealand fjord. *Trans Roy Soc NZ* 6:215–227
- Brandt JF (1835) *Polypos, acalephas discophoras et siphonophoras, nec non echinodermata continens*. Volume 1. *Sumptibus Academiae, St. Petersburg*
- Bucklin A (1982) The annual cycle of sexual reproduction in the sea anemone *Metridium senile*. *Can J Zool* 60:3241–3248
- Bucklin A (1985) Biochemical genetic variation, growth and regeneration of the sea anemone, *Metridium*, of British shores. *J Mar Biol Assoc UK* 65:141–157
- Bucklin A (1987) Growth and asexual reproduction of the sea anemone *Metridium*: comparative laboratory studies of three species. *J Exp Mar Biol Ecol* 110:41–52
- Bucklin A, Hedgecock D (1982) Biochemical genetic evidence for a third species of *Metridium* Coelenterata: Actiniaria. *Mar Biol* 66:1–7

- Bucklin AC (1980) *The reproduction and population biology of Metridium (Coelenterata, Actiniaria)*. PhD Thesis, University of California, Berkeley
- Carlgrén O (1893) Studien über Nordische Actinien. Kongl Vetensk Acad Handl Band XXV 10(102–109):148
- Carlgrén O (1899) Zoantharien. Hamb Magal Samm 4:1–48
- Carlgrén O (1928) Ceriantharier. Zoantharier Och Actiniarier Medd Grönl 23(Supplement):253–308
- Carlgrén O (1933) The Godthaab Expedition 1928 Zoantharia and Actiniaria. Medd Grönl 798:1–55
- Carlgrén O (1934) Some Actiniaria from Bering sea and Arctic waters. J Wash Acad Sci 24:348–353
- Carlgrén O (1949) A survey of the Ptychodactylaria, Corallimorpharia and Actiniaria. Kongl Vetensk Acad Handl 1:1–121
- Carlgrén O (1951) The actinian fauna of the Gulf of California. Proc US Natl Mus 101:415–449
- Carlton JT (2011) The inviolate sea? Charles Elton and biological invasions in the world's oceans. In: Richardson D (ed) Fifty years of invasion ecology: the legacy of Charles Elton. Blackwell, Oxford, pp 71–100
- Chadwick NE (1987) Interspecific aggressive behavior of the corallimorpharian *Corynactis californica* (Cnidaria: Anthozoa): effects on sympatric corals and sea anemones. Biol Bull 173:110–125
- Couch RQ (1844) A Cornish fauna, being a compendium of the natural history of the country. Pt. 3. The zoophytes and calcareous corallines. Le Gillet, Truro
- Couthouy JP (1839) Descriptions of new species of mollusca and shells, and remarks on several polypi found in Massachusetts Bay. Boston J Nat Hist 2:53–111
- Daly M, Brugler MR, Cartwright P, Collins AG, Dawson MN, France SC, McFadden CS, Opresko DM, Rodriguez E, Romano S, Stake J (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. Zootaxa 1668:127–182
- Dalyell JG (1848) Rare and remarkable animals of Scotland, represented from living subjects: with practical observations on their nature, vol 2. J Van Voorst, London
- de Blainville HMD (1824) Mollusques, Vers et Zoophytes. Dictionnaire des Sciences naturelles, vol 30, p 470. Available online at <https://www.biodiversitylibrary.org/page/25300797#page/77/mode/1up>
- de Blainville HMD (1830) Zoophytes. In: Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts. Tome 60. FG Levrault, Paris
- Delle Chiaje S (1822) Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli. Fratelli Fernandes, Napoli, 109 pls
- Delle Chiaje S (1825) Memoria sulla storia e notomia degli animali senza vertebre del regno di Napoli. Volume 2. C Batelli, Naples
- den Hartog JC, Ates RML (2011) Actiniaria from Ria de Arosa, Galicia, northwestern Spain, in the Netherlands Centre for Biodiversity Naturalis, Leiden. Zool Meded Leiden 85:11–53
- Dixon GY, Dixon AF (1891) Report on the marine invertebrate fauna near Dublin. Proc Roy Irish Acad 32:19–33
- Duerden JE (1898) On the relations of certain Stichodactylinae to the Madreporaria. J Linn Soc London Zool 26:635–653
- Dunn DF, Hulsemann K (1979) Metridiidae Carlgrén, 1893 Anthozoa and Metridiidae Sars, 1902 Copepoda; request for a ruling to eliminate the homonymy. Z.N.S.2263. Bull Zool Nomencl 361:53–56
- Ehrenberg CG (1834) Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Abh Königl Akad Wiss Berlin 1:225–380
- Ellis J (1767) Beruch einer Naturgeschichte der Corallarten und anderen vergleichen Mercorper. Gabriel Nicolaus Raspe, Nürnberg, pp 152, 46 Pl
- Ellis J (1768) An account of the Actinia Sociata or clustered animal-flower, lately found on the sea-coast of the new ceded island. In a letter from John Ellis... to the Right honourable the Earl of Hillsborough. Phil Trans Roy Linn Soc London 57:428–437
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes, collected from various parts of the globe. Systematically arranged and described by the late Daniel Solander. Volume 4. Benjamin White and Son, London
- Elmhirst R (1925) Associations between the amphipod genus *Metopa* and Coelenterates. Scot Nat 155:149–150
- Fautin DG (2016) Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). Zootaxa 4145:1–449
- Fautin DG, Hand CH (2000) *Metridium farcimen*, the valid name of a common North Pacific sea anemone Cnidaria: Actiniaria: Aconitaria. Proc Biol Soc Wash 1134:1151–1161
- Fautin DG, Bucklin A, Hand C (1989) Systematics of sea anemones belonging to the genus *Metridium* (Coelenterata: Actiniaria), with a description of *M. giganteum*, new species. Wasmann J Biol 47:77–85
- Francis L (1988) Cloning and aggression among sea anemones (Coelenterata: Actiniaria) of the rocky shore. Biol Bull 174:241–253
- Gemmill JF (1920) The development of the sea-anemones *Metridium dianthus* (Ellis) and *Adamsia palliata* (Bohad). Phil Trans R Soc London Ser B 209:351–375
- Gimenez LH, Battini N, Gonzalez-Munoz R, Glon H (2023) Invader in disguise for decades: the plumose sea anemone *Metridium senile* in the Southwestern Atlantic Ocean. Biol Invasions 25:2159–2173
- Glon HE, Costa M, de Lecea AM, Goodwin C, Cartwright S, Díaz A, Brickle P, Brewin PE (2020) First record of the plumose sea anemone, *Metridium senile* Linnaeus, 1761, from the Falkland Islands. BioInvasions Rec 9:461–470
- Glon H, Quattrini A, Rodríguez E, Titus BM, Daly M (2021) Comparison of sequence-capture and ddRAD approaches in resolving species and populations in hexacorallian anthozoans. Mol Phylog Evol 163:107233
- Glon H, Häussermann V, Brewin PE, Brickle P, Kong S, Smith ML, Daly M (2023) There and back again: the unexpected journeys of *Metridium* de Blainville, 1824 between the old oceans and throughout the modern world. Biol Bull 244:9–24
- Gmelin JF (1788) Carolia Linne Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. (ed. 13). GE Beer, Lipsiae
- Goddard JH, Love MS (2010) Megabenthic invertebrates on shell mounds associated with oil and gas platforms off California. Bull Mar Sci 86:533–554
- Gosse PH (1855) Description of *Peachia hastata*, a new genus and species of the class Zoophyta, with observations on the family Actiniadae. Trans Linn Soc (London) 21:267–276
- Gosse PH (1858) Synopsis of the families, genera, and species of the British Actinia. Ann Mag Nat Hist 1:414–419
- Gosse PH (1860) Actinologia Britannica. A history of the British sea-anemones and corals. Van Voorst, London
- Gravier C (1920) Larves d'Actiniaires provenant des campagnes scientifiques de S. A. S. le Prince Albert I de Monaco. In: Résultats des Campagnes Scientifiques Accomplies sur son Yacht par Albert I Prince Souverain de Monaco 57, pp 3–25
- Greene CH, Schoener A (1982) Succession on marine hard substrata: a fixed lottery. Oecologia 55:289–297

- Griffiths CL, Kruger LM, Smith CE (1996) First record of the sea anemone *Metridium senile* from South Africa. *African Zool* 31:157–158
- Grizel H, Heral M (1991) Introduction into France of the Japanese oyster (*Crassostrea gigas*). *ICES J Mar Sci* 47:399–403
- Haddon AC (1886) First report on the marine fauna of the south-west of Ireland. *Actinozoa Proc R Irish Acad* 4:615–618
- Haddon AC (1889) A revision of the British Actiniae. Part I. *Sci Trans R Dublin Soc* 4:297–361
- Hand C (1955) The sea anemones of central California. Part III: The Acontiarian anemones. *Wasmann J Biol* 13:189–251
- Hand C (1961) Two new acontiate New Zealand sea anemones. *Trans R Soc NZ Zool* 14:75–89
- Harris LG (1991) Comparative ecology of subtidal actiniarians from the coasts of California and the Gulf of Maine, USA. *Hydrobiologia* 216:271–278
- Häussermann V, Molinet C, Díaz Gómez M, Försterra G, Henríquez J, Espinoza Cea K et al (2022) Recent massive invasions of the circumboreal sea anemone *Metridium senile* in North and South Patagonia. *Biol Invasions* 24:3665–3674
- Häussermann V, Försterra G (2005) Distribution patterns of Chilean shallow-water sea anemones Cnidaria: Anthozoa: Actiniaria, Corallimorpharia, with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic. *Sci Mar* 69:91–102
- Hertwig R (1882) Report on the Actiniaria dredged by H.M.S. Challenger during the years 1873–1876. *Rep Sci Res Voy Challenger Zool* 61:1–136
- Hoffmann RJ (1976) Genetics and asexual reproduction of the sea anemone *Metridium senile*. *Biol Bull* 1513:478–488
- Hoffmann RJ (1981) Evolutionary genetics of *Metridium senile*. II. Geographic patterns of allozyme variation. *Biochem Genet* 19:145–154
- Holdsworth EWH (1855) Description of two new species of *Actinia*, from the south coast of Devon. *Proc Zool Soc London* 23:235–237
- Hollard MH (1848) Études sur l'organisation des Actinies. Imprimerie de Marc Ducloux, Paris
- Johnston G (1838) A history of British zoophytes. WH Lizars, London
- Jordan RCR (1855) Some account of the Actiniadæ found upon the coast near Teignmouth, Devon. *Ann Mag Nat Hist* 15:81–91
- Kostina EE (1988) Biogeographical characteristics of sea anemones of the Pacific boreal region. *Biol Morya* 1988:14–21
- Kramer A, Francis L (2004) Predation resistance and nematocyst scaling for *Metridium senile* and *M. farcimen*. *Biol Bull* 207:130–140
- Laird MC, Griffiths CL (2016) Additions to the South African sea anemone Cnidaria, Actiniaria fauna, with expanded distributional ranges for known species. *African Invert* 57:15–37
- Le Sueur CA (1817) Observations on several species of the genus *Actinia*; illustrated by figures. *J Acad Nat Sci Philadelphia* 16(149–154):169–189
- Li Y (2013) Study on the species composition and flora characteristics of Chinese sea anemones (Cnidaria: Anthozoa). PhD thesis, Institute of Oceanology, Chinese Academy of Sciences, Qingdao
- Li Y, Xu K-D (2020) Species diversity and faunal characteristics of the order Actiniaria (Cnidaria: Anthozoa) in the seas of China. *Oceanol Linnol Sin* 51:434–443
- Linnaeus C (1761) *Fauna Suecica sistens Animalia Suecica Regni: Distributa per Classes, Ordines, Genera, Species, cum Differentiis Specierum, Synonymis Auctorum, Nominibus Incolarum, Locis Natalium, Descriptionibus Insectorum*. Sumtu & Literis, Stockholm
- Linnaeus C (1767) *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Regnum Animale. Laurentii Salvii, Holmiae*
- Lissner AL, Taghon GL, Diener DR, Schroeter SC, Dixon JD (1991) Recolonization of deep-water hard-substrate communities: potential impacts from oil and gas development. *Ecol Appl* 1:258–267
- Manuel RL (1988) *British Anthozoa*. Academic Press, London
- Martin JP, Garese A, Sar AM, Acuña FH (2015) Fouling community dominated by *Metridium senile* Cnidaria, Anthozoa, Actiniaria in Bahía San Julián Southern Patagonia, Argentina. *Sci Mar* 79:211–221
- Masuda MM, Stone RP (2003) Biological and spatial characteristics of the weathervane scallop *Patinopecten caurinus* at Chiniak Gully in the central Gulf of Alaska. *Alaska Fish Res Bull* 10:104–118
- McMurrich JP (1901) Report on the Hexactiniae of the Columbia University Expedition to Puget Sound during the summer of 1896. *Ann NY Acad Sci* 141:1–52
- McMurrich JP (1911) The Actiniaria of Passamaquoddy Bay, with a discussion of their synonymy. *Trans R Soc Can* 4:59–83
- McMurrich JP (1914) Modesty overworked. *Science* 39:785–786
- Milne Edwards H (1857) *Histoire naturelle des coralliaires, ou polypes proprement dits*. 1. Librairie Encyclopédique de Roret, Paris
- Molinet C, Häussermann V, Astorga M, Barahona N, Espinoza K, Diaz M, Diaz P, Henríquez J, Matamala T, Soto D (2023) Population expansion of the invasive sea anemone *Metridium senile* in the spatial mesoscale of a sea urchin bed in north-western Patagonia. *Biol Invas* 254:1101–1118
- Müller OF (1776) *Zoologiae Danicae prodromus, seu Animalium Daniae et Norvegiae indigenarum: characteres, nomina, et synonyma imprimis popularium*. Typis Hallagerii, Copenhagen
- Nafilyan Z (1912) Matériaux pour la faune des Actinies des côtes de France. *Les Actinies de Roscoff. Mem Soc Zool Fr* 25:5–44
- Nelson ML, Craig SF (2011) Role of the sea anemone *Metridium senile* in structuring a developing subtidal fouling community. *Mar Ecol Prog Ser* 421:139–149
- Nordgaard O (1905) Hydrographical and biological investigations in Norwegian Fiords. *Bergens Museums Meereskrifter* 2:164–174
- Oken L (1815) *Lehrbuch der Naturgeschichte*. Dritter Theil: Zoologie. Erste Abtheilung: Fleischlose Thiere. A Schmid, Jena
- Östman C, Kultima JR, Roat C, Rundblom K (2010) Acontia and mesentery nematocysts of the sea anemone *Metridium senile* Linnaeus, 1761 Cnidaria: Anthozoa. *Sci Mar* 74:483–497
- Parker GH (1900) Synopses of North-American invertebrates. XIII. The Actiniaria. *Am Nat* 34:747–758
- Parker T, Tunnicliffe V (1994) Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *Biol Bull* 187:336–345
- Parry G (1951) The Actiniaria of New Zealand. A check-list of recorded and new species, a review of the literature and a key to the commoner forms Part I. *Rec Canterb Mus* 6:83–119
- Pax F (1920) Die Aktinienfauna von Büsum. *Schriften der Zoologischen Station Büsum für Meereskunde* 6(5):1–24
- Pax F (1922) Untersuchungsfahrt des Reichsforschungsdampfers "Poseidon" in das Barentsmeer im Juni und Juli 1913, Zoantharien und Actiniarien. *Helgol Meeres* 132:249–254
- Pax F (1928) Über das Vorkommen der Seenelke *Metridium dianthus* Ell. in der Adria. *Zool Garten* 198:118–120
- Pei Z (1998) *Coelenterata Actiniaria Ceriantharia Zoanthidea*. Science Press, Beijing
- Pennant T (1777) *British Zoology*, vol. IV. Crustacea. Mollusca. Testacea. London. i-viii, 1–154, pls. 1–93
- Pennant T (1812) *British Zoology*. A new edition in four volumes, vol IV. Wilkie & Robinson, London, pp xvi+379, 95 pls
- Pennington AS (1885) *British zoophytes: an introduction to the Hydrozoa, Actinozoa, and Polyzoa found in Great Britain, Ireland, and the Channel Islands*. L. Reeve and Co, London

- Purcell JE (1977) Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* Coelenterata, Actiniaria. *Biol Bull* 1532:355–368
- Purcell JE, Kitting CL (1982) Intraspecific aggression and population distributions of the sea anemone *Metridium senile*. *Biol Bull* 162:345–359
- Rapp W (1829) Über die Polypen im Allgemeinen und die Actinien insbesondere. Verlage des Grossherzog, Weimar
- Riemann-Zürneck K (1975) Actiniaria des Südwestatlantik II. Sagaritiidae Und Metridiidae. *Helgol Wiss Meeres* 27:70–95
- Riemann-Zürneck K (1986) Zur Biogeographie des Südwestatlantik mit besonderer Berücksichtigung der Seeanemonen Coelenterata: Actiniaria. *Helgol Meeres* 40:91–149
- Rodríguez E, Fautin D, Daly M (2023) World list of Actiniaria. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/>. Accessed 17 Nov 2023. <https://doi.org/10.14284/568>
- Sebens KP (1981) The allometry of feeding, energetics, and body size in three sea anemone species. *Biol Bull* 161:152–171
- Stephenson TA (1920) On the classification of Actiniaria. Part I. – Forms with acontia and forms with a mesogloal sphincter. *Q J Microsc Sci* 64:425–574
- Stephenson EM (1925) On the anatomy and relationships of new or little known British Actiniaria. *J Mar Biol Assoc UK* 134:891–909
- Stephenson TA (1935) The British Sea Anemones, vol II. The Ray Society, London
- Stimpson W (1853) Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contrib Knowl* 6:1–66
- Stuckey FGA (1914) Description of a collection of actinians from the Kermadec Islands. *Trans NZ Inst* 46:132–134
- Teng G, Jin X, Fu C, Guan L, Jin Y, Chen Y et al (2021) Is seafloor litter contributing to sea anemone blooms? *Sci Tot Environ* 759:143479
- Tilesius GT (1809) De nova Actiniarum specie gigantea, Kamtschatica. *Mem Acad Imp Sci St. Pétersbg* 1:388–422
- Torrey HB (1898) Observations on monogenesis in *Metridium*. *Proc California Acad Sciences* 1:345–360
- Torrey HB (1902) Papers from the Harriman Alaska Expedition. XXX. Anemones, with discussion of variation in *Metridium*. *Proc Wash Acad Scie* 4:373–410
- Tugwell G (1856) A manual of the sea-anemones commonly found on the English Coast. John Van Voorst, London
- Uchida T (1938) Actiniaria of Mutsu Bay. Report of the Biological Survey of Mutsu Bay 13, 4(3):281–317
- Verrill AE (1864) Revision of the Polypi of the eastern coast of the United States. *Mem Boston Soc Nat Hist* 1:1–45
- Verrill AE (1865) Classification of polyps. (Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition under Captains Ringgold and Rodgers, U.S.N.). *Ann Mag Nat Hist* 16:191–197
- Verrill AE (1914) Priority overworked. *Science* 39:607–609
- Verrill AE (1922) The Actiniaria of the Canadian Arctic Expeditions, with notes on interesting species from Hudson Bay and other Canadian localities. *Rep Can Arctic Exped 1913–1918(8)*:89–164
- Walsh PJ (1981) Purification and characterization of two allozymic forms of octopine dehydrogenase from California populations of *Metridium senile*: The role of octopine dehydrogenase in the anaerobic metabolism of sea anemones. *J Comp Physiol* 143:213–222
- Walsh PJ, Somero GN (1981) Temperature adaptation in sea anemones: physiological and biochemical variability in geographically separate populations of *Metridium senile*. *Mar Biol* 62:25–34
- Walton CL (1908) Actiniae collected by the S.S. “Huxley” in the North Sea during the summer of 1907. *J Mar Biol Assoc UK* 8:215–226
- Williams RB (1975) Catch-tentacles in sea anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. *J Nat Hist* 9:241–248
- Wright EP (1859) Notes on the Irish Actinidae, etc., with especial reference to their distribution. *Nat Hist Rev Q J Sci* 6:113–125
- Yan T, Lin M, Cao W, Han S, Song X (2021) Fouling characteristics of cnidarians Hydrozoa and Anthozoa along the coast of China. *J Oceanol Limnol* 396:2220–2236
- Zamponi MO (1978) Sobre la anemona *Paraisometridium pehuensis*, gen. y sp. nov. (Actiniaria: Metridiidae). *Neotropica* 24:117–122

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.