Synopsis of the Family *Xeniidae* (Cnidaria: Octocorallia): Status and Trends

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Abstract. During an examination of xeniid octocorals held in the collections of the California Academy of Sciences (CAS) it was determined that identification to the species level was severely limited by the incomplete data present in most species descriptions published prior to 1950. A lack of consistent use of morphological characteristics by authors was found to be the most common difficulty, followed by limited or non-existent *in situ* data of the species being described. Descriptions from the later part of the twentieth century offered a more complete and detailed account of species. This paper presents the status of the Xeniidae by reviewing its two hundred year taxonomic history, examines the worldwide distribution of xeniids to date, and identifies the current challenges in xeniid systematics. It provides an overview of trends in modern taxonomy including *in situ* data collection, molecular analysis, and scanning electron microscopy. This last technique illustrates the micro-structural features of the sclerites or skeletal elements, a major taxonomic character of octocorals including the Xeniidae. The modern taxonomic methods outlined here are applicable for both xeniids and octocorals in general.

Key words: Cnidaria, Octocorallia, Xeniidae, Phylogenetics, Taxonomy.

Introduction

The family Xeniidae (Ehrenberg 1828) is often an abundant component of shallow-water octocoral communities throughout the Indian Ocean, Red Sea and Central West Pacific Ocean (Fig. 1). Among the genera in this family some species of *Heteroxenia* and *Xenia* are known for their characteristic rhythmic pulsation in the autozooid polyp tentacles. Xeniids are rapid colonizers of artificial surfaces (Schuhmacher 1974; Benayahu and Loya 1987) and natural hard substrates (Fabricius and Alderslade 2001; Wood and Dipper 2009) through both sexual reproduction and vegetative propagation.

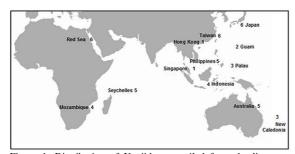


Figure 1: Distribution of Xeniidae compiled from the literature. Locations are shown with the number of xeniid genera present.

Colonies are zooxanthellate and most feature several longitudinal rows of pinnules on each side of the polyp tentacles. There has been relatively little work published on the taxonomy of xeniids compared to similarly abundant alcyoniids belonging to the genera *Sarcophyton*, *Sinularia* and *Lobophytum* (McFadden et al. 2006a, 2009). This is likely due to limited variation in characters among xeniid species and the uniformity of the sclerites, both of which make them difficult to identify.

Most descriptions of xeniid type material dating back prior to the twentieth century omit information of colony characters or do not include sclerite details. Coupled with this is the lack of actual type specimens. Many Anthelia, Cespitularia, Heteroxenia and Xenia type specimens are now missing from museum collections (Y. Benayahu pers. com). Those that are present often consist of only a few polyps or have dried out (A. Johnson pers. com) due to a lack of collection maintenance over time (Fig. 2). In the present study, we provide a historical context for the development of Xeniidae taxonomy and outline the progress made with modern tools now used to describe specimens to the species level.

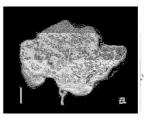




Figure 2: *Xenia elongata* (Dana, 1846); a) photo of holotype in dry condition, scale 1 cm, b) Colony drawing after Dana, 1846.

Historical Remarks

Octocorals were included in the collections of early expeditions to tropical seas, however they were part of larger invertebrate collections and no systematized sampling occurred. The first Xeniidae colonies were collected over 200 years ago as part of Napoleon's invasion of Egypt during the years 1798-1799 when specimens of Anthelia glauca and of Xenia umbellata were brought back to Europe. Both specimens were given brief descriptions by Lamarck (1816) and accompanied by detailed drawings of the colonies and their polyps. His work was published a year later by Savigny (1817). No measurements of the colonies were given nor details of their sclerites included, and both type specimens have been lost. Ehrenberg (1828) established the family Xeniidae making note that the octocoral polyps were soft, fleshy and fully extended. Later, the family Xeniadae was introduced by Gray (1859) as part of a broader work on the taxonomy of octocorals. Verrill (1865) suggested the family Xenidae from material collected by Dr. William Stimpson on the North Pacific Exploring Expedition. Both families were given brief mention but never formally adopted by later authors. It was not until 1889 that Wright and Studer provided the first systematic description for the family Xeniidae based on material collected on the Challenger Expedition. They noted that colonies consisted of non-retractile polyps united at the base with sclerites in the form of calcareous disks.

The genera Sympodium (Ehrenberg, 1834), Cespitularia (Milne-Edwards & Haime, 1850), Xenia (Lamarck, 1816) and Heteroxenia (Kölliker, 1874) were further defined by Hickson (1931) as members of the Xeniidae based on the presence of a welldeveloped pair of dorsal mesenteries in the gastric cavity of the polyps. In his revision of the genera of the Stolonifera, Hickson (1894) suggested abandoning the xeniid genus Anthelia Lamarck, 1816 and moving the associated species to the genus Clavularia. Then Gohar (1939) moved Anthelia back into the family Xeniidae. The confusing history of Anthelia was outlined in reviews by Gohar (1940) and Alderslade (2000). Gohar (1939) also introduced the xeniid genus Efflatounaria based on type material with retractile polyps and void of sclerites. Funginus (Tixier-Durivault, 1987) was originally described as a new xeniid genus but on re-examination of the type specimen it was determined to most likely be a species of Heteroxenia (Alderslade, 2001).

By the beginning of the twenty-first century significant works on xeniid genera were being published. The genus *Sansibia* (Alderslade, 2000) was

introduced for a number of species previously described as Anthelia. This new genus supported a distinction between the elongated rod-like sclerites with minute tooth-like projections typically found in species of Anthelia with those specimens which contained flattened platelets or spheroids. The monogeneric family Asterospiculariidae (Utinomi, 1951) was shown to have a sclerite microstructure similar to that of sclerites found in species of Xenia. The two species of this family were moved into the family Xeniidae under the genus Asterospicularia (Alderslade, 2001). In the same paper Alderslade introduced the new xeniid genera Bayerxenia, Ingotia, Ixion, Orangaslia and Ovabunda. With the introduction of these new genera a further distinction was need to separate genera with only the dorsal pair of mesenteries being well developed from those with all eight mesenteries equally developed. The family was divided into two subfamilies, Xeniinae for genera with only the dorsal pair of mesenteries (Anthelia, Bayerxenia, Cespitularia, Efflatounaria, Heteroxenia, Ovabunda, Sansibia, Sympodium and Xenia) and Ixioninae for the genera exhibiting all eight mesenteries fully developed in the gastric cavity (Asterospicularia, Ingotia, Ixion and Orangaslia). Ovabunda was established for a number of nominal Xenia species that exhibit sclerites comprising aggregations of spherical microscleres bound by organic material. Species belonging to this genus are present in the Red Sea and Indian Ocean. The xeniid Fasciclia (Janes 2008) exhibits morphological characteristics of a membranous basal attachment and sclerite micro-architecture found in Anthelia and the columnar stalk of bound autozooid polyps observed in species of Xenia. Yamazatum (Benayahu, 2010) was shown to have four different sclerite forms that were visible under light microscopy.

Modern Investigation

Scanning Electron Microscopy

With the limited resolution of light microscopy, xeniid sclerites were considered to have a uniform platelet or biscuit-like shape (Fig. 3) that only varied in size (Kükenthal 1902; Roxas 1933; Verseveldt and Cohen 1971).

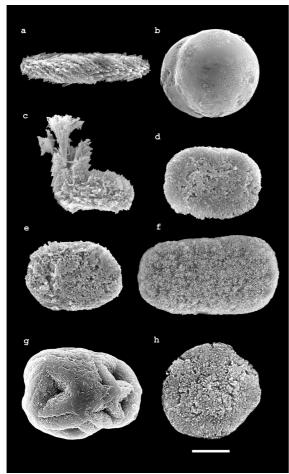


Figure 3: SEM sclerite images from xeniids; a) Anthelia ternatana, b) Cespitularia simplex, c) Fasciclia ofwegeni, d) Heteroxenia elizabethae, e) Ovabunda aldersladi, f) Sympodium caeruleum, g) Yamazatum iubatum, h) Xenia puertogalerae

In the study of xeniids, the scanning electron microscope (SEM) was first utilized by Kawaguti (1969) to show the development of the sclerites in the mesogloea of Heteroxenia elizabethae Kölliker, 1874. Just over a decade later Bayer et al. (1983) suggested examining the surface detail of xeniid sclerites for with SEM technology. taxonomic purposes Micrographs published by Benavahu (1990) revealed the microstructure of xeniid sclerites for the first time in two Red Sea species. This technology was further utilized by Reinicke (1997) to illustrate the sclerite microstructure of some additional Red Sea specimens including Sympodium caeruleum Ehrenberg, 1834. Xenia umbellata Lamarck, 1816, Xenia faraunensis Verseveldt and Cohen, 1971, and Heteroxenia fuscescens Ehrenberg, 1834 which he had originally been asked to collect for Dr Phil Alderslade (P. Alderslade, pers. com). The genera Bayerxenia, Ingotia, Ixion, Orangaslia, and Ovabunda established by Alderslade (2001) were based in large part on the micro-architecture of their sclerites. He noted that that at present the findings "indicate that the basic building blocks of the (xeniid) sclerites in all genera are calcite rods, and their differences in assembly can be used as generic level characters", something that had been previously overlooked by investigators. Sclerite microstructure was noted in the genus *Fasciclia* (Janes, 2008) where the fine surface detail of the sclerites showed a considerable structural similarity to those found in *Anthelia*. The genus *Yamazatum* (Benayahu, 2010) has a distinct sclerite surface feature that was revealed with SEM technology (Fig. 3).

The introduction of the environmental SEM (ESEM) has made high-resolution examination of sclerite microstructures easier (Fig. 4). ESEM technology provides the convenience of imaging material without extensive sample preparation. By comparison, preparation for SEM work on octocoral sclerites requires them to be extracted from coral tissue, thoroughly cleaned, and mounted on an SEM stub. The stub is then placed in a sputter coater to coat the sclerites with a molecular layer of gold so they can be imaged.

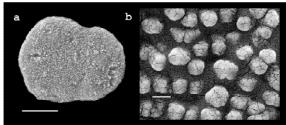


Figure 4: *Heteroxenia mindorensis* Roxas, 1933; a) SEM of an autozooid polyp sclerite, scale bar = 0.005 mm, b) ESEM high-resolution image of the sclerite surface, scale bar = 200 nm.

In the first published account of ESEM imaging in xeniid octocorals (Aharonovich and Benayahu 2011) Ovabunda species sclerites revealed that the surface of the microscleres have granular crystals. These crystals appear to interlock with adjacent microscleres, maintaining the sclerite shape. Both the organic component found in Ovabunda sclerites (Janes 2008) and the granular surface crystals observed with the ESEM can be used as diagnostic features for the taxonomy of this genus. Utilizing these new microscopic technologies for taxonomic identification of new genera and species has proved valuable in recent years. However, the need to reexamine previously described xeniid specimens where sclerite ultra-structures are unknown is vital, otherwise many new species may be synonyms of previously described species.

Molecular Tools

Advances in molecular systematics have provided additional ways to clarify genus level relationships in octocorals, allow comparisons to be made between specimens with little or no morphological variation and identify new morphological characters useful for taxonomic identification (McFadden et al. 2006a; 2009). To date, however, only two phylogenetic studies of octocorals have included Xeniidae, and neither has included more than two representatives of any one genus (McFadden et al. 2006b; McFadden et al. 2011). Combined, the results of these two studies taxonomic suggest confusion among morphologically similar genera Ovabunda, Xenia, and Heteroxenia, with members of the latter two genera co-occurring in more than one distinct clade (Fig. 5). Recent, unpublished results also suggest that the definition of Cespitularia is unclear, with some species belonging to a clade with Efflatounaria while others fall with Xenia (C. McFadden, pers. comm.). Finally, the mtMutS tree presented in McFadden et al. (2006b) and Fig. 5 places Anthelia outside of Xeniidae, while the COI tree in McFadden et al. (2011) supports a monophyletic Xeniidae.

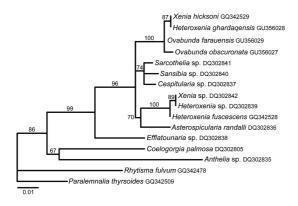


Figure 5: Maximum likelihood phylogeny of Xeniidae based on a 726 nt fragment of the octocoral-specific mitochondrial gene mt MutS. *Coelogorgia, Paralemnalia* and *Rhytisma* are included as non-Xeniidae outgroup taxa. All sequences from GenBank (accession numbers follow species names). Numbers above branches are bootstrap values.

Challenges exist in the use of molecular analysis for xeniids. Many specimens housed in museum collections are stored in formalin, which can significantly degrade the sample tissue. Also, not all species are reliably distinguished using the currently available genetic markers (McFadden et al. 2011). The advantage of molecular phylogeny will be its use in combination with traditional taxonomy. This can improve accuracy by identifying which morphological characters separate genera and assist in distinguishing specimens to the species level.

Focused Sampling

Historically, octocoral collections have relied on material being acquired indiscriminately as part of larger coral surveys. The process of selective sampling provides an opportunity to conduct detailed surveys, *in situ* imaging with underwater digital cameras and habitat data collection. Selective sampling surveys have already been shown to yield a rich octocoral diversity of taxonomic significance (Reinicke 1997; Grasshoff and Bargibant 2001; Ofwegen 2008a, 2008b; Janes 2008).

A literature compilation of the distribution of xeniids is shown in Fig. 1. Areas with the richest diversity of xeniid genera include the Red Sea, Indonesia, Japan, Australia and the Seychelles. However, both the Red Sea and the Seychelles have received extensive investigation so it is unknown if the figures for some of the other locations reflect limited collection efforts and/or low diversity. Published accounts of xeniids from Australia (Verseveldt 1977), the Philippines (Roxas 1933) and Indonesia (Schenk 1896) are quite limited. A few studies have revealed that some locations display a high level of soft coral diversity (Benayahu 1995, 1997; Ofwegen 1996, 2002, 2007).

Outlook

Xeniid taxonomy is only beginning to see the advantages of contemporary taxonomic approaches utilized by scleractinian researchers (Zlatarski 2008). Improvements in xeniid systematics have benefited from the use of SEM and ESEM technologies, molecular analysis and selective sampling in the field. However advances such as DNA barcoding have yet to be realized (McFadden et al. 2011). The taxonomy of xeniid octocorals is important to our understanding of octocoral biodiversity and in a broader sense, the conservation of tropical coral reefs.

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