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New record of the coral-boring sponge *Amorphinopsis* cf. *excavans* in Kāne‘ohe Bay, Hawai‘i

Mestrado em Biologia Marinha

Supervisor:

Regina Lopes da Cunha

Co-supervisors:

Rob Toonen

Jan Vicente

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Abstract

The Hawaiian archipelago is currently recognized as a hub of species introductions. In Kāne‘ohe Bay, several marine alien species have been reported over the last decades, including sponges, which benefit from its nutrient-rich waters. Here we report the presence and the coral-excavating habit of the Indo-Pacific sponge *Amorphinopsis* cf. *excavans* in the bay. A thorough traditional taxonomic assessment is performed, along with a genetic analysis of both ribosomal and mitochondrial genes, revealing the identity of the sponge. The results underscore the polyphyletic nature of the genus and highlight the need for an integrative approach to resolve its phylogenetic framework. Existing literature on *A. excavans* and its extended distribution range justify its classification as a species complex until further clarification. Limited dispersal capabilities of sponge larvae and the species' encrusting ability suggest an introduction by integrating the fouling community of trans-Pacific vessels. The sponge is actively boring into the two primary reef-building species of coral in the bay - *Montipora capitata* and *Porites compressa*, therefore posing a significant environmental threat to Hawai‘i's native ecosystem. Considering the expected increase in bioeroding sponges under future climate change scenarios, the development of management strategies is advised.

Resumo

O Havai é constituído por uma cadeia de 137 ilhas, atóis, recifes de coral e montes submarinos localizados no centro do Oceano Pacífico, sendo considerado o arquipélago geograficamente mais isolado do planeta. Apesar desse isolamento, o seu clima tropical e posição estratégica tornaram-no um centro urbano, turístico e militar de grande importância, contando com mais de um milhão de habitantes e cerca de 10 milhões de visitantes anuais. Como consequência, foram estabelecidas várias ligações comerciais e de transporte com outras regiões do mundo, o que facilitou a introdução inadvertida de múltiplas espécies não nativas. Atualmente, poucas regiões do mundo apresentam um número tão elevado de espécies introduzidas quanto o Havai.

Na Baía de Kāneʻohe, localizada no lado leste da ilha de Oʻahu, encontra-se não só o maior volume de água resguardada de todo o arquipélago, mas também um dos ecossistemas de recife de coral mais bem estudados do mundo. Nesta baía, foram já registadas várias espécies marinhas não-nativas nas últimas décadas. Entre estas, encontram-se cerca de 30 espécies de esponjas (Porifera), que beneficiam das águas calmas e ricas em nutrientes proporcionadas pela configuração única deste local. Recentemente, foram identificados vários novos registos para a baía, incluindo espécies novas para a ciência. Neste estudo, é reportado e discutido um desses registos em particular, de uma espécie não-nativa, dadas as implicações ambientais que lhe estão associadas.

A morfologia simples e a falta de características distintivas desta espécie dificultaram a sua identificação, pelo que foi utilizada uma estratégia integrativa para se alcançarem conclusões definitivas. Inicialmente, foram recolhidas quatro amostras de indivíduos diferentes da espécie, complementando uma amostra anteriormente recolhida. Com base nas características morfológicas da espécie, foi primeiramente realizada uma avaliação taxonómica tradicional, a partir da observação direta do material e de secções histológicas, utilizando também técnicas de microscopia ótica e de microscopia eletrónica de varrimento. Os parâmetros descritos incluem o seu aspeto, o tipo e as dimensões das espículas, a organização interna e externa do esqueleto, entre outros. Os resultados foram comparados com as descrições de espécies já conhecidas na literatura. Para complementar esta abordagem, foram também realizadas análises genéticas a genes ribossómicos (28S rRNA) e mitocondriais (Cox1). Para permitir o alinhamento com todas as sequências parciais disponíveis no GenBank, várias regiões de cada

gene foram sequenciadas nas amostras havaianas, nomeadamente os domínios D2 e D3-D4 do gene nuclear e o fragmento Folmer e uma extensão do mesmo no gene mitocondrial, resultando em quatro árvores filogenéticas distintas. Apenas a combinação destes dois métodos permitiu identificar a espécie em questão com um elevado grau de confiança, e como pertencente ao táxon *Amorphinopsis* cf. *excavans*. Este estudo sublinha, assim, a necessidade de uma abordagem integrativa na classificação de esponjas com características morfológicas plásticas e/ou pouco distintivas.

Neste contexto, foi também realizada uma revisão taxonómica da espécie, analisando todas as descrições morfológicas existentes na literatura. Esta revisão revelou algumas discrepâncias nas identificações anteriores, as quais necessitam de uma avaliação genética para confirmar a classificação atribuída. Por outro lado, os resultados da análise molecular evidenciaram também a natureza polifilética do género *Amorphinopsis* em ambos os marcadores genéticos analisados, um padrão comum noutros géneros da família Halichondriidae. Este cenário taxonómico incerto, aliado à distribuição geográfica extensa da espécie, algo improvável considerando a capacidade limitada de dispersão natural das esponjas, justifica que *A. excavans* seja classificada como um complexo de espécies (cf.*)* até que estudos futuros forneçam os esclarecimentos necessários para a sua classificação fiável.

Embora não existam provas concretas da introdução desta espécie no arquipélago, vários fatores tornam esta hipótese muito plausível. A biodiversidade da baía foi intensamente estudada em investigações anteriores e, no entanto, a espécie nunca tinha sido detetada até agora, apesar da sua presença evidente em secções superficiais dos corais. Além disso, amostras recolhidas em Omã apresentaram uma identidade genética superior a 99% relativamente aos exemplares havaianos, sugerindo que a distribuição da espécie não pode ser explicada apenas por uma taxonomia conservativa. Um estudo adicional revelou que *A. excavans* é capaz de encrustar bóias de sinalização em portos de Singapura, indicando não só a sua presença num dos portos mais movimentados do Sudeste Asiático, mas também a sua capacidade de colonizar superfícies artificiais. Esta característica legitima a possibilidade da integração da espécie na comunidade incrustante dos cascos de navios oriundos deste porto, que mantêm ligações comerciais frequentes com o Havai. Acredita-se que a maioria das esponjas introduzidas no arquipélago chegaram por este meio, sendo provável que o mesmo tenha ocorrido com *A.* cf. *excavans*.

A esponja *Amorphinopsis* cf. *excavans* foi observada particularmente na zona sul da Baía de Kāneʻohe, o que seria expectável, já que é a zona da baía onde existe maior concentração de nutrientes na coluna de água, que representam a maior fonte de alimento para animais filtradores como as esponjas. No entanto, a distribuição atual da espécie na baía não foi alvo de estudo neste trabalho, e por isso carece de iniciativas de monitorização futuras. A espécie encontra-se a erodir/escavar duas espécies de corais na zona sul da Baía de Kāneʻohe, *Montipora capitata* e *Porites compressa*, esclarecendo dúvidas anteriores sobre a sua capacidade de bioerosão. Estas espécies de coral são fundamentais para a estrutura do recife da baía, formando a base do ecossistema marinho local. Além disso, *P. compressa* é uma espécie endémica, tornando a sua degradação uma preocupação ambiental ainda maior. Embora os mecanismos exatos de bioerosão utilizados por *A.* cf. *excavans* não sejam conhecidos, prevê-se que estas interações sejam agravadas pelas alterações climáticas, como a acidificação dos oceanos, que facilita o processo de erosão através de um aumento da concentração de pCO_2 e uma redução do pH da água. Além disso, muitas esponjas bioerosivas demonstram uma maior resistência a temperaturas elevadas, beneficiando assim também do declínio dos recifes de corais fragilizados pelo stress térmico e pela eutrofização em ambientes futuros.

O caso da esponja *Mycale grandis*, introduzida há cerca de 30 anos na baía, ilustra as potenciais consequências da proliferação descontrolada de esponjas introduzidas. Esta espécie sobreviveu a tentativas de controlo e erradicação e está hoje presente em diversas zonas do arquipélago, infestando as mesmas espécies de corais que *A.* cf. *excavans* e comprometendo a estrutura do recife. Considerando este precedente e o impacto potencial de esponjas bioerosivas em cenários futuros, *A.* cf. *excavans* representa uma ameaça séria para o ecossistema único da Baía de Kāneʻohe. Assim, a implementação de estratégias de controlo precoces é essencial para mitigar os impactos ambientais desta espécie.

Keywords

Non-indigenous; Excavating sponge;
Molecular Phylogeny; Taxonomy

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Table of contents

List of abbreviations, acronyms and symbols

28S rRNA - structural ribosomal RNA (rRNA) for the large subunit (LSU) gene of eukaryotic cytoplasmic ribosomes
COI - Cytochrome C Oxidase subunit I
DOC - Dissolved Organic Carbon
OTU - Operational Taxonomic Units
POC - Particulate Organic Carbon

Part 1. GENERAL INTRODUCTION

1.1 Porifera

1.1.1 What is a sponge?

(a) Most primitive phylum in Metazoa

Sponges (Porifera) are the most primitive phylum of all extant metazoans, coming at the very base of the animal phylogenetic tree (Nielsen, 2008; Philippe et al., 2009). The common ancestor of all Metazoan phyla is thought to have been a sponge-like organism (Müller et al., 1994a, Müller, 1995), and the first to cross the “metazoan threshold”, by developing critical characteristics such as cell-cell adhesion molecules, an immune system, and intracellular signal pathways (Müller, 2001). As a result, the Porifera are often considered “living fossils” (Muller, 1998), with a body plan that remains one of the simplest in the animal kingdom.

Due to their unique morphology, the classification of sponges as true metazoans was historically controversial, and they were sometimes designated as "zoophytes" or "plant-animals" because of their plant-like appearance (Müller, 2004). However, their early divergence in the animal tree of life makes them essential for understanding the evolutionary pathways of early metazoans and reconstructing the paleogenomics of the last common ancestor of animals (Taylor et al., 2007).

(b) Sponge design

Sponge morphology varies significantly both within and between species, ranging from over a meter in length to just a few millimeters thick, and from tall upright structures to thin encrusting layers (Van Soest et al., 2012). Their structure is supported by a skeleton composed of siliceous or calcareous microscopic structures (spicules) and/or collagenous fibers (spongin), embedded in a collagenous matrix (mesohyl). The arrangement, composition, and density of these elements determine the sponge's shape and consistency. Most sponges have a skeleton divided into the ectosome, a thin surface layer, and the choanosome, the internal section (Uriz et al., 2003). These components create a network of canals and chambers through which water flows, entering via small openings (pores) and exiting through larger openings (oscula). This network forms the so-called “aquiferous system”, which facilitates oxygen and nutrient intake while expelling waste, gametes, and larvae (Leys & Hill, 2012).

Lacking organs or complex systems, sponges rely on specialized cells for their life functions. Choanocytes generate water currents for feeding, gas exchange, and waste removal while capturing food particles. Archaeocytes are totipotent cells responsible for digestion, nutrient transport, and regeneration. Pinacocytes form the outer layer and line water channels, regulating flow by adjusting pore and oscula size (Simpson, 1984; Leys & Hill, 2012). While most sponges are filter feeders, some are carnivorous (Vacelet & Boury-Esnault, 1996), and others, particularly shallow-water species, host photosymbionts (Usher, 2008).

1.1.2 Uses and applications

(a) Historical uses

Sponges have been used throughout history for various purposes, including decoration, painting, padding, anesthesia, food, and even contraception (Pronzato & Manconi, 2008). However, none of these applications have matched the cultural and economic significance of "bath sponges." Since antiquity, several species, particularly five from the genera *Spongia* and *Hippospongia*, have been continuously harvested across the Mediterranean. These sponges are highly valued for their silica-free spongin skeletons, which provide exceptional softness, elasticity, and water retention (see Pronzato & Manconi, 2008 for detailed descriptions; Voultsiadou et al., 2011; Jesionowski et al., 2018). The global demand for natural sponges, primarily for bathing and cleaning, was historically substantial. While the advent of synthetic alternatives and the development of sponge farming have helped reduce pressure on Mediterranean bath sponge populations, some beds have still suffered significant depletion (Duckworth, 2009; Voultsiadou et al., 2011).

(b) Source of bioactive substances

More recently, sponges have been sought not only for their physical properties but also for their chemical richness. Despite lacking physical defenses or a conventional immune system, sponges rarely suffer from biofouling by competing invertebrates (Abarzua & Jakubowski, 1995), and only a fraction of species are actively consumed by predators (Pawlik et al., 1995). This is largely due to the extensive array of toxic or deterrent secondary metabolites produced by sponges and their many associated symbionts (Pawlik, 1993; Perdicaris et al., 2013). These chemical compounds exhibit a wide range of molecular structures and are being extensively studied for medical and pharmaceutical applications, particularly for their antimicrobial, anti-inflammatory, antitumor, and antiviral properties (e.g., Laport et al., 2009; Essack et al., 2011; Drechsel et al., 2020). Currently, sponges are the most prolific source of marine bioactive compounds, with nearly 10,000 new molecules isolated in the past 50 years, driving significant research efforts in this field (Thakur et al., 2005; Maslin et al., 2021).

1.1.3 Ecological role of Porifera in coral reefs

(a) Production and interaction with other organisms

Several species of sponges have established symbiotic relationships with cyanobacteria and zooxanthellae, particularly within coral reefs, promoting primary production (Usher, 2008; Webster & Taylor 2012). Some species also participate in secondary production by being palatable, and consumed by a multitude of predators, some being specialists, and others more opportunistic (Wulff, 2006).

An immense diversity of microbial and macrofaunal communities is also supported by sponges (Wulff, 2006; Taylor et al., 2007). Many of the defensive chemicals produced by sponges are, in fact, synthesized by the diverse bacteria and protists they harbor (e.g., Piel et al., 2004; Tianero et al., 2019). Additionally, their canal systems provide microhabitats where microorganisms can thrive while evading predation (Wulff, 2006; Bell, 2008). This includes a wide range of invertebrate groups found in coral reefs, such as crustaceans, polychaetes, cnidarians, ophiuroids, and mollusks, as well as some species of small fish (Wulff, 2006). For instance, Ribeiro et al. (2003) documented 2,235 individuals from 75 different associated fauna species living within a single sponge species in southeastern Brazil.

(b) Influence on carbon cycling

Sponges play a vital role in linking carbon dispersed in the water column to the benthos and the broader food web, particularly in coral reefs, as outlined in the "sponge-loop hypothesis" (De Goeij et al., 2013). As highly efficient filter feeders, sponges pump and filter large volumes of water relative to their body size every day (Vogel, 1977; Morganti et al., 2019), retaining up to 90% of organic particles smaller than 10 µm (Pile et al., 1996; Yahel et al., 2003). Similar to the microbial loop in the open ocean, where bacterioplankton play a key role (Azam et al., 1983), sponges absorb dissolved organic carbon (DOC), which is typically unavailable to most organisms, and convert it into particulate organic matter (POC) through cell shedding (De Goeij et al., 2013; Alexander et al., 2014). This carbon is then transformed into detritus, which can be consumed by detritivores, effectively creating a pathway between DOC and higher trophic levels (Rix et al., 2017).

In this way, sponges establish a powerful recycling mechanism where a significant portion of the carbon fixed and released by the community is retained within the ecosystem. This helps explain how coral reefs can maintain high productivity despite thriving in nutrient-poor waters, a long-standing puzzle for scientists (Maldonado, 2016; De Goeij et al., 2013). In addition to carbon, sponges and their symbionts process other essential nutrients, including nitrogen, phosphorus, and silica. As abundant members of coral reef ecosystems, sponges can influence not only the availability of these nutrients but also their fluxes and cycling within the system (Bell, 2008; Maldonado et al., 2012; Pawlik et al., 2020). However, understanding the precise ecological roles of sponges in nutrient cycling at a large scale remains a challenging task, and significant knowledge gaps still persist (De Goeij et al., 2017).

1.1.4 Bioerosion in coral reefs

(a) Boring sponges and the excavating process

Bioerosion is defined as the breakdown of hard materials of any type by the direct action of living organisms (Neuman, 1966). In coral reefs, bioerosion is primarily carried out by a group of sponges commonly known as boring or excavating sponges, which use the coral framework as their substrate. In Caribbean reefs, for instance, boring sponges can account for up to 90% of the total macrobioerosion (MacGeachy, 1977). The first official description of a boring sponge was published nearly 200 years ago by Grant (1826), who documented *Cliona celata*, a species found excavating a common oyster. Since then, nearly 300 species have been recognized as borers across 13 different families. Interestingly, Clionaidae remains the most abundant and most studied family (Schönberg et al., 2017a).

Coral-boring sponges can display different morphologies, which may represent distinct species or merely developmental stages of the same species (Vosmaer, 1931; Schönberg et al., 2017a, b). Most species are either entirely endolithic, with all sponge tissue developing inside the coral skeleton and leaving only inhalant and exhalant openings visible on the surface (alpha morphology), or they expand on the surface of the coral, forming a crust that can range from thin to extending into the substrate (beta morphology) (see Fig. 1 in Murphy et al., 2016, for a side-by-side comparison). The beta form also allows the integration of photosynthetic symbionts due to the large, exposed surface area, as seen in many clionids (Rützler, 2002; Weisz et al., 2010).

The excavating process typically begins with chemical boring, where the sponge etches cuspate fissures into the coral framework using specialized etching cells. This process not only dissolves part of the substrate but also weakens it (Cobb, 1969; Rützler and Rieger, 1973; Pomponi, 1977). The exact agent responsible for the dissolution of coral $CaCO_3$ remains unidentified, and it likely varies between sponge species. As fissures meet, carbonate "chips" (approximately 15-100 µm in diameter) become dislodged from the substrate and are transferred out of the sponge through its aquiferous system as part of the mechanical boring process (Warburton, 1958; Cobb, 1969; Rützler and Rieger, 1973).

It was traditionally believed that the material dissolved through chemical boring was minimal compared to the extraction via mechanical boring (e.g., Rützler and Rieger, 1973; Acker and Risk, 1985). However, this is not the case for all species, as in some, chemical action plays a more significant role than chip removal (Zundelevich et al., 2007).

(b) Influence of climate change

In healthy coral reefs, bioerosion by sponges is a crucial process that helps maintain the ecosystem's proper functioning (Bell, 2008). The carbonate chips produced by sponges are one of the main contributors to sediment availability on coral reefs (Rützler, 1975; Carballo et al., 2017; De Bakker, 2024), which are vital for stabilizing reef structures (Hubbard et al., 1998;

Mallela & Perry, 2007). These chips also promote habitat heterogeneity and coral dispersal by weakening and further fragmenting the reef (Goreau & Hartman, 1963; Tunnicliffe, 1977). Furthermore, bioerosion facilitates carbonate recycling by dissolving dead coral and rubble back into the system, making these materials available for new calcifying organisms to use in constructing their skeletons (Nava & Carballo, 2008). This relationship between erosion and calcification, however, implies a balance in which calcification must exceed the rate of erosion in order to maintain a positive $CaCO_3$ budget (Glynn & Manzello, 2015). Climate change impacts are threatening to disrupt that balance, pushing reefs towards negative carbonate budget states (Perry et al., 2008, 2014; Molina-Hernández et al., 2020).

The rise in sea surface temperatures over the past decades has had a profound impact on coral health (Cheng et al., 2019). The thermal tolerance of their photosymbionts can be exceeded after certain temperature thresholds, resulting in the loss of the coral's photosynthetic capacity, often leading to coral death (Coles & Jokiel, 1977; Gates et al., 1992; Weis, 2008). The breakdown of this symbiotic relationship causes the visual whitening of the coral tissue, a phenomenon referred to as "bleaching", which can extend to large-scale events (Heron et al., 2016; Hughes et al., 2017, 2018). Eutrophication, driven by rising temperatures and land-based pollution, leads to algal blooms and hypoxic states that severely affect photosynthesis and coral metabolism (Bruno et al., 2003; Lesser, 2023). Simultaneously, the ocean absorbs a significant portion of the excess carbon dioxide (CO_2) in the atmosphere (Doney et al., 2009). Higher levels of pCO_2 in the ocean decrease the water's pH, reducing the availability of carbonate ions needed for coral skeleton formation (Anthony et al., 2011; Cornwall et al., 2021). In short, due to the combination of ocean warming, acidification, eutrophication, and other local factors, corals in many parts of the world are under great stress, experiencing unprecedented mortality rates, a trend expected to persist and possibly escalate in the future (Oliver et al., 2019; Klein et al., 2022).

On the other hand, these impacts are not manifesting in boring sponges in the same way. Boring sponges are already naturally resistant to unfavorable environmental conditions, as most species live sheltered in cryptic spaces of the reef structure or even within coral skeletons, making them less exposed to temporary environmental shifts compared to other free-living species (Schönberg et al., 2017a). Additionally, like most sponges, they possess an incredible capacity for regeneration (Bell, 2002; Halperin et al., 2016) and exhibit highly versatile reproduction strategies (Schönberg et al., 2017a). Despite the influence of climate change, boring sponges are not as profoundly affected as corals. Increases in water temperature can cause physiological stress to some excavating sponge species (Bell et al., 2018; Strano et al., 2022), but many others appear to be significantly more tolerant than corals (Carballo et al., 2013), and some are even stimulated to grow (Marquez et al., 2006). Species that harbor zooxanthellae in symbiosis are less susceptible to bleaching (Vicente, 1990; Fang et al., 2016), and while eutrophication may be detrimental to shallow-water corals, it provides higher nutrient loads that benefit filter-feeding organisms like boring sponges (Holmes, 2000; Ward-Paige et al., 2005).

The disparity between the responses of corals and boring sponges, two of the main space competitors in coral reefs, gives boring sponges a physiological advantage during climate-induced stress, such as bleaching events and eutrophic states. This advantage offers a window of opportunity for sponge settlement, colonization, and success. A similar scenario occurs with ocean acidification. Boring sponges do not use carbonate ions to create their skeletons, which are either entirely organic or based on silica components. As a result, their physical development is less affected by a decrease in pH and higher pCO_2 levels (Fang et al., 2013). In fact, more acidic environments can facilitate the bioerosion process (Wisshak et al., 2012). Nearly all species of boring sponges studied in relation to environmental acidification have shown enhanced bioerosion performance (with limits), particularly in terms of the chemical component of bioerosion (e.g., Wisshak et al., 2013, 2014; Enochs et al., 2015; Webb et al., 2017).

Considering these factors, where sponges are generally favored and sympatric corals are suppressed, it is clear why many scientists expect boring sponges to become “winners” in future climate scenarios (Fabricius et al., 2011; Bell et al., 2018).

(c) Challenges in sponge bioerosion research

In the face of a changing planet, understanding bioeroding sponges in a functional context has never been more important. However, while it is anticipated that bioerosion rates by sponges will likely increase in the near future, several obstacles hinder the advancement of scientific knowledge on this group of organisms. These challenges include:

1. Cryptic Nature: Most environmental studies require estimates of the abundance and volume of boring sponges at the study site. Yet, these sponges are often cryptic or

endolithic, making them difficult to detect, let alone estimate their body volumes (Rützler, 1975; Schönberg, 2015; Murphy et al., 2016).

2. Species-Specific Excavation: The excavation process is usually species-specific, but only a few species have been the target of thorough research (Schönberg et al., 2017a). We are likely still far from understanding the full diversity of boring species due to both their cryptic nature and challenges in sponge systematics (as discussed below).
3. Lack of Standardization: There is often a lack of standardization across methods, which prevents effective comparison of results (De Bakker et al., 2018). For example, total sponge bioerosion rates have been reported to range from 0.3 to 29.5 kg m^2 y^{-1}, and different values have been found for the same species (Schönberg, 2008; Fang et al., 2013; Wisshak et al., 2013).
4. Environmental Influences: Bioerosion and sponge metabolism are influenced by a range of environmental factors, such as temperature, pH, substrate type, nutrient availability, and biological interactions (Schönberg et al., 2017b). Consequently, experimental results obtained in controlled environments may not always reflect in situ conditions.

Although excavating sponges are probably the best-studied endolithic borers in coral reefs (Fang & Schönberg, 2015), and research on sponge bioerosion has significantly increased since the recognition of their role in carbonate cycling (Schönberg et al., 2017a), we still lack a comprehensive understanding of how they affect the carbonate budget of coral reefs. This knowledge gap prevents us from fully anticipating and mitigating potential negative impacts in the future.

1.1.5 Sponge systematics

(a) Traditional taxonomy

The simple bauplan of sponges has long posed a challenge for the classification of Porifera and, ultimately, for sponge research. While some species exhibit distinct morphologies that allow for easy visual identification, many others lack sufficient variability in morphological characters to enable straightforward individualization (Leal et al., 2010; Xavier et al., 2010).

In cases of high phenotypic plasticity, the same taxon may even display apparently distinct forms (e.g., Hill, 1999; Lopez-Legentil et al., 2010; DeBiasse et al., 2015). The strongest characters used in sponge classification are typically the skeleton arrangement and the shape/size of mega/microscleres, however, these features often remain limiting for accurate identification, particularly between closely related species, and their homoplasy has been demonstrated in multiple instances (e.g., Manuel et al., 2003; Erpenbeck et al., 2006; Cárdenas et al., 2011; Morrow et al., 2013). This issue has led to consistent revisions in the systematics of Porifera since the beginning of spongiology in the mid-19th century (Hooper & Van Soest, 2002), as accurate phylogenetic reconstruction through morphology relies on good character assessments (Erpenbeck et al., 2012).

In 2002, J. Hooper, R. W. M. van Soest, and their co-authors published *Systema Porifera*, which remains the most comprehensive overview of Porifera systematics to date. The organization of species in this work is almost exclusively based on sponge morphology, incorporating existing literature along with extensive re-evaluation of type specimens. While *Systema Porifera* continues to serve as the foundation of sponge taxonomy today, it also highlighted how the classification of species was often based on rather superficial divergences - arguably insufficient to reliably discriminate taxa or establish a robust phylogenetic framework for this group.

(b) DNA Barcoding

The advent of genetic approaches came to confirm these concerns, but it also came as a solution to them. As anticipated, many discrepancies arose between the prevailing classification and the new phylogenetic relationships revealed by molecular studies, exposing the polyphyly of many groups, particularly within Demospongiae (Cárdenas et al., 2012; Morrow et al., 2012, 2013; Redmond et al., 2013). These discoveries culminated in significant updates to the classification in *Systema Porifera*, following the revision by Morrow and Cárdenas (2015). This revision led to the abandonment of seven orders, the resurrection or upgrade of six, and the creation of seven new orders, bringing the total number of orders to 22. The class Homoscleromorpha was also formally recognized, alongside a host of other minor changes.

Both mitochondrial DNA (mtDNA) gene cytochrome oxidase subunit 1 (CO1) and the structural ribosomal RNA for the large subunit gene of eukaryotic cytoplasmic ribosomes (28S rRNA) are used as barcodes for sponges, and both can be effective for sponge identification. However, while CO1 is the most commonly used region for amplifying genetic material in metazoans (Hebert et al., 2003), it often performs poorly in sponges (Vargas et al., 2012). This is especially true in Calcarea, where high nucleotide substitution rates hinder the amplification of target mtDNA regions (Lavrov et al., 2013), and in Demospongiae, where it can be too conserved at the species level due to slow evolutionary rates (Erpenbeck et al., 2006; Pöppe et al., 2010). On the other hand, the 28S rRNA region does not have the same limitations as CO1 and offers sufficient variability to provide higher taxonomic resolution within Porifera (Voigt & Wörheide, 2016; Martineau et al., 2024).

(c) Obstacles

Currently, there are 9,455 species of sponges accepted in the World Porifera Database (de Voogd et al., 2025), yet only a fraction of these have been sequenced (Benson et al., 2009), and over 25,000 species are estimated to exist (Appeltans et al., 2012). The revision of higher taxa classification was possible with limited genetic material, but genus-level systematics remain largely uncertain for several groups (e.g., Please et al., 2021; Turner et al., 2024; Leal et al., 2025). This is because, although the integrative approach, combining morphological and molecular data, has significantly improved the classification of sponges, particularly in more challenging taxa (Cárdenas et al., 2012; Boury-Esnault et al., 2013), it is also demanding in terms of both time and cost. This is partly due to the relatively low success of sponge barcoding and the high abundance and diversity of associated microorganisms. These microorganisms can lead to the co-extraction and amplification of non-target DNA, complicating the interpretation of sequences or misattributing them to non-target species (Vargas et al., 2012). Additionally, expert sponge taxonomists are often required to validate results, and such experts are not always readily available (Wägele et al., 2011). While integrative taxonomy is the most reliable method to establish a classification system for Porifera, it slows the rate at which our knowledge of sponges expands. This presents a challenge, especially given the urgency imposed by climate change, which is one of the reasons why addressing sponges in functional groups has been suggested, particularly for environmental studies (Schönberg, 2021).

(d) Note on Halichondriidae and Suberitida

Until the revision by Morrow and Cárdenas in 2015, the family Halichondriidae was part of the order Halichondria. This order was primarily based on shared negative characters, as there were no clear synapomorphies to define the group, which is reflected in its complex history (see Erpenbeck et al., 2012 for a comprehensive review). The fact that the group was never recovered as monophyletic in several molecular studies (e.g., Morrow et al., 2012; Erpenbeck et al., 2012) confirmed that it was phylogenetically incorrect, leading to its abandonment (Morrow & Cárdenas, 2015). On the other hand, these studies also highlighted the close relationship between Halichondriidae and Suberitidae within the order. The establishment of this clade had been previously proposed by Chombard and Boury-Esnault (1999), and it was finally formalized as the order Suberitida, which also includes Stylocordylidae according to other genetic studies (Morrow & Cárdenas, 2015).

1.2 Marine introduced species

1.2.1 Pathways and implications

Terms like introduced, non-native, alien, and exotic all refer to species that occur outside their natural range (Walther et al., 2009). Currently, the World Register of Introduced Marine Species (WRiMS) lists nearly 3,000 accepted marine introduced species (Costello et al., 2025), which can be found across all phyla, habitat types, and geographical regions (Costello et al., 2021). Most species are introduced unintentionally, which is why the exact origin or dispersal method of these species is often unclear (Alidoost Salimi et al., 2021). However, the majority of introductions are attributed to international shipping, primarily through two pathways: biofouling and ballast water exchange (Molnar et al., 2008). Incrusting organisms such as algae, sponges, bivalves, cirripedes, ascidians, most cnidarians, and associated fauna can form communities on vessel hulls, allowing them to be transported between ports (Lewis & Coutts, 2009; Shevalkar et al., 2020). On the other hand, pelagic organisms and larvae can be carried in the ballast water of cargo ships, which adjust their ballast to maintain stability according to cargo specifications (Bailey et al., 2015; Saglam et al., 2018). Another common pathway is aquaculture, where species are intentionally introduced to new locations, and, due to insufficient preventive measures, both the target species and associated organisms may be accidentally released into local environments (Naylor et al., 2001). Occasionally, species are dispersed through the aquarium hobby, as seen with the notorious lionfish *Pterois volitans* (Padilla et al., 2004; Walters et al., 2011).

The number of times alien species are introduced to non-native regions far exceeds the number of times they actually succeed in establishing themselves (Williamson et al., 1996). This is because these species must contend with the environmental pressures of fully developed ecosystems with which they did not co-evolve and for which they have no adapted life strategies (Kennedy et al., 2002; Sax et al., 2005). The species that succeed are typically generalists that can tolerate a wide range of environmental conditions, have efficient reproduction, and possess fast dispersal strategies (Geburzi et al., 2018). These species can become invasive if they spread aggressively or negatively impact the ecosystem (Ricciardi, 2012). The effects of such invasions can be numerous, including outcompeting native species, disrupting community dynamics and food chains, causing economic harm by reducing fishery yields and damaging ship hulls, and altering essential processes like nutrient cycling (Bax et al., 2003; Lovell et al., 2006; Molnar et al., 2008). Consequently, marine invasions are the second leading cause of biodiversity loss in the world’s oceans (Blakeslee et al., 2010), and this relatively small group of species has already significantly altered multiple marine ecosystems globally (Gallardo et al., 2016).

1.2.2 Introduced sponges

Porifera has largely been overlooked in the study of marine introduced species, primarily due to the incomplete knowledge of their natural ranges and the taxonomic challenges previously discussed (Turner, 2020; Alidoost et al., 2021). Compared to other marine organisms, sponges generally have very limited natural dispersal capabilities. Their larvae lack effective swimming mechanisms and are short-lived, surviving only minutes to a few days, as they can only feed after settlement (Maldonado, 2006). Similarly, their asexual propagules typically settle close to the parent sponge (Blanquer et al., 2009). Since sponges cannot travel long distances on their own, natural dispersal to new regions is highly unlikely, raising questions about species with widespread geographic distributions (Carballo et al., 2013).

Despite these limitations, the review of Alidoost et al. (2021) identified 34 sponge species as introduced in tropical regions, although the World Register of Introduced Marine Species (WRiMS) currently recognizes only 31 (Costello et al., 2025). The introduction pathway is known for only about 40% of these species, while the rest are attributed to shipping activity (Alidoost et al., 2021). This aligns with expectations, as the aquaculture and aquarium trade for sponges is minimal. However, it should be noted that while sponges are not commercially cultivated, they have been documented using oyster farms in colder waters as dispersal vectors (Henkel & Janussen, 2011; Fuller & Hughey, 2013). Ballast water exchange between nearby ports could facilitate sponge transport, but long-distance dispersal via this method is less likely due to the limitations of larvae (Mariani et al., 2006). In most cases, introduced sponges are believed to reach new locations through vessel biofouling, later dispersing once they establish themselves in a new harbor (Davidson et al., 2014).

1.2.3 Hawaii and the case of *Mycale grandis*

The Hawaiian Archipelago is a chain of 137 islands, atolls, and seamounts stretching over 2,500 km in the central Pacific Ocean, approximately 3,850 km from California and 6,200 km from Japan. The islands are entirely of volcanic origin, formed by an intraplate thermal hotspot. As a result, the Big Island of Hawaiʻi is geologically young, at around 500,000 years old, while the northernmost atolls are over 28 million years old (Spalding et al., 2019). Approximately 60% of Hawaiʻi's shoreline is bordered by coral reefs, which support what is possibly the highest level of endemism of any shallow-water tropical ecosystem on Earth (Fautin et al., 2010; Spalding et al., 2019). However, the combination of a relatively young, fragile, and isolated ecosystem with ever-increasing shipping traffic has led Hawaiʻi to have one of the highest numbers of introduced marine species (Carlton & Eldredge, 2009, 2015), a pattern also observed in Porifera. Of the 34 introduced sponge species reviewed by Alidoost et al. (2021), 24 have been reported from Hawaiʻi.

While most of these species have yet to show a clear negative impact on Hawaiian reefs, *Mycale grandis* stands out as an aggressive non-native sponge and a major threat to native corals (Coles & Bolick, 2007). This species forms thick encrustations and can reach up to 1 m in diameter. Native to Australia, Indonesia, Malaysia, and India, *M. grandis* was first reported in Pearl Harbor, Hawaiʻi, in 1996, likely introduced via biofouling on ships' hulls (Coles et al., 1997; Coles, 2007). Since then, it has spread across several areas of the archipelago, particularly in degraded habitats with high nutrient loads, such as the south basin of Kāneʻohe Bay, where it overgrows native reef-building corals like *Montipora capitata* and *Porites compressa* (Coles et al., 2007). The sponge significantly increased in biomass and expanded its distribution, particularly during the mid-2000s, and is now firmly established as a prominent member of affected regions. Its coverage ranges from 2.1% on fringing reefs to 32.3% in mangrove areas near Coconut Island in Kāneʻohe Bay (Coles & Bolick, 2007; Shih, 2018). Shin & Popp (2020) found that, in this bay, *M. grandis* cycles a substantial portion of the water column, potentially influencing local water biochemistry and Vicente et al. (2015) predicted that its survival rates will remain unaffected by future climate change scenarios. Efforts to control *M. grandis* have included both mechanical removal and compressed air injection, which have provided some level of population control. However, complete eradication has proven unfeasible due to rapid regrowth, high costs, and the labor-intensive nature of these methods (Coles et al., 2007).

1.3 Importance of this study

In this work, we report a new record of an introduced boring sponge for the Hawaiian archipelago, currently only detected in Kāneʻohe Bay, Oʻahu. Over the years, multiple non-native sponges have been recorded in this bay (O'Connor et al., 2008; Carlton & Eldredge, 2009, 2015; Pons et al., 2017), yet little attention has been given to them. More recently, several other species have been found following the work of Vicente et al. (2022). So why dedicate a thesis to this species alone?

Unlike most other introduced sponge species in Hawaiʻi, the ecological impact of this sponge was evident from the moment it was first detected, as it actively overgrows the two main reef-building corals of Kāneʻohe Bay: *M. capitata* and *P. compressa*. Upon closer inspection, it became clear that the sponge was not only overgrowing but also bioeroding the coral skeleton. As previously discussed, two major groups of sponges that are increasing in abundance and negatively affecting marine ecosystems are (1) boring sponges, whose activity is being amplified by climate change, and (2) introduced sponges, spread by today's intense global boat traffic. This species belongs to both groups.

Additionally, Kāneʻohe Bay, as a semi-enclosed system largely separated from the open ocean, has recorded water parameters resembling future climate scenarios, including higher water temperatures and eutrophication events (Jokeil et al., 1993; Bathen, 1968; Bahr et al., 2015). At the same time, the potential impact of non-native sponges in the bay has already been acknowledged, particularly following the case of *M. grandis*.

Beyond the intrinsic value of Hawai‘i’s native fauna, much of which found nowhere else, these reefs hold immense economic importance through tourism, fishing, or education (Cesar & van Beukering, 2004), as well as deep cultural significance for Native Hawaiian knowledge (Gregg et al., 2015). The combination of ecological, economic and cultural importance of these reefs with the threat posed by this new species makes its identification a priority. This study provides such identification as well as a preliminary assessment of its origins and potential impacts, laying the groundwork for future in-depth research and, hopefully, effective management strategies.

Finally, this case also presented an opportunity to conduct a taxonomic review of the species, previously suggested as necessary by other researchers (Carvalho et al., 2004), and to demonstrate that identifying challenging species requires integrative approaches.

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Part 2. MANUSCRIPT

New record of the coral-boring sponge *Amorphinopsis* cf. *excavans* in Kāne‘ohe Bay, Hawai‘i

Author: João Diogo Pontes

Affiliation: Universidade do Algarve

Contact email: a78849@ualg.pt

Keywords

Non-indigenous; Excavating sponge;
Molecular Phylogeny; Taxonomy

2.1 Abstract

The Hawaiian archipelago is currently recognized as a hub of species introductions. In Kāne‘ohe Bay, several marine alien species have been reported over the last decades, including sponges, which benefit from its nutrient-rich waters. Here we report the presence and the coral-excavating habit of the Indo-Pacific sponge *Amorphinopsis* cf. *excavans* in the bay. A thorough traditional taxonomic assessment is performed, along with a genetic analysis of both ribosomal and mitochondrial genes, revealing the identity of the sponge. The results underscore the polyphyletic nature of the genus and highlight the need for an integrative approach to resolve its phylogenetic framework. Existing literature on *A. excavans* and its extended distribution range justify its classification as a species complex until further clarification. Limited dispersal capabilities of sponge larvae and the species’ encrusting ability suggest an introduction by integrating the fouling community of trans-Pacific vessels. The sponge is actively boring into the two primary reef-building species of coral in the bay - *Montipora capitata* and *Porites compressa*, therefore posing a significant environmental threat to Hawai‘i’s native ecosystem. Considering the expected increase in bioeroding sponges under future climate change scenarios, the development of management strategies is advised.

2.2 Introduction

Hawaiʻi is the most isolated archipelago in the world (Gillespie & Baldwin, 2009), and exhibits high endemism of marine species (Eldredge & Evenhuis, 2003; Kane et al., 2014). However, as the only developed landmass in the center of the largest ocean on the planet, Hawaiʻi is also the "cross-roads" of the Pacific maritime shipping traffic (Carlton, 1994; Godwin, 2003). While the native species of the archipelago are the result of slow and sporadic colonization events through natural dispersal mechanisms (Kay et al., 1987; Bowen et al., 2020), commercial shipping has been known to introduce nonindigenous marine species to the Hawaiian Islands (Coles et al., 2002). Such introductions possess a threat not only to autochthonous species, but to the resilience of the Hawaiian underwater ecosystems.

Sponges (Porifera) play several important functional roles on coral reefs and are therefore vital components of these ecosystems (Diaz et al., 2001; Bell, 2008). However, they are also one of the most successful phyla of marine introduced biota. Their primitive structural features and their simple life strategies enable them to easily adapt to new environmental conditions, sometimes outcompeting native species (van Soest et al., 2012). Most sponge species have a very limited dispersal capacity, given the short planktonic phase of their larvae (Maldonado, 2006). Ocean currents can be a viable route for species dispersal between habitats in proximity (Mariani et al., 2006), but given the remarkably isolated position of Hawaiʻi, many of its emergent and reef-surface dwelling sponge species within harbors are believed to have been artificially introduced (Carlton & Eldredge, 2015). As filter feeders, sponges can establish and thrive in shipping ports, where organic matter is usually abundant given the exposure to terrestrial sources of organic matter from river runoff, confinement from the open ocean and long residence time of the water (Paulay et al., 1997; Kelly et al., 2003; Lau and Mink, 2006). Harbors and shipping ports can then act as distribution points of alien sponge species to other parts of the world, including Hawaiʻi, either by ballast water exchange containing larvae, upon arrival to new ports (Coles et al., 1999), or, and most commonly, by integrating the marine fouling community of the ships (Godwin, 2003). In Hawaiʻi, hull fouling is thought to be the vector for the initial introduction of close to 100% of documented non-native sponge species (Davidson et al. 2014).

In Oʻahu, the entrance point of most nonnative sponge species are Honolulu Harbor, Pearl Harbor, and Barber's Point Harbor (Godwin, 2003). After colonization, sponges can then easily disperse to other nearby harbors such as Kāne‘ohe Bay, through artificial vectors like recreational vessels that may also transport biofouling invertebrates (Leonard, 2009). With an area of approximately 45 km^2, Kāne‘ohe Bay is the largest body of sheltered water in the entire archipelago, where an offshore coral barrier protects the shallow reef systems of the bay from strong open ocean energy (Jokiel, 1991). While this protection may be what fostered the development of the thriving marine ecosystem that characterizes the bay today, it also resulted in extended water residence times, reaching up to two months in its most southern region (Lowe et al., 2009). The supply of nutrients from stream runoff and the continuous production of organic matter by a developed reef system, combined with slow water renewal and almost inexistent wave action, create a protected nutrient rich environment that provides the right set of conditions for the success of sponges. The high traffic of recreational vessels, and the fact that it is one of the most extensively studied coral reef systems in world (Bahr et al., 2015), make it unsurprising that Kāne‘ohe Bay has one of the highest percentages of recorded non-indigenous marine fauna of any region in Hawai‘i, many of which are sponges (Coles et al., 2002).

In coral reefs there is strong competition for space between sponges and corals (van Soest et al., 2012). While most corals have various sets of chemical defense mechanisms (Lang & Chornesky 1990), many sponge species are still capable of overgrowing and further excavating their skeletons (eg. Vicente, 1990; López-Victoria & Zea, 2005; Márquez et al., 2016). A large part of reef bioerosion in coral reefs is carried out by these sponges (Schönberg et al., 2017b), which is an important process within these ecosystems since it helps reshape the reef’s structure and boosts the marine calcium carbonate ($CaCO_3$) cycle (Bell, 2008). However, reef bioerosion works in a delicate dynamic balance with reef accretion (Glynn, 1997). If introduced in a nonnative community, with no natural mechanisms of control, excavating sponges can tip the balance, increasing in abundance at the cost of coral loss (Wulff, 2012). Besides displacing native species, these bioeroders don’t provide the same set of ecological functions, particularly in habitat building, and contribute to the disintegration of the reef framework (Schönberg et al., 2017b). The negative impacts of sponge overgrowth have been documented on several occasions within other coral reefs of the world (see Table 1 in Ashok et al., 2020 for examples), including alien species. For example, the invasive sponges *Terpios hoshinota* and *Chalinula nematifera*, often referred as “coral-killing” sponges, have overgrown various coral species and caused multiple outbreaks in non-native regions over the past decades. (Ávila & Carballo, 2009; Elliott et al., 2016; Fiedler et al., 2024).

Between 1950–2020 approximately 50 species of sponge were identified in Kāneʻohe Bay (De Laubenfels, 1950, 1951, 1954, 1957; Bergquist, 1967, Pons et al., 2017). Many of these records are considered non-indigenous artificial introductions (Coles et al., 2002), including *Mycale grandis*, a species native to Australia and the Indo-Pacific, first reported in the bay in the late 1990s, and currently considered the most widespread introduced sponge in Hawaiʻi (Coles & Bolick, 2007; Shih & Popp, 2020). Recent efforts targeting both emergent and cryptobenthic sponges showed that sponge diversity has been grossly underestimated, adding 142 new species records for the bay only (Vicente et al., 2022). However, the classification of species from Vicente et al. (2022) was based on operational taxonomic units (OTUs) identified by a limited taxonomic assessment using spicule composition and sequence barcoding. Here, we present not only the missing pieces for a full integrative classification of the taxon classified as *Amorphinopsis* sp. 1 in that work, through paratype sampling, histology, barcoding of paratypes and a comparative analysis with other congeners in the literature, but also document a new record of a bioeroding sponge with invasive potential for Kāneʻohe Bay and Hawaiʻi, found to be excavating *Montipora capitata* and *Porites compressa*, the two primary reef-building species of coral in the bay.

2.3 Materials and Methods

2.3.1 Sample collection

One sample was collected on November 2018 (for BKON_2782) and four were collected on December 2023 with a small knife while freediving on an adjacent patch reef slope on the South side of Moku o Loʻe (Coconut Island), and a patch reef slope (up to 5 m deep) close to the Yacht Club in South Kāneʻohe Bay on the island of Oʻahu, Hawaiʻi (Fig. 2.1).

Samples were stored in whirl paks © until further processing in the lab. In situ photos of the surrounding reef environment and of sponges were taken prior to collection, insuring good representation of the morphological features from undisturbed specimens. Observations of the color, consistency, surface and general morphology were recorded, along with the attached substrate. The samples were then fixed in ethanol (95%) and RNA later. Ethanol was replaced 48h and 96h after storing. All samples were collected under special activities collection permit (SAP) nos. 2019–03 and SAP 2024-45 covering the period of January 13, 2018 through April

10, 2019 and June 20, 2023 through June 19, 2024 respectively. Samples have been deposited at the Bernice Pauahi Bishop Museum (catalog number beginning with acronym BPBM) in Oʻahu, USA and at the Florida Museum of Natural History (catalog number beginning with acronym UF) in Florida, USA.

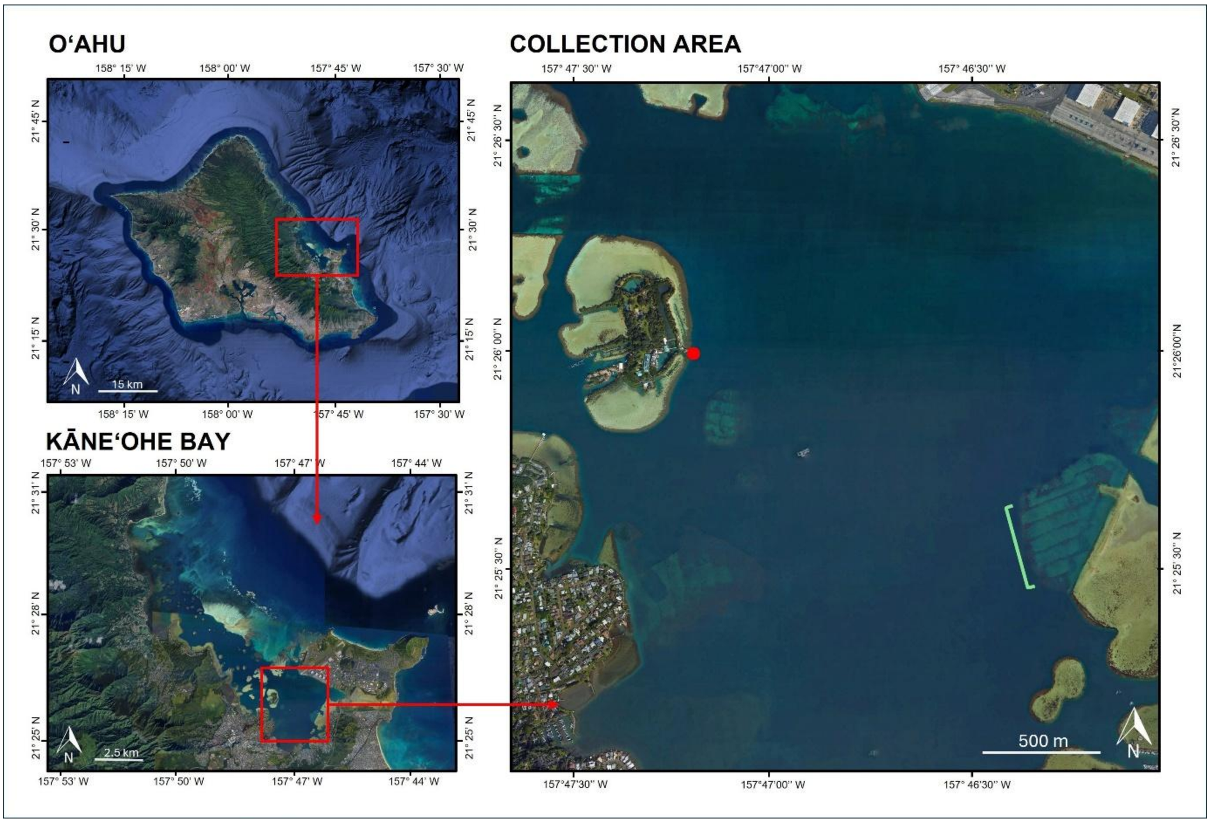

Figure 2.1. *Satellite image of the southeast end of O'ahu, Kāne'ohe Bay, and collection area (south portion of Kāne'ohe Bay). Moku o Lo'e (Coconut Island) on the top left corner of the collection area and collection sites in red for BPBM C1880 and green for the remaining samples. Image obtained using Google Earth Pro, © Google, Data © 2024.*

2.3.2 DNA extraction and sequencing

Small subsamples with no visible signs of infaunal organisms were removed from each sponge sample preserved in RNA later and processed for DNA extraction with the E-Z 96 Tissue DNA Kit (Promega Bio-Tek, Norcross, GA, USA) following the manual's protocol.

DNA amplification was performed for both the 28S rDNA D-Region and Folmer (5') region of the COI gene. The primers used to amplify each gene region are presented in Table 2.1. The Polymerase chain reactions (PCRs) were performed in thermal cyclers with a 39.2µL cocktail consisting of 20 µL of GoTaq® Green Master Mix; 14.4 µL of H2O; 3.2 µm of bovine serum albumin (BSA) (100 mg/mL); 0.8 µL of each primer (10 mM) and 0.8 µL of sample DNA (1–30 ng/µL). PCR products were visualized on 1% agarose gels stained with GelRed that were ran at 70 mV, 180 mA for 50 min. If strong bands with the correct size product were visible on the Gel imager, a second electrophoresis was performed with the PCR products on a 2% agarose gel made with 1 x modified (no EDTA) TAE and ran at 50 mV, 180 mA and for 90 min. The resulting bands were excised by hand from the gel using a UV transilluminator, and centrifuged through a custom-made column filter at 5,000 rpm for 10 min.

The PCR was started by the denaturation of the DNA strands at 94°C for 3 min, followed by 34 cycles of denaturation (94°C for 30 s), annealing (45°C for 20 s) and extension (72°C for 1 min). The final extension was 8 min, after which the finished product was maintained at 12°C in the thermal cycler. The annealing time was extended to 45 s for the LSU300F/LSU1200R, LSU900F/LSU1642R, and dgLCO1490/ dgHCO2198 primers; and to 80 seconds for the LCO1490 forward and COX1-R1 reverse primers. Separate sequencing reactions were performed using both primer directions on an ABI Prism 3730 XL automated sequencer using the Big Dye TM terminator v. 3.1 at the University of Hawaiʻi Advanced Studies of Genomics, Proteomics and Bioinformatics sequencing facility.

Table 2.1*- Primers used for DNA sequencing.*

	Primers	*5'- 3' Sequence*	*Reference*
28S (C2 – D2 region)	C2 FWD	GAAAAGAACTTTGRARAGAGAGT	Chombard et al. 1998
	D2 RV	TCCGTGTTTCAAGACGGG	
28S (D2 region)	LSU300F	CAAGTACCGTGAGGGAAAGTT	Olsen (NHM London,Pers. Comm)
	LSU1200R	GCATAGTTCACCATCTTTCGG	
28S (D3 – D5 region)	LSU900F	CCGTCTTGAAACACGGACCAA	Olsen (NHM London,Pers. Comm)
	LSU1642R	CCAGCGCCATCCATTTTC	
CO1	dgLCO1490	GGTCAACAAATCATAAAGAYATYGG	Meyer, Geller & Paulay, 2005
	dgHCO2198	TAAACTTCAGGGTGACCAAARAAYCA	
CO1	LCO1490 FWD	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994); Rot et al., 2006
	COX1-R1 REV	GCGACTACATAATAAGTRTCRTG	

2.3.3 Phylogenetic analysis

Forward and reverse reads were assembled, trimmed, and edited by eye using Geneious 6.1.8 (Kearse et al., 2012). Sequences were checked for contamination using the online BLAST server (Altschul et al., 1990). Results that showed at least 90% sequence identity to sponges were aligned using the ClustalW with default parameters. The sequences of both 28S and CO1 were later separated into two sections given the lack of continuity between all sequences of interest available in GenBank, resulting in four phylogenic trees. Alignments consisted of 425 bp and 269 bp for 28S, and 496 bp and 409 bp for CO1. RaxML (Stamatakis, 2006) included in Geneious 10 was used for maximum likelihood (ML) analysis with the GTR+GAMMA model of nucleotide substitution, 100 starting maximum parsimony trees, and 1.000 bootstrap replicates. Resulting bootstrap values of >50 from the ML posterior probabilities are shown on the tree. The phylogenetic trees for 28S were both rooted on *Tethya seychellensis* (KC869475), and CO1 trees were rooted on *Tethya coccinea* (JQ034584) and *Liosina paradoxa* (AY625663). Only sequences linked to taxonomic work were used in the analysis.

2.3.4 Sectioning and spicule preparation

Sponge pieces (3–5 mm^3) containing both ectosomal and choanosomal tissue were cut, placed inside small disposable cassettes, and dehydrated in an automated tissue-transfer processing machine, following a series of 35%, 50%, 70%, and 100% ethanol concentrations. Each sample was then embedded in paraffin, making sure that the surface of the ectosome (in the samples representing this tissue) was facing the cutting section of the wax block. Using a microtome, transversal sections (~300 µm thick) were cut from each sample. Several sections of the choanosome tissue were made and 2 to 3 mostly intact sections were mounted on histology slides. Only 1-2 sections for the ectosomal tissue were mounted. Paraffin was removed from the section by melting in an incubator at 60 °C followed by a hot plate and a final wash with xylene. When the tissue was dry and free of wax, Permount mounting medium and a cover slip was placed over the slide while ensuring no bubbles were present inside the sample. The drying process of each plate took a few days and more medium was added around the edges of the slide as the mounting medium dried and no bubbles were observed between the cover slip and slide.

For spicule preparation, small subsamples were removed from each specimen and dissolved in household bleach (5 – 6 % sodium hypochlorite solution), leaving only the spicules. Samples imaged with SEM (Scanning Electron Microscopy) were also boiled in nitric acid for 1–2 min or until the solution turned clear. The supernatants were discarded, and spicules were rinsed with distilled water three times to remove all the bleach or acid. On the last change the supernatant was replaced by 95% ethanol for storage. The spicules were resuspended, and some drops were mounted and observed under light microscopy, photographed at different magnifications with a digital camera, and measured using ImageJ (Abràmoff et al. 2004) http://imagej.nih.gov/ij/). The length and the width of 30 oxeas and 30 styles were measured, expressed as minimum–mean [±1 standard deviation (SD)]-maximum length / width in µm. For SEM, black double sided adhesive carbon tape was added on the top of metal stubs and a circular (18 mm diameter) cover slip was placed on the other side of the adhesive tape followed by a drop of the cleaned spicule suspension. Samples were then left to air dry. The procedure was repeated for 2 additional replicates. The stubs were then brought to the Biological Electron Microscope Facility at the University of Hawaiʻi Mānoa, where they were first coated with argon in a Hummer 6.2 Sputter Coater and then imaged under a S-4800 Field Emission Scanning Electron Microscope. Clean and isolated spicules were selected at maximum resolution for both spicule types representing different size ranges.

2.4 Results

2.4.1 Systematic Description

Phylum Porifera Grant, 1836
Class Demospongiae Sollas, 1885
Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012
Order Suberitida Chombard & Boury-Esnault, 1999
Family Halichondriidae Gray, 1867
Genus *Amorphinopsis* Carter, 1887

Amorphinopsis* cf. *excavans
(Figures 2.2 & 2.3, Table 2.2)
Amorphinopsis sp.1 in Vicente et al., 2022b

Synonyms and References.
Spongosorites sp. – Sewell, 1913: 346
Amorphinopsis excavans var. *digitifera* - Annandale, 1915: 469, Fig. 5 pl. XXXIV; Kumar, 1925: 225

Amorphinopsis excavans var. *robinsonii* - Annandale, 1918: 198, Plate II, fig. 3; plate IX, fig. 1
Amorphinopsis excavans – Carter 1887: 77, Plate V, figs. 12-15; Thomas, 1973: 58, Plate III, Fig. 8; Thomas, 1985: 316, Plate VI, Fig 9; Thomas et al., 1996: 132; Hooper, 1997: 25, Figs. 15-16; Hooper & Van Soest, 2002: 790, Figs 1A-D; Lim et al., 2008: 115; Alvarez & Hooper, 2011 57, Figs 1A, 2;
Amorphinopsis sp.1 – Vicente et al., 2022b: Fig. 5

Type locality. King Island, Mergui archipelago, Andaman Sea Coral Coast

Material examined. BPBM C1895, BPBM C1899, BPBM C1900, BPBM C1901 Patch reef south of Kāneʻohe Bay, Oʻahu (21°25'12.9"N 157°46'20.7"W); 1– 3 m, coll. Jan Vicente, 2024-12-11. **BPBM C1880** Fringing reef on south side of Moku O Loʻe **(**21°43'35"N 157°78'64"W); 3 m, coll. Jan Vicente, 2018-11-16.

2.4.2 Description (Fig. 2.2)

Laminar, thickly encrusting (2 mm to 6 cm thick) or slightly massive, spreading laterally (up to 30 cm wide). Sponge is firm but is compressible and can be torn easily. Surface smooth and mostly even but can have dispersed oval oscules (1-4 mm in diameter), which can also be clustered (Fig. 2.2, F). Oscules did not contract in spirit. Oscula were absent when sponges exhibited laminar morphology. The sponge surface is greyish or bluish green in live specimens growing on the reef surface and can be brownish yellow when growing in shaded habitats (Fig. 2.2, G & H). The tissue from the sponge interior is also yellow (Fig. 2.2, I-K). In spirit the skeleton becomes uniformly grey. When laminar, the sponge tissue simply overgrows coral (Fig. 2.2, J), more developed stages spread into the interior of the coral skeleton (Fig. 2.2, I & K).

2.4.3 Spicules (Fig. 2.3, A-E)

Oxeas fusiform, smooth, acerate, uniformly curved or slightly angulated in the center, and in a large range of sizes (166-450-771µm x 6-13-18µm). Styles smaller, slightly curved, blunt rounded end tapering to a sharp tip, in a narrower range of sizes (112-155-227.5µm x 3.8-6-8.9 µm). Styles are almost always smaller than oxeas. Oxeas are observed more frequently than styles. Measurements for individual specimens are given in Table 2.2.

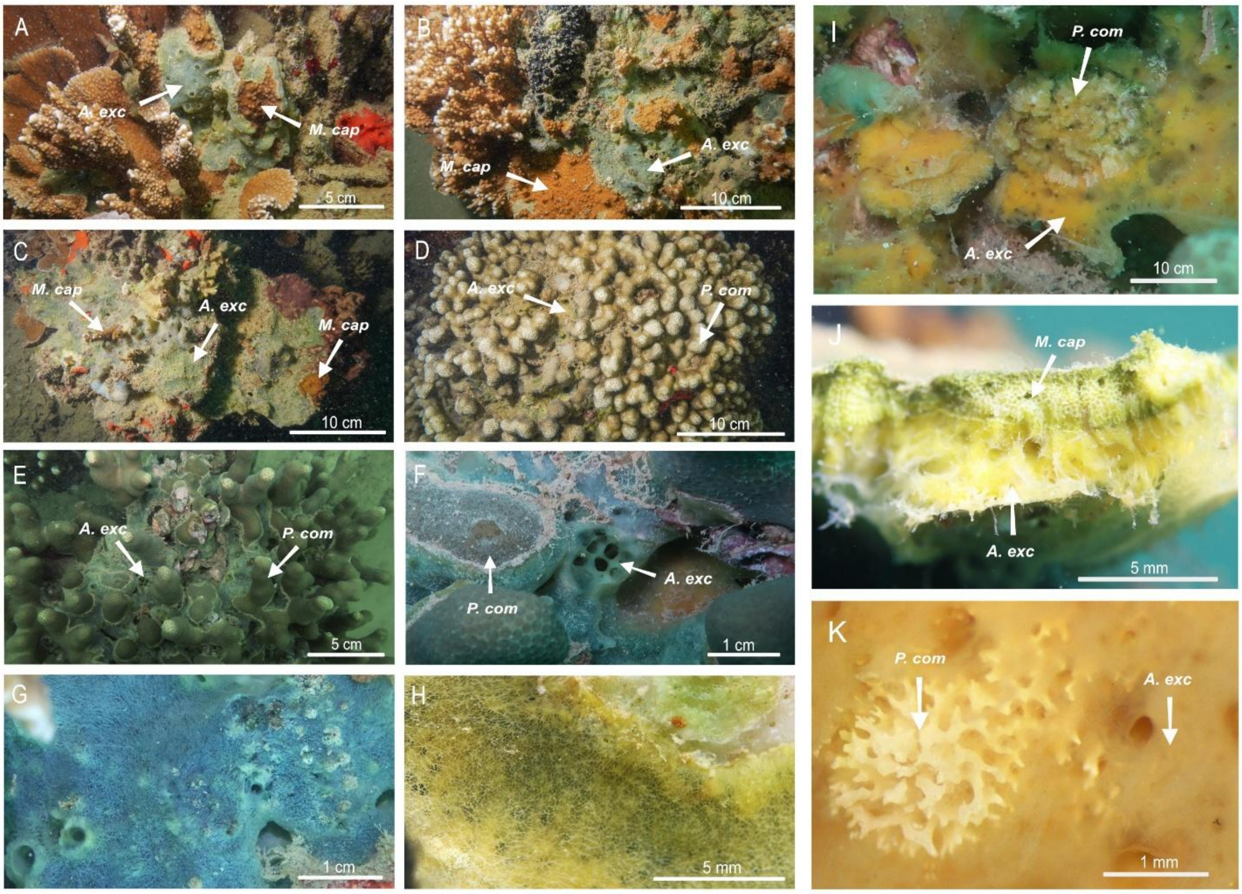

***Figure 2.2**. In situ images of the collected specimens: A, BPBM C1900; B, BPBM C1901; C, BPBM C1899; D, BPBM C1895; E, BPBM C1880. Specimens A-C overgrowing Montipora capitata, specimens D & E overgrowing Porites compressa. F, cluster of oscules. G & H, close-up on the surface of specimens when exposed to light (G) or in shade/interior of sponge (H). I, boring activity inside P. compressa skeleton. J, sponge overgrowing M. capitata in a thin layer; K, sponge boring M. capitata skeleton. Arrows in figures pointing to Amorphinopsis cf. excavans (A.exc); M. capitata (M. cap); P. compressa (P.com).*

Table 2.2. *Spicule measurements of oxeas and styles for Amorphinopsis* cf. *excavans. Measurements are shown as minimum–mean (±1 standard deviation)–maximum. N=30 for oxeas and N=30 for styles.*

Voucher	**Oxeas**		**Styles**	
	Length (µm)	**Width (µm)**	**Length (µm)**	**Width (µm)**
BPBM C1880	200.0-(373.1±116.8)-548.4	6.3-(10.2±2.4)-16.0	111.7-(152.0±25.7)-204.6	5.0-(6.3±1.0)-8.6
BPBM C1895	165.7-(345.9±108.9)-526.9	6.06-(11.2±3.7)-19.1	126.1-(154.6±17.7)-182.3	4.4-(6.3±1.0)-8.6
BPBM C1899	279.7-(523.4±105.3)-771.1	6.897-(13.1±3.2)-18.9	112.2-(155.4±23.2)-203.9	5.0-(6.7±1.1)-8.9
BPBM C1900	281.3-(480.2±87.7)-597.3	7.2-(13.2±3)-18.3	113.3-(150.2±20.6)-217.5	3.8-(5.5±0.8)-8.1
BPBM C1901	221.4-(452.1±142.6)-753.5	7.3-(12.6±3.4)-18.7	120.1-(159.6±21.6)-227.5	5.0-(6.3±0.7)-7.7

2.4.4 Skeleton (Fig. 2.3, F-H)

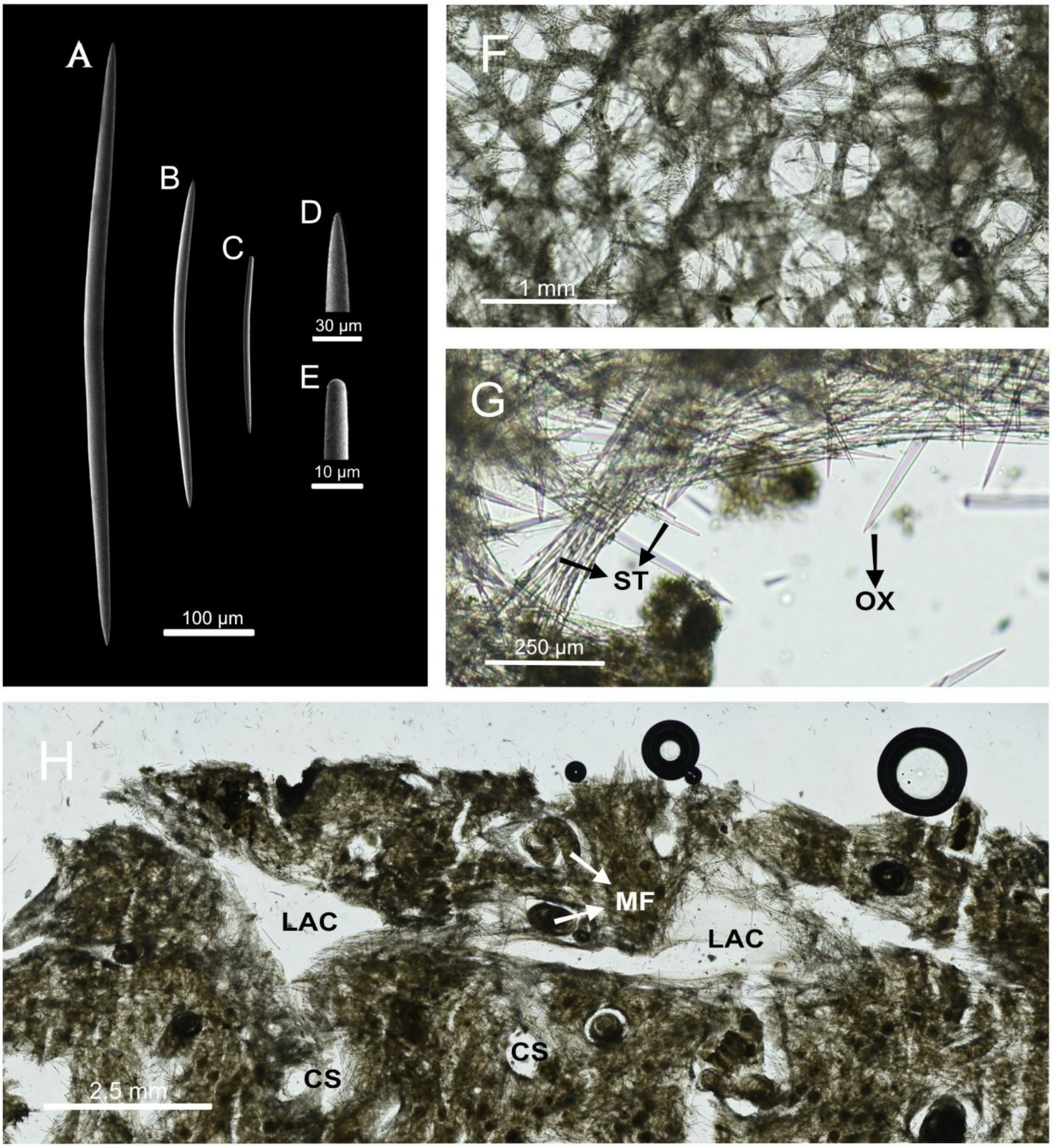

Figure 2.3. *Skeleton and spicule composition of collected specimens. A-E SEM of spicules; A & B, oxeas in two different sizes; C, style; D, close-up of oxea acerate ends; E, close-up of style blunt end. F-G, tangential sections of the ectosomal skeleton, highlighting tracts made mostly of styles (st) with protruding large oxeas (ox); H, cross section of choanosome, highlighting lacunae (lac), choanosomal spaces (cs), and associated microfauna (mf).*

Ectosomal skeleton (100 µm thick) detachable (Fig. 2.3, F) composed mainly of styles (Fig. 2.3, G, st), with small oxeas occasionally complementing, oriented in thin rather well-defined tracts, and sporadically protruded by larger oxeas (Fig. 2.3, G, ox). The tracts are united by bundles of less organized megascleres and create a structured mesh with numerous regular small spaces free of spicules (100–200 μm in diameter) (Fig. 2.3, F). The regular arrangement of spicule tracts is clear on the surface. In most cases the ectosome is slightly raised in the outline of oscules. Spicules close to the surface layer are mostly paratangential. Choanosomal skeleton (Fig. 2.3, H) is composed mainly of larger oxeas, with oxeas and occasional styles of smaller size filling in the gaps. Tracts are more scarce and less delimited, overlayed by large meshes of confused reticulation of intercrossing spicules and collagenous material. The ducts are more occasional and wider (diameter >300 μm), often leading to large lacunae up to 1mm wide (Fig. 2.3, H; lac). Numerous sections of associated microfauna can be found in the mesohyl, incorporated in the dense collagenous material (Fig. 2.3, H, mf). No spongin is present.

2.4.5 Distribution

Adaman Sea Coral Coast (Carter, 1887; Annadale, 1915); Malacca Strait (Annadale, 1918); East, South and Western India (Kumar, 1925; Thomas, 1972; Thomas, 1996), Seychelles (Thomas, 1973), Sri Lanka (Thomas, 1972); Singapore (Lim et al., 2008, 2009); Northern Australia (Bonaparte Coast) (Alvarez & Hooper, 2011).

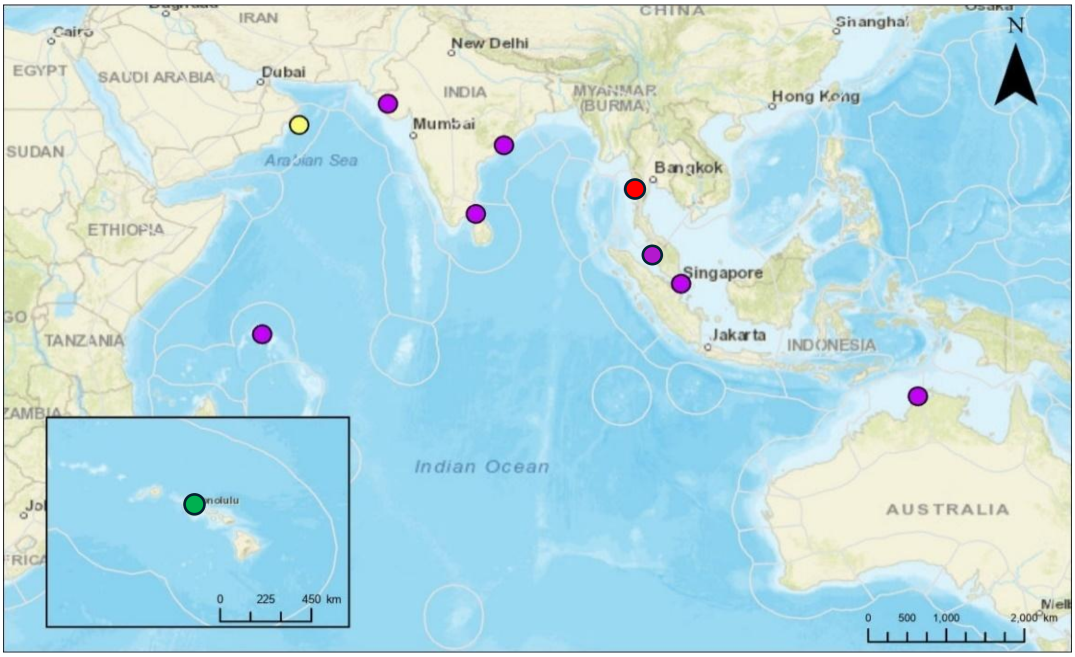

Figure 2.4. Documented distribution of Amorphinopsis excavans. Red mark represents type locality; purple marks represent the distribution available in World Porifera database without available DNA sequences; yellow circle represents specimens with sequence data used in phylogeny (AY319313 & AF437297); and green circle represents the new material collected in Hawai'i. The exact GPS coordinates were not available for all locations, therefore some circles show an approximate location.

2.4.6 Habitat and Ecology.

Found on live or dead coral skeleton, either encrusting or bioeroding. The specimens described here were all found overgrowing live coral colonies of either *Porites compressa* or *Montipora capitata* in shallow reef habitats of Kāneʻohe Bay.

2.4.7 Taxonomic remarks

The order Suberitida is composed of three families. The members of the family Stylocordylidae are easily distinguishable from the current material given their unique club-shaped morphology and that they are confined to deep-sea habitats (Erpenbeck and Van Soest 2002). The family Suberitidae is composed of sponges whose skeleton clearly differs from the current material as it is built with styles and derived forms of styles, and lack true oxeas, with some exceptions. The first exception is the monotypical genus *Pseudospongosorites* whose single species *Pseudospongosorites suberitoides* (Diaz, van Soest & Pomponi, 1993) has exclusively oxeas as spicules (no styles). The other exception are of those belonging to the genus *Aaptos*, where the skeleton is radial and predominantly comprised of strongyloxeas, and smaller oxeas (often centrotylote) that are only occasionally present (McCormack & Kelly, 2002). The Halichondriidae, on the other hand, have skeletons formed mainly of oxeas, styles, or both (occasionally complemented with variations of both spicule types) and have a confused arrangement of spicules in the choanosome, which is the major synapomorphy for the group (Erpenbeck and Van Soest 2002).

Alvarez and Hooper (2011) point out that the discrimination between the species and genera in the Halichondriidae is based exclusively on a few skeletal traits, which are simplistic and leave room for doubt. Regardless, the combination of oxeas and styles found in the Hawaiian specimens is only present in two genera within Halichondriidae. The *Axinyssa* genus lacks a continuous ectosomal skeleton (Van Soest et al. 1990) and the genus *Ciocalapata* has much longer styles relative to our specimens (often > 800 µm long (Lage et al., 2013)). In addition, no species in both genera have an encrusting growth form (Erpenbeck and Van Soest 2002). *Spongosorites* spp. occasionally bares true styles (eg. *Spongosorites cabliersi* Santín, Grinyó & Lo Iacono, 2021 (Santín et al., 2021)) with a broad size range. *Vosmaeria crustacea* Fristedt, 1885 is the only species with true styles in a single size category out of the two species in the genus, however, this species is only found in cold waters of the Arctic Ocean (Erpenbeck & Van Soest 2002). *Laminospongia subtilis* Pulitzer-Finali 1983 is the only species in the genus and differs from the Hawaiian material due to its laminar habit, the lack of a specialized ectosomal skeleton, and so far has only been found in the Mediterranean. Lastly, *Cyocalipta* spp. are distinct from any other Halichondriid because of the finger-shaped fistular habit whose branches possess a central column with extra-axial thick supporting tracts, not found in other genera with similar fistular habit. The combination of 1. spicule types (oxeas and styles), 2. A distinguishable ectosome made of styles forming a network of meshes with paratangential tracts, and 3. Confused arrangement of oxeas of different size categories in the choanosome all support that the Hawaiian material belong within the *Amorphinopsis* genus (Erpenbeck and Van Soest 2002).

Amorphinopsis is a taxonomically challenging group, given its history of “ping-pong” assignments of species within the genus to other genera which is a reflection of poor and simplistic descriptions, making it difficult to distinguish between species (Carvalho et al., 2004). There are currently 18 species assigned to the genus (de Voogd et al., 2024). These have, as a key, the combination of oxeas and styles as megascleres in the skeleton, except for *Amorphinopsis fenestrata* (Ridley, 1884) and *Amorphinopsis maza* (de Laubenfels, 1954). Even though the spicule composition of *A. fenestrata* is entirely made of styles, the habit and skeleton characteristics justified its transfer to this genus by Alvarez & Hooper (2011). *Amorphinopsis maza* has strongyloxeas instead of true oxeas (Hooper & Van Soest, 2002). Neither are therefore a match with the Hawaiian material.

While the habit can vary a lot within the same species on several occasions (hence the genus name *Amorphinopsis*), the encrusting habit of the Hawaiian specimens is not found in some of the species. *Amorphinopsis megarrhaphea* (Lendenfeld, 1888) has a distinct massive and lobose habit, attached to a small base. *Amorphinopsis mollis* Annadale, 1924 is known only from the holotype, described as massive, cavernous and spherical, and only found in a costal lake on an island in Southern Java. *Amorphinopsis armata* (Lindgren, 1897) is also represented just by the type, and has a massive habit with small humps and oxeas much larger than the Hawaiian material, with means around 900 µm and extremes over 1200 µm (type reexamined by Carvalho et al., 2004). *Amorphinopsis fistulosa* (Vacelet, Vasseur & Lévi, 1976) has a massive base buried in the sediment from which tubular papillae emerge and has clearly differently shaped styles which are longer (200-350 µm) yet with the same width (4-7 µm) relative to the Hawaiian specimens. *Amorphinopsis kempi* Kumar, 1925 (also known from just the type) has several cylindrical processes rising from a basal plate, the styles are larger (500-600 µm) and oxeas smaller (<400 µm) than the Hawaiian material. *Amorphinopsis siamensis* (Topsent, 1925) has a ramose, erect habit, with anastomosing branches and oxeas frequently over 1,000 µm long and 40 µm thick (type specimen reexamined by Erpenbeck & Soest, 2002 and Carvalho et., 2004). *Amorphinopsis subacerata* (Ridley & Dendy, 1886) consists of massive anastomosing branches with oxeas up to 1,200 µm long. *Amorphinopsis dichotoma* (Dendy, 1916) single description (of the type) highlights its digitiform morphology to separate it from *Amorphinopsis foetida* (Dendy, 1889) (suggested by Carvalho et al., 2004 as synonyms). *Amorphinopsis pallescens* (Topsent, 1892) has only two descriptions, and both disagree with the Hawaiian material in either habit or in the dimension of oxeas - the description of the holotype is reported as encrusting but the oxeas of the type material are much smaller (80-160 µm) and is found in the Mediterranean. *Amorphinopsis filigrana* (Schmidt, 1862) is also reported from the Mediterranean and its single description of the holotype (Schmidt, 1862) is very simplistic, without a formal description or mention of spicule compositions or measurements. Based on the distribution and the paucity of comparative characteristics we are unable to consider this species as conspecific. The habit of *Amorphinopsis papillata* (Baer, 1906) is not clear, as it has only been described through the holotype from French Polynesia, yet the size range of oxeas measure 703 to 1242 µm in length x 11 to 30 µm in thickness are much larger than the in Hawaiian specimens. Therefore, these species can be excluded as possible matches with the Hawaiian material.

The five remaining species in the genus are more challenging to differentiate relative to the specimens found in Kāneʻohe Bay, as they all have very similar habit, spicule composition and skeletal structure. In *A. foetida*, the volcano-shaped fistula and large oscules (up to 8 mm wide) described by Hooper et al. (1997) have been used before as a discriminating character (Carvalho et al., 2009; Lim et al., 2009), but that specimen has been in the meantime concluded to be better allocated to *A. fenestrata* (Alvarez & Hooper, 2011) given that the skeleton had two size categories of oxeas instead of one. Regardless of this, the species has only been very scarcely characterized as encrusting, and when it is, the specimens were described with “flatten lobes” and no spicule measurements (Lévi, C.,1961), “tubercular branches and conules” (Thomas, P.A., 1981), “tubular oscules bearing projections (papillae)” (Thomas, P. A. 1976), and very general traits not associated with a single specimen (Thomas, P. A., 1985). None of these descriptions of encrusting specimens match the morphology of the Hawaiian material.

Amorphinopsis sacciformis (Thiele, 1900) has been described as thinly encrusting by Hooper et al., (1997), and distinguished from *Amorphinopsis excavans* Carter, 1887 and *Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004, given the large oxeas, up to 1100 µm long, of that specimen, which can be applied to the Hawaiian specimens as well, whose oxeas are invariably smaller than 800 µm. On the other hand, Alvarez & Hooper (2011) concluded that the same specimen was better allocated to *A. excavans* and the syntype *Ciocalypta sacciformis* Thiele, 1900 should be interpreted as *Halichondria*. The species seems to not be clearly defined considering its descriptions (see Table S1), yet these do not mention an encrusting habit, so the species will therefore not be considered as a possible match to the Hawaiian specimens.

Amorphinopsis atlantica is only found in the west Atlantic, yet, considering that other species found in the Caribbean and the Atlantic have been introduced in Hawaiʻi (eg., *Haliclona (Soestella) caerulea* (Hechtel, 1965), *Suberites aurantiacus* (Duchassaing & Michelotti, 1864) and *Geodia cf. papyracea* Hechtel, 1965, (de Laubenfels, 1950; Eldredge & Smith, 2001; Coles, DeFelice & Eldredge, 2002; Nunley et la., 2025; Vicente et al., 2025), weakens the argument that the geographic barrier of the American continent would prevent dispersal of *A. atlantica* to the Pacific. The sponge has also been linked to a behavior typical of an invasive species (Veloso-Junior et al., 2023) since it has been reported growing on many different types of substrate, such as rocks, mangrove pneumatophores, dead coral, mud, fish traps, piers, and in harsh conditions, such as the intertidal (often exposed to sunlight and desiccation) and estuarine environments with high tolerance to changes in salinity and sediment density (Carvalho et al. 2004; Santos et al. 2018; De la Cruz-Francisco et al. 2019). However, it has not been clearly reported as growing on coral reefs, such as those of Kāneʻohe Bay. Carvalho et al (2004) added that the size range of the two spicule types (oxeas and styles) consistently overlap in *A. atlantica*. In our specimens BPBM C1899 and BPBM C1900 there is no overlapping sizes, while in BPBM C1895 and BPBM C1901 the size ranges overlap only slightly (see Table 2.2). We consider differences in spicule composition, the massive morphology, the fact that *A. atlantica* has not been reported as a bioeroding species, and the different habitat type as enough evidence to consider it to be heterospecific from the Hawaiian material.

Amorphinopsis maculosa (Pulitzer-Finali, 1996) has only been described once after the holotype by Alvarez and Hooper (2011), and the ectosome of those specimens are characterized by disorganized brushes of solely small styles. The Hawaiian material has styles concentrated on the surface of the sponge, but oxeas of variable size are also present. In addition, the specimens seem to have a more massive growth morphology than our specimens (see Fig. 1C in Alvarez and Hooper (2011).

Amorphinopsis excavans is the type species for the genus, and the one that fits best with the description of the Hawaiian material in question. The skeleton of this species has been described as a confused arrangement mainly of large oxeas in the choanosome producing long and oval lacunae, with a specialized ectosome of regular tracts of smaller spicules, both identical to the Hawaiian specimens (Fig. 2.3, F-H). A high concentration of styles on the ectosomal skeleton is mentioned as an important feature by multiple descriptions of *A. excavans* (Thomas, 1973; Hooper et l, 1997; Hooper and Van Soest 2002). The blunt end of the styles in the ectosomal tracts are difficult to distinguish due to other spicules overlaying them. However, the smallest of spicules are clearly concentrated there (Fig. 2.3, G, st) which, in the Hawaiian specimens, correspond to styles. Some authors provide size categories for oxeas (Hooper & Van Soest, 2002), and even for styles (Kumar, 1925), yet most descriptions are of a single continuous range of sizes for both types. The lengths are more conserved in the styles, which range from around 120 to 250 µm (average ~ 190 µm), and are very variable for oxeas, from around 180 µm to 900 µm (average ~ 500 µm) (see Table S1), and are similar to the measurements of the Hawaiian specimens, which are just slightly smaller on average in both spicule types (Table 2.2). The descriptions of Annadale (1915 & 1918) include the presence of styles whose lengths stand out between all other descriptions in the literature (up to 548 µm Annandale (1915) and 680 µm measured by Kumar (1925)). These however correspond to two distinct morphologies in the species, previously considered variants (*Amorphinopsis* var. *digitifera* & *Amorphinopsis* var. *robinsonii*, sensu Annadale 1915, 1918) given the short projections/branches found on the surface of the sponge. The differences in style length and distinct growth morphologies differentiate it from the encrusting habit of the Hawaiian sponges and are potentially heterospecific. The specimen described by Pulitzer-Finali (1996) on the other hand has oxeas in a smaller size category expected for the species. The ectosome of this specimen is not detachable from the body and the brown color in spirit make it likely that it corresponds to a different species. The color of Carter's specimen is described as "pinkish, almost white", a trait only corroborated by Thomas' descriptions (1972; 1973), while most descriptions refer to a shade of yellow or green, depending on whether it is growing in a dark area (including the interior part of the sponge), or exposed to sunlight, respectively (Lim et al., 2008; Alvarez & Hooper, 2011), a dichotomy also observed in the Hawaiian material. It is possible that Carter might be referring to the color in spirit, since he doesn't specify it in his description, and it's consensual in the literature that when preserved in ethanol the sponge becomes white/beige. The original representation of the holotype shows a very clear arrangement of tracts on the ectosome united by small regular elevations, which were hypothesized to be the result of desiccation (Hooper & Van Soest, 2002), yet this arrangement is also present upon closer inspection of the surface of the Hawaiian specimens. Oscules may or may not be present. In the holotype they are not present, however it is also described as laminar or very thin. In the thinner areas of the collected specimens oscules are also not seen, so these are likely not present during early stages of development as the sponge encrusts the substrate, in which it may still be too thin to develop oscules and must therefore rely only on the pores for internal circulation. In turn, pores were also not visible in the holotype, following Carter's description, but considering that these are positioned behind the external membrane and seen only through the spaces between the spicule tracts, it is possible that such openings were not clear if the specimen was described after desiccation. Annadale (1918) emphasizes the capacity for both pores and oscules to contract, yet such feature has not been described by any other author and has not been observed in the Hawaiian specimens, neither before nor after preservation in ethanol.

Regardless of how strong/weak the previously discussed characters might be for a species id, the fact that the Hawaiian sponges were found encrusting and boring into coral assures that *A. excavans* is the closest match from the literature. The species has been reported on several occasions as encrusting coral, including the holotype. Some of these refer to old, presumably dead coral rock (Carter, 1887) while some are dubious as if the coral was alive (eg. Thomas 1972, 1973; Hooper et al., 1997). Hooper & Van Soest (2002) explain that the excavating habit is a result of holes produced by clionids that are later penetrated by *A. excavans*, and that therefore the species is not actually excavating the coral. This position was questioned by Schönberg et al (2017a) given the clear description of the excavating habit by Carter (1887), and hence the sponge was retained as a bioeroding species in that work. Considering the absence of clionids inside the coral skeleton of completely healthy *Porites compressa* and *Montipora capitata* colonies where the Haawaiian specimens were found excavating (Figure 2.2), we confirm that this species may indeed bioerode calcifying scleractinians. We observed this behavior in all five specimens.

2.4.8 Phylogeny

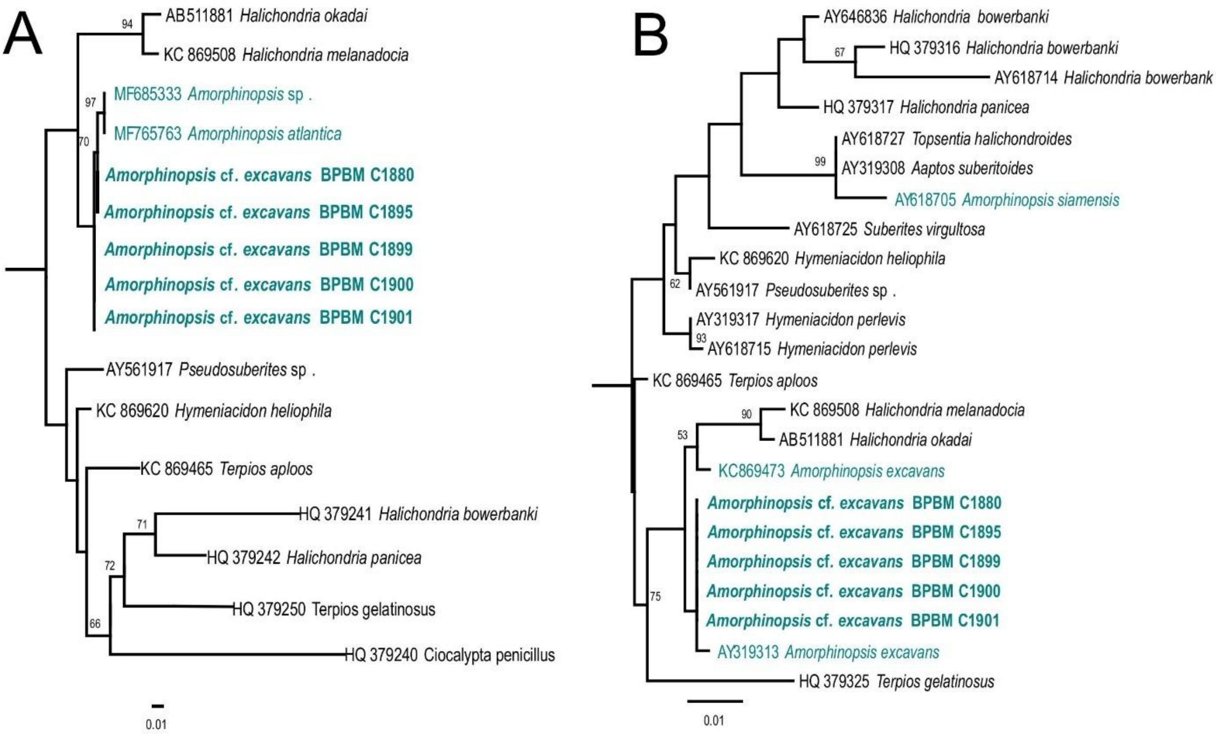

Figure 2.5. *Maximum-likelihood phylogeny using 28S partial sequences. A, partial sequences (386 bp) from a section of the 28S region of the D2 domain in 12 species; B, partial sequences (570 bp) of the D3-D4 domain of the 28S region from 23 specimens in 14 species;. Both trees are rooted on Tethya seychellensis (KC869475). Only bootstrap support values of >50 from the ML posterior probabilities are shown in the nodes (1000 bootstrap replicates). Specimens in blue are in the genus Amorphinopsis and specimens in* ***bolt*** *represent new sequences from the Hawaiian specimens.*

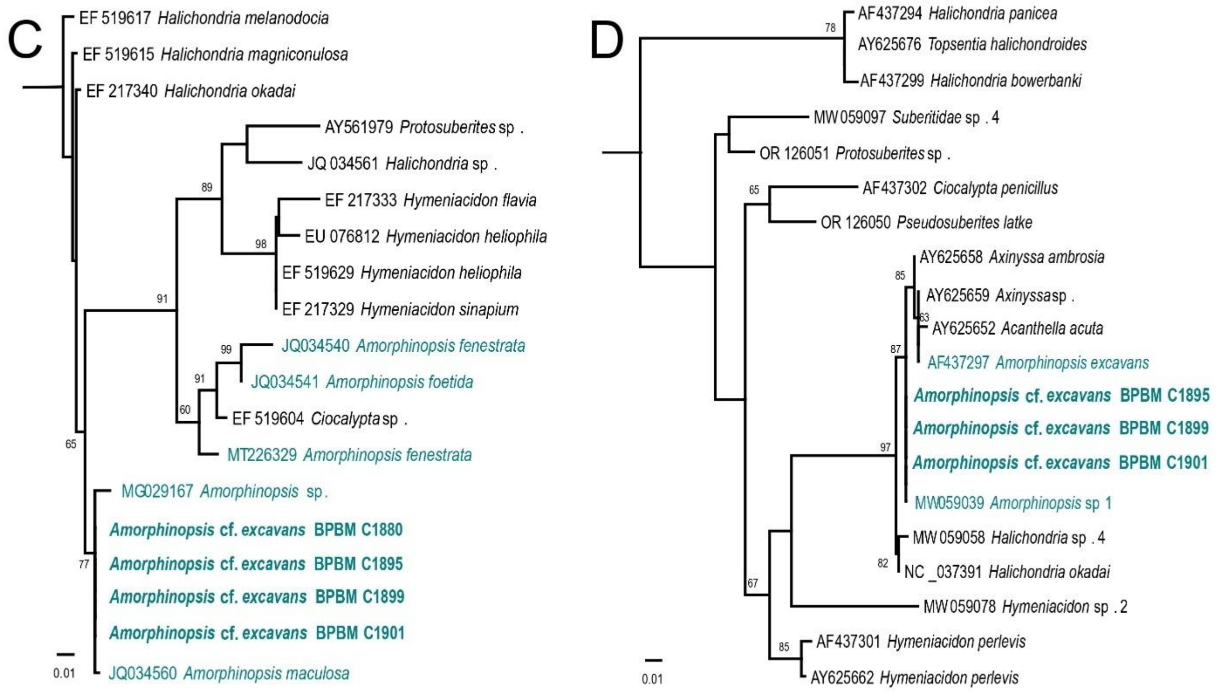

Figure 2.6. *Maximum-likelihood phylogeny using CO1 partial sequences. C, partial sequences (496 bp) from the Folmer fragment of the CO1 region from 15 suberitid species; D, partial sequences (409 bp) from the extension of the Folmer fragment of the CO1 region from xx 16 suberitid species. C is rooted in Tethya coccinea (JQ034584) and D is rooted in Liosina paradoxa (AY625663). Only bootstrap support values of >50 from the ML posterior probabilities are shown in the nodes (1000 bootstrap replicates). Specimens in blue are in the genus Amorphinopsis and specimens in* ***bold*** *represent new sequences from the Hawaiian specimens.*

CO1 and 28S sequences were obtained for all specimens. However, the sequence length varied according to the use of primers targeting multiple products of interest with differing sequence fragment sizes. Within overlapping regions, CO1 sequence fragments were 100% identical among all five specimens, and 28S sequence fragments were 100% identical within the D3-D4 domain, yet varied between 99.5-100% of identity in the D2 domain as a result of a single nucleotide mutation between cytosine (C) and guanine (G), and one nucleotide in voucher specimen BPBM C1880 which could not be determined (N) due to a weak signal. These differences are most likely localized mutations within the population, as no morphological differences in the sponges justify the separation into different species/sub-species. The sequences were separated into two trees for both markers since the sequences of related species available in GenBank were scarce and did not always cover the same regions in the gene.

Within the 28S D2 fragment (386 bp) the highest % identity match was with *A. atlantica* MF765763 (99.3%) and *Amorphinopsis* sp. MF685333 (99.1 %) (Fig. 2.6, A). Within the 28S D3-D4 (570 bp) fragment the closest relatives were *A. excavans* AY319313 (99.8%), *A.*

excavans KC869473 (99.5%), *Terpios aploos* KC869465 (98.9%), *Halichondria okadai* AB511881 (98.6%), *Halichondria melanodocia* KC869508 (98.1%) (Fig. 2.6, B). On the other hand, in the CO1 Folmer fragment (496 bp) the Hawaiian sponges had the highest identity with *A. maculosa* JQ034560 (99.8%), *Amorphinopsis* sp. MG029167 (99.2%), *Halichondria okadai* EF217340 (98.8%), *Halichondria magniconulosa* EF519615 (98.6%), *H. melanodocia* EF519617 (97.8%) (Fig. 2.6, C). For the COI extension fragment (409 bp) the closest relatives were *Axinyssa ambrosia* AY625658 (99.4%), *Axinyssa* sp. AY625659 (99.4%), *A. excavans* AF437297 (99.2%), *H.okadai* NC_037391 (99.2%), *Acanthella acuta* AY625652 (98,7%) and *Halichondria* sp. 4 MW059058 (98.7%) (Fig. 2.6, D).

Our results show that all Hawaiian specimens belong to the same species, which is clearly placed in the Halichondriidae family within the Suberitida order. The results highlight the polyphyly of this family, yet the genus *Amorphinopsis* are often the closest relatives to the Hawaiian specimens. Particularly, all sequences of *A. excavans* used in this analysis have identity percentages > 99%.

2.5 Discussion

Using an integrative taxonomic approach with a thorough literature review of halichondrid species (de Voogd et al., 2024) and a complete analysis of the genetic material available in GenBank, we find that the collected specimens, previously classified as *Amorphinopsis* sp. 1 in Hawaiʻi (Vicente et al., 2022) most likely belong to the species complex *Amorphinopsis* cf. *excavans* - the first record of this taxa in the Hawaiian archipelago. Field and microscope observations reveal it to be an encrusting species that overgrows and further excavates scleratinian corals in Kāneʻohe Bay, namely *Montipora capitata* and *Porites compressa,* two of the main reef-building species of coral in the bay.

The genetic approach was instrumental in validating the taxonomic assessment of the collected specimens. The halichondriids are known for their basic body plan and subsequent lack of diagnostic characters, which poses challenges to reliable classification solely through traditional taxonomy based on morphology (Erpenbeck et al., 2006; Alvarez & Hooper, 2011). This issue is clear in *Amorphinopsis* spp., defined by simple spicule types, basic skeleton organization, and no consistent body shape or habit - traits that have consistently proven inadequate for the characterization of halichondrid sponge species (Turner et al, 2024). However, genetic work within the genus remains minimal and limited to only 6 species, particularly combinations of both traditional and genetic approaches, creating obstacles to the reliable classification of taxa. Consequently, it's only natural that some level of polyphyly is observed in our phylogenetic trees (Fig. 2.5 & 2.6), as is generally the case within Halichondriidae (Erpenbeck et al., 2012) and Suberitida (Turner et al., 2024). For example, some sequences of *Amorphinopsis* spp. have relatively low molecular identity with the Hawaiian specimens and *A. excavans*, namely *A. siamesis*, *A. fenestrata* and *A. foetida*, while others outside of the genus have high identity, such as *Axinyssa ambrosia*, *Axinyssa* sp. and *Halichondria okadai*. Furthermore, *Amorphinopsis maculosa* JQ034560 and *Amorphinopsis atlantica* MF765763 had the highest molecular identity with our specimens, other than *A. excavans,* out of any species in the genus - and for the former as high as the highest obtained with *A. excavans* (specimen AY319313). While it must be noted that the sequence MF765763 is the only one available for *A. atlantica*, and *A. maculosa* has no taxonomic work associated with any of its sequences, the fact that these two species were also some of the most challenging to differentiate morphologically suggests that they could be conspecific. Much like the general scenario of sponge taxonomy, these results emphasize the need for more genetic work to be conducted in combination with traditional taxonomy on the species of the genus, in order to validate both the classification of specimens and their heterospecificity. Here we produced both COI and 28S fragments from the same species of *Amorphinopsis* cf. *excavans* in Hawai‘i, but were still limited in our analysis by the lack of sequence availability for conspecifics and congeners from other regions.

Amorphinopsis excavans has been reported from the west Indian Ocean to the Indo-Pacific, northern Australia, and now Hawai‘i (Fig. 2.4), a very extensive distribution range if we consider the limited natural dispersal capacity of sponge larvae (Maldonado, 2006). Such phenomena are often the result of over-conservative taxonomy (Klautau et al., 1999, Carballo et al., 2013), where similar species are described under the same name despite belonging to different taxa (see Table 1 in Xavier et al. 2010 for examples). Given the paucity of clear diagnostic characters and the high level of trait variability/plasticity within *Amorphinopsis* spp., it would not be surprising if this is the case for *A. excavans*, where cryptic species remain undetected by the lack of DNA barcoding. Indeed, some of the species' descriptions leave room for doubt on whether the specimens belong to the species *A. excavans*, specifically the two distinct morphologies described by Annadale (*Amorphinopsis* var. *digitifera* & *Amorphinopsis* var. *robinsonii*, sensu Annadale 1915, 1918) and the specimen described by Pulitzer-Finali (1996). These specimens require genetic analyses to confirm their conspecificity. Furthermore, genetic divergences or environmental influences could also affect the boring strategy of the sponge. As suggested by Schönberg et al (2017a), the species may be a facultative bioeroder, which could explain why the specimens analyzed by Hooper & Van Soest (2002) led them to conclude that the species was not truly excavating. Due to the unresolved taxonomic state of the species, we decided to give *A. excavans* the status of species complex (cf) until further genetic work is conducted on specimens from other regions.

At the same time, the *A. excavans* vouchers AF437297 and AY319313 had some of the highest molecular identities to the Hawaiian sponges – 99.2% and 99.8 %, respectively – and both come from Oman, at the farthest geographic distance from the Hawaiian specimens (Fig. 2.4). Therefore, taxonomic challenges can't explain the large range observed for the species – or at least not on their own. *Amorphinopsis* cf. *excavans* is not inconspicuous or cryptic, rather, the sponge overgrows large patches of shallow scleractinian corals, and it seems to be well established, particularly in the southern portions of Kāneʻohe Bay. Given the extensive surveys of marine fauna in the archipelago (Eldredge & Evenhuis, 2003) and the thorough documentation of the bay, one of the most-studied reef systems in the world (Bahr et al., 2015), it is highly unlikely that this species has been overlooked. Therefore, it is almost certain that this species does not occur naturally in Hawaiʻi and has been artificially introduced, which would also explain its extended distribution. This scenario follows what has been revealed for other species, such as *Hymeniacidon perlevis*, the most globally-distributed sponge species, also within Halichondriidae, which has recently had its range attributed to human dispersal (Turner, 2020). The most recent catalogue of the sponge fauna in Kāneʻohe Bay before Vicente et al., (2022) was conducted by Pons et al (2017), which suggests that the inoculation of the species was recent. However, additional vouchers from collections in the 1990s in Pearl Harbor need to be revisited with a thorough taxonomic assessment by a sponge expert to confirm a possible window of introduction (Coles, 1997).

Close to 100% of introduced sponge species in Hawaiʻi are believed to have reached the archipelago by integrating the fouling community of commercial vessels (Davidson et al. 2014) given its unmatched isolated position and the low dispersal capabilities of sponge larvae (Maldonado, 2006). It must be noted that the larvae of this genus have never been examined, but natural dispersal remains highly unlikely. Surveys of the marine fouling organisms of ship hulls have previously been conducted in Hawaiʻi (Godwin, 2003; Godwin et al., 2004) and *A.* cf. *excavans* was not reported. However, Lim et al. (2009) did an assessment of sponges present in the fouling community of navigation buoys of the port of Singapore, where *A. excavans* was found to be a common occurrence. This finding shows that the species is capable of encrusting artificial smooth substrates, similar to those found in the hulls of vessels, suggesting that this opportunistic species can use ships as dispersal vectors. Furthermore, it reveals that the species is present in one of the biggest and busiest ports in the world, which has frequent connections with the ports of Hawaiʻi. Indeed, *Mycale grandis,* the most aggressive and successful introduced sponge in Hawaiʻi (Coles et al. 2007) is also present in this port (Bakker et al., 2024), so it may be acting as a source of dispersion for other alien marine species as well. The most likely scenario is an initial introduction to one of Oʻahu's main harbors (Pearl Harbor or Honolulu Harbor), followed by a dispersal to Kāneʻohe Bay, either naturally or by fouling the hulls of recreational vessels, which are abundant in the bay and can also play a role in dispersion through biofouling (Leonard, 2009). Validation of this hypothesis would require monitoring efforts to detect the presence of the sponge in the main Hawaiian harbors and in the fouling community of commercial and recreational vessels.

Our collections were done haphazardly and did not consider abundance estimates of *A.* cf. *excavans* in Kāneʻohe Bay. Nevertheless, the species was frequently found overgrowing corals in the southern area of the bay, which is where the specimens here described were collected. This is expected given the long residence time of the water, ranging between 1 to 2 months (Lowe et al. 2009), as well as the influence of stream runoff (Coles et al., 2002), leading to high levels of nutrients and organic matter, including DOC, which serves as the main energy source for other excavating sponge species (Mueller et al., 2014). Other areas of Kāneʻohe Bay are also nutrient-rich compared to the exposed reef, and since this species is a good disperser, it is possible that it is or will soon be dispersed throughout the bay.

Research on sponge bioerosion has focused primarily on clionid sponges (eg.,Wisshak et al., 2012; Márquez et al., 2016; Achlatis et al., 2017; Webb et al., 2017), as they represent one of the most pervasive and disruptive groups of boring organisms in coral reefs around the world (Holmes, 2000; Rützler, 2002). However, boring sponges are a taxonomically diverse and widespread group (see Schönberg et al., 2017a for a list of species), which implies that attention should be given to specific divergences in the mechanics and chemistry involved, as they may have evolved independently and could impact the coral differently. The biology and ecology of *A. excavans* have scarcely been studied, including the dynamics driving its excavating habit. While the species seems to be restricted to areas of high nutrient concentration, a holistic understanding of its excavating capacity, rates of ammonification or nitrification, dispersal rates and current distribution in Kāneʻohe Bay is necessary to properly evaluate the current environmental risks associated with this introduction, as well as to design successful management strategies.

Controlling introduced sponges is not a straightforward process, as existing control methods are often not effective. Natural control does not always happen with sponges, since not all species are palatable, and even if so, predation might not occur in the community they were introduced to. A study on sponge response to predation in the Caribbean (Wulff, 2005) found that a species of *Amorphinopsis* was heavily predated by the parrotfish *Sparisoma aurofrenatum*. This fish does not occur in Hawaiʻi, yet other species of parrotfish are common in Kāneʻohe Bay, which could possibly feed on *A.* cf. *excavans*. Other fish species in Hawaiʻi, such as the Moorish idol (*Zanclus cornutus*) (Hobson, 1975), are known to include sponges in their diet, yet they are unable to effectively control other introduced sponges in the bay (Vicente et al., 2020). Most introduced sponges in Hawaiʻi are palatable and not chemically defended against fish and cowries (Vicente et al., 2020). The lack of defense mechanisms can be leveraged by faster growth rates (Leong & Pawlik, 2010) and perhaps increased dispersal and ability to encrust vessel hulls (Leong & Pawlik, 2010, Vicente et al., 2020), traits that may also apply to *A.* cf. *excavans*. It is important to address whether the sponge is palatable, and, if so, if predator abundance management can be used to control the species. Human-mediated control approaches have also been applied in other cases of invasive species. For example, in Kāneʻohe Bay, *M. grandis* has been the target of several methods of control, including mechanical and air-injection, both highly time-costly, with some implication to the corals, and high levels of sponge regrowth (Coles & Bolick 2006, 2007). It must be noted though that *M. grandis* is a massive sponge that does not excavate the coral it grows on, yet approaches for excavating sponges are not as studied. Manual removal of the boring sponge *Cliona delitrix*, for example, had high levels of regrowth after 12 months, even when the sponge was removed in its entirety (Halperin et al., 2016). Regardless of the method employed, it is consensual that manual approaches for sponge removal are logistically impractical and ineffective when applied at a large scale, given the time and costs involved. Thus, the development of innovative and scalable approaches is encouraged to address the presence of *A.* cf. *excavans* and other introduced sponges in Kāneʻohe Bay.

It is estimated that the presence of bioeroding sponges in coral reefs might intensify in the face of climate change. The increasing number of coral bleaching events can provide available dead coral substrate for sponge settlement, or at least reduce the defense capacity of corals (Schoenberg & Ortiz, 2009; Carballo et al., 2013). While many excavating sponges host photosynthetic symbionts and are thus affected by bleaching (Achlatis et al., 2017), we did not observe any chlorophyll leaching from *A.* cf. *excavans* tissue when preserved in ethanol, suggesting the absence of photosymbionts in this species, although specific analyses would be required to confirm this statement. Kāneʻohe Bay has already experienced several bleaching events (Bahr et al., 2017), enhanced by summertime water temperatures that can rise up to 2 °C higher than the surrounding open ocean (Bathen, 1968, Bahr et al., 2015). Both species of coral encrusted by *A.* cf. *excavans* (*Porites compressa* and *Montipora capitata*) were affected during these events (Grottoli et al., 2004; Bahr et al., 2017). Higher levels of pCO2 associated with ocean acidification can further accelerate bioerosion rates by lowering pH and facilitating the boring process (Wisshak et al., 2012, Schönberg et al., 2017b). In Kāneʻohe Bay, pCO2 levels range between 400-500 μatm (Fagan & Mackenzie, 2007), however, global projections suggest significant increases in the near future (Feely et al., 2009) and that many sponges will likely tolerate higher acidification scenarios (Vicente et al., 2016; Bell et al., 2018; Jury et al., 2024). Lastly, higher availability of nutrients and organic matter associated with eutrophication is also beneficial to filter feeders such as sponges, including excavating species (Holmes, 2000), especially if not dependent on autotrophy (Webb et al., 2017). As mentioned before, given the high residence time of water (Lowe et al. 2009), southern portions of Kāneʻohe Bay are more prone to suffer from eutrophication events in the future. Direct extrapolation of findings on other excavating species to *A.* cf. *excavans* is unreliable, and their tolerance/success in future scenarios is not transversal to all species (Achlatis et al., 2017). Thus, understanding how this species and its excavating mechanisms will respond to these multiple future environmental stressors is a pressing necessity.

2.6 Conclusion

The comprehensive taxonomic and genetic analysis performed in this study revealed that the excavating sponges collected in Kāneʻohe Bay belong to the species complex *Amorphinopsis* cf. *excavans,* here considered as a species complex given its current taxonomic scenario. The phylogenetic analyses highlighted some degree of polyphyly within the genus, or possibly conspecificity among heterospecifics. In turn, the extensive distribution of *A. excavans* may also be in part related to a lack of molecular characterization, leading to cryptic species being erroneously grouped under the same name. These taxonomic issues are understandable considering the few simplistic and inconsistent morphological characters that define the species within the genus (Hooper & Van Soest, 2002), yet they are just another clear example of the implications of incomplete taxonomy within Porifera. Like other authors have emphasized, the genetic approach must not be seen as complementary in taxonomic studies involving simple metazoans such as sponges, but rather as standard procedure. Likewise, available sequences must be linked to detailed morphological descriptions. Further studies including integrative analysis of both newly collected and previously described specimens are needed to reliably assign specimens to species and resolve their phylogenetic relationships.

We also conclude that the species was recently introduced to Hawai’i, based on the following observations: 1. It is a conspicuous species capable of encrusting large areas, and yet it had never been historically recorded in the Kāneʻohe Bay; 2. Low dispersal capability of sponge larvae make range expansion to the most remote archipelago in the world through natural vectors unlikely; and 3. This species has been observed fouling on navigational buoys in the Central Indo-Pacific which makes it capable of also integrating the fouling community of vessels, which are the most commonly used dispersal vectors for introduced sponges in Hawaiʻi. However, insights into the exact mechanisms by which the inoculation occurred require a reassessment of the fouling community of vessels throughout the main harbors of Oʻahu.

Unlike what was previously described (Hooper & Van Soest, 2002), this species clearly exhibits a bioerosive behavior on scleratinian corals, specifically two of the main reef-builders in the archipelago. The reefs of Kāneʻohe Bay have suffered from multiple human-induced disturbance events and proved to be very resilient once the stressor is controlled (Bahr et al., 2015). In particular, the population of the invasive *M. grandis* eventually stabilized some years after its introduction (Shih & Popp, 2020), providing some optimism. Nonetheless, the exact implications of this activity for the underwater ecosystem of Kāneʻohe Bay call for a full understanding of the biology and ecology of the species. Does it start by an overgrowth followed by the excavation process, or does its tissue infiltrate the coral skeleton from within? How fast does it develop and at what rate can it disperse to other regions of the archipelago? Is it restricted to nutrient-rich environments, or could it adapt to other habitats? Will it benefit from the consequences of climate change? We hope this study serves as a foundation to inspire others to pursue the answers to some of these questions, along with more effective prevention and control methods for introduced sponges in Hawaiʻi.

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2.9 Supplementary Materials

Table S1. *Summary of morphological data of Amosphinopsis spp.*

Species	External morphology	Skeleton morphology	Site description	Distribution
***Amorphinopsis armata* (Lindgren, 1897)**	Massive, with small humps; consistence fibrous and quite firm, oscula and pores not perceived; 2.5 cm high and 2 cm wide.	**Choano**: confused. **Ecto**: Up to 2mm thick, made of a light and loose fabric free of spicules with large canals. **Oxeas**: one or more irregular bends and gradually tapered, ends often rounded (1700 x 48 µm). **Styles**: mean 900 µm and maximum over 1200 µm (styles measured by Carvalho et al., 2004).	Attached to a stone, 54 m depth.	Indo-south China Sea.
***Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004**	Encrusting to massive cushion-shaped, lobate; color alive dark-greyish-green with or without yellow tinges on the exposed surface, occasionally white, areas protected from light exposure generally bright yellow, or completely yellow; surface smooth, detachable, subectosomal canals visible by the naked eye; oscules 2-7 mm across, scattered, flush on the surface; slightly compressible, becomes friable when dried.	**Ecto:** spicules dispersed, no tracts or reticulation. **Choano:** confused but with irregular, vague, pauci- to multispicular tracts (50-100 mm wide) which tend to display a plumose arrangement when approaching the surface. **Oxeas:** single size category, straight or slightly curved (150-452-900 x 4.8-9.1-17.9 µm). **Styles:** smooth, straight or slightly curved: length (160- 209-260 x 4.8-6.5-9.7 µm)	0.5-16 m depth, rocky coasts, on vertical surfaces or in overhangs; rarely exposed to direct sunlight.	São Sebastião and Ilhabela, São Paulo state; and Arraial do Cabo, Cabo Frio region, Rio de Janeiro state. Brazil.
***Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004, sensu Santos et al., 2018**	Thickly encrusting (2 cm thick) to massive, 35 x 15 cm (length x width) or lobate; some may present ramose shape, surface rugose, easily detachable, texture firm and compressible; oscules of 0.1–1 cm in diameter; color in vivo usually yellow to dark green or both distributed in different regions, brownish in spirit.	**Ecto:** detachable, formed by small oxeas and styles tangentially arranged, subectosomal skeleton with some smaller spicules and may present lacunae. **Choano** lacunar, confused but with irregular, vague, pauci- to multispicular tracts of large oxeas, with large rounded lacunae 300–1800 µm approx. **Oxeas** smooth, straight or slightly curved, some anisoxeas modifications are also present (180–568.8–1000 x 5–15.2–31.2 µm). **Styles**: smooth, usually straight (130–283.2–650 x 2.4–9.9–20 µm).	Growing on semi-exposed surfaces, subject to considerable sedimentation and epibiosis, on rather shallow habitats. intertidal mangrove area of river, substrata dead corals, rocks, sand, mud, pneumatophores of mangrove trees.	Brazil: Northeastern and Southeastern Region.
***Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004, sensu de la Cruz-Francisco et al., 2019**	Encrusting (1.5 cm thick) to massive, ~ 15 cm x 8 cm, may have prolonged branches up to 7 cm long and 0.4 cm thick, rough surface, compressible; color yellow when alive, brown in spirit; usually partially covered by sediment.	**Ecto:** indefinite cross-linking, spicules dispersed. **Choano:** with multi-spicular fibers of large oxeas. **Oxeas:** Slightly curved (331-552.9-774 x 7-10.4-16 µm). **Styles:** slightly curved and smooth (138-166.2-205 x 5-6.9-9 µm).	Tampamachoco lagoon; high turbidity, meso-polyhaline, covering the surface of bivalves.	Belize, northeast and southeast Brazil, Mexico.

***Amorphinopsis atlantica* Carvalho, Hajdu, Mothes & van Soest, 2004, sensu Veloso-Junior et al., 2023**	Encrusting, massive, cushion-shaped or lobate; rough surface easily detachable; slightly compressible; yellow to dark greyish green in vivo, bright yellow in areas protected from direct sunlight, brownish in spirit; subectosomal canals visible to the naked eye.	**Ecto:** scattered spicules in a complex arrangement. **Choano:** lacunar and formed by multiple spicular fibers of large oxea. **Oxeas:** straight or slightly curved, with needle-shaped or blunt tips (145.8-441.2-689 x 3.3-11.8-19.9 µm). **Styles:** straight or slightly curved, with blunt tips (132.5-159.9-212 x 3.3-4.8-6.6 µm).	Rigid parts of mangrove trees, hard substrates lying in the mud, fish traps made from mangrove stakes, attached to rocks, piers, and concrete constructions associated with oysters, barnacles, macroalgae, young crabs, and specimens of the anemone, *Diadumene lineata* (Verril, 1869). Some sponges were constantly exposed to sunlight and desiccation.	Northeastern and southeastern Brazil, Gulf of Mexico, North Caribbean, South Caribbean, Colombia and Venezuela.
***Amorphinopsis dichotoma* (Dendy, 1916)**	Cylindrical stem dividing at half the total height of the specimen into two approximately equal branches diverging from one another at an acute angle, each branch terminating in a bluntly pointed apex, stem slightly enlarged with a few grains of coarse sand and shell-fragment attached; surface stellately reticulate; some small, inconspicuous vents, chiefly in single series along the sides of stem and branches; pale yellow in spirit ; texture stiff, resilient; total height of specimen 46 mm; diameter of stem and branches 4-5 mm.	**Choano:** very irregular reticulation of loose spicular fibre composed of the larger oxea. Central axis surrounded by wide subdermal cavities traversed by spicular columns supporting the dermal membrane. The axis is very thick and the radiating spicule columns very short. Numerous loose fascicles of large oxea run lengthwise through the axis, separated from one another by a fair amount of soft tissue and crossed here and there by scattered oxea. Radiating columns support the dermal membrane are loose fascicles of similar spicules, ending in surface brushes of short styli. **Ecto:** translucent dermal membrane, supported by a reticulation of small styles, mostly arranged in the brushes at the ends of the radial columns, overlying extensive subdermal cavities. **Oxeas:** slightly curved, fusiform, symmetrical, gradually and sharply pointed at each end (800 x 20 C). **Styles**: short, usually slightly bent, well rounded off, but somewhat narrowed at one end, and gradually sharp-pointed at the other (200 x 8 µm). .	Shallow water.	Western India (Okhamandal in Kattiawar).
***Amorphinopsis excavans* Carter, 1887**	Laminar, continuous, very thin, spreading horizontally over a piece of old coral, which it has excavated vertically; consistence soft; color pinkish, almost white; surface even, following that of the object on which it may be growing, presenting a beautiful arrangement of the spiculation on the surface, which gives it the appearance of a fabric formed of little stars. Pores and vents not seen. Horizontal diameter of specimen about 3 inches; the	**Oxeas:** skeletal, acerate, fusiform, slightly curved, smooth, and very gradually sharp-pointed, varying much in size, up to 706 x 32 µm. **Styles:** acuate, slightly curved, slightly fusiform, smooth and sharp-pointed, head obtuse, not inflated, varying in size, up to 141 x 7 µm.	Growing over and incrusting and penetrating old coral.	King island, Mergui archipelago, Adaman sea.

	portion which lies in the excavations about 4 an inch in vertical diameter.			
Amorphinopsis excavans* Carter, 1887, sensu Annandale, 1915, of *Amorphinopsis excavans* var. *digitífera Spicule measurements by Kumar, 1925	Upright branches embedded in small stones and shells, branches up to 30 x 14 x 7 mm, specimen 100 x 40 mm.; color in spirit dirty white; consistency hard but can be torn easily, surface obscurely and reticulate or hispid; no pores or oscula visible; internal structure cavernous with several large canals running vertically up each branch..	**Choano:** dense, irregular network. In the branches its fibres curve upwards and outwards towards the external surface; as a rule they are directed mainly towards the inner side of the branch. They frequently fuse together to form strands of great thickness, but seem to contain little or no horny matter. There is a horizontal reticulation of fibres below the external layer of small spicules. The larger spicules are closely packed together in the fibres and lie quite parallel to one another. **Ecto:** layer of small spicules is horizontal over the greater part of the surface but in the hispid parts the spicules are vertical and little upright bunches can sometimes be detected that project through the dermal membrane. The bunches are arranged with considerable regularity at fairly equal distances. Sometimes they coincide in position with the terminations of skeletal strands. The spiculation differs from that of the typical form in the complete absence of large stout styli and in the fact that the large amphioxi are on an average considerably shorter. **Oxeas:** 300 / 500 / 800 x 25 µm. **Styles:** 200/ 500-680 x 17 µm.	Rock-pool.	Fisher Bay, Tavoy I., off the coast of Tenasserim, Myanmar.
Amorphinopsis excavans* Carter, 1887, sensu Annandale, 1918, of Amorphinopsis *excavans* var. *digitifera	Encrusting in a 5 mm layer; color alive greenish-grey, grey in spirit; consistency tough and elastic, not very hard, surface uneven, covered with a network of low ridges which often bear at the nodes short upright conical projections up to 3 mm high. No pores or oscula visible, but “the conical projections on the surface apparently represent conuli in which the orifices are closed by contraction”	**Choano and Ecto**: The upright spicule-fibres are well defined and below the external surface are splayed out. There is also an irregular skeletal reticulation of spicules of various forms and sizes and a distinct external layer of small spicules arranged horizontally in the ectosome. Large horizontal channels with a circular or horizontally oval cross-section run through the substance of the sponge, especially in the region immediately below the ectosome. There is a stout horny basal membrane. **Oxeas:** curved with median swelling, rare, 24 to 25 times longa as broad, extremities sharp and gradually pointed 200-440 µm long; without median swelling, common, slender, curved or geniculate, length 26-33 times as great as the maximum breadth, extremities sharply and gradually pointed. **Styles:** scarce, up to 548 µm , smaller 150 – 300 µm, 23 times as long as broad. The head is not at all dilated but abruptly rounded; the diameter of the spicule is uniform for about ¾ of its length. The tip is gradually and sharply pointed. Sometimes with a median swelling.	Growing on wooden piers in a salt-water creek.	Port \Veld, Perak, Malay Peninsula.
***Amorphinopsis excavans* Carter, 1887, sensu Thomas, 1973**	Encrusting; small; with internal ramifications throughout the coral rock; color pale white; no oscules seen; pores found in groups between dermal reticulation with elliptical outline, around 0.003 mm wide	**Choano:** irregular bands of oxeas running towards the outer layer and supporting the ectosome. **Ecto:** well developed reticulation of oxeas bound together with spongin, small styles abundantly represented. **Oxeas:** considerably variable in size and shape, uniformly curved or slightly angulated at the centre, tips sharply pointed, rarely satir-stepped or stylote; up to 610 x 20 µm. **Styles:**	Overgrowing a piece of coral rock, which is disintegrated to the maximum.	Indian Ocean, Australian region.

		slightly curved or sharply pointed, up to 300 x 8 µm.		
***Amorphinopsis excavans* Carter, 1887, sensu Thomas, 1972 & 1985**	Color white when alive; oscules and pores present, circular, in groups of 2-6, 1 to 1,5 mm wide	**Ecto:** well developed. **Choano:** irregular, oxeas rranged in irregular bundles in the peripheral parts. **Oxeas:** usually angulate in the centre (188-451-547 x 6-15-21) µm. **Styles:** abundant in the dermal region 166 x 5 µm (average)	Boring into coral. 2-5 m depth.	Indian Ocean, Australian region
***Amorphinopsis excavans* Carter, 1887, sensu Pulitzer-Finali, 1996**	Color cream white or brown when alive, light brown in spirit; cushion shaped or irregular; consistency though to hard	**Ecto:** not separable, slightly hispidated by small erect styles. **Choano:** halichondroid. **Oxeas:** 230-100 x 25-38 µm, small oxeas not abundant. **Styles:** 170-280 x 4.5-9 µm	6 m depth.	
***Amorphinopsis excavans* Carter, 1887, sensu Hooper et al., 1997**	Up to 15 mm thick; surface convoluted and opaque, optically smooth; oscules small, discrete, 1-2 mm diameter, scattered over surface, with slighlty raised membraneous lip; color yellow-brown when alive, beige-white in spirit; texture firm but compressible, easily torn.	**Ecto:** thin peel, detachable, composed of tangential layer of larger oxeas, mostly in bundles lying on surface, with small styles oriented paratangential to ("echinating") and protruding through surface; with sparse collagen and detritus. **Choano:** Tightly packed confused halichondroid reticulate skeleton of larger oxeote spicules, mostly formed by multispicular bundles bound together with very little collagenous material, producing small elongate cavities (lacunae) and oval meshes throughout skeleton. Towards periphery, spicule tracts becoming more paratangential, subplumose, producing larger lacunae free of spicules. Sparse collagen dispersed throughout mesohyl. **Oxeas:** choanosomal, fusiform, slightly curved at centre, tapering to sharp points (175-506.6-642 x 8-12.8-18) µm. **Styles:** ectosomal, slightly curved at centre, with rounded bases and tapering fusiform points (164-190.3-244 x 2-4.1-8) µm	Gravel substrate; intertidal to 54 m depth, thickly encrusting over Pocillopora coral fronds and large fragments of siliceous detritus.	Widespread in coral reefs of the Indo-west Pacific - Gulf of Manaar, Sri Lanka; Bay of Bengal, India; Andaman Sea, Burma; South China Sea, Vietnam; Sulu Sea, Philippines; Gaspar Strait, Java Sea, Banda Sea and Arafura Sea, Indonesia; Vernon Islands, NT; Torres Strait, Old.
***Amorphinopsis excavans* Carter, 1887 sensu Erpenbeck and Van_Soest_2002** (fragment of type examined)	Encrusting on a piece of dead coral; size 6 x 3 cm; surface smooth but displays some conules in the dry state; no visible openings; consistency firm when dry.	**Ecto:** tangential, consisting of thick intercrossing tracts of larger oxeas, the spaces in between filled with loose oxeas of all sizes as well as small styles. **Choano:** confused, with thick but vaguely delimited tracts and many loose individual spicules. **Oxeas:** most common, large size variation, long, fat, fusiform, curved, (520-700 x 18-20) µm, or shorter, fusiform, (200-375 x 8-12) µm. **Styles**: thickest in the middle, blunt end tapering 120 x 6 µm, concentrated in the surface	Coral reefs.	Mergui Archipelago, off the coast of Birma.
***Amorphinopsis excavans* Carter, 1887 sensu Lim et al., 2009**	Encrusting; up to 10 x 5 x 3 cm (length x width x thickness) in size; color alive not exposed to sunlight bright yellow, exposed to sunlight dark greyish-green with or without a yellow tinge; beige in spirit; oscules not visible, texture firm but compressible; fragile and friable when dried; surface opaque, usually smooth but some parts can	**Ecto:** peels easily, consists of vague, intercrossing tracts of oxeas and styles. Small styles are oriented paratangential to “echinating” and protrude through the surface. Collagen sparse. **Choano:** tightly packed, confused, with vague, irregular tracts of spicules bound together with very little collagenous spongin producing elongated and oval cavities throughout the skeleton. Towards the periphery, spicules tracts become more paratangential.	Encrusting navigation buoys.	Singapore.

	be convoluted.	No significant size differences of the spicules were observed for both oxeas and styles at the surface and the choanosomal skeleton. **Oxeas:** smooth, straight or slight curved (260–636–980 x 5–14.7–25) µm. **Styles**: smooth, straight or slightly curved; size (160–212–350 x 5–5.2–7) µm.		
***Amorphinopsis excavans* Carter, 1887 sensu Alvarez & Hopper, 2011**	Thinly to thickly encrusting (up to 50 mm thick); massive to lobate, or developing short projections and small lumps; generally growing in patches and following substrate, semi-buried in substrate; color olive green, yellow inside; oscula round to ovate, conspicuous, 10 mm diameter; surface hispid, bumpy.	**Ecto:** thin, detachable tangential layer, composed by a disorganised criss-cross reticulation of paucispicular-multispicular tracts of oxeas, up to 100 µm thick, with small styles tangentially to paratangentially oriented, sometimes in disorganised tufts. **Choano:** halichondroid, with large oxeas oriented in all directions, sometimes grouped in directionless multispicular tracts; slightly cavernous at subectosomal area with short multispicular tracts supporting the ectosomal skeleton. **Oxeas:** hastate, in a large range of sizes, 213.4-(598±221)-945.3 x 5.9-(16.3±5.5)-25.1 µm. **Styles:** 140.8-(193.8±41.3) -264.9 µm x 4.1-(5.5±0.9)-7.5 µm		Mergui Arhipelago, Singapore, northern Australia.
***Amorphinopsis fenestrata* (Ridley, 1884) of "*Leucophloeus fenestratus*"**	Dry, upright, flattened, , 70 mm. high x 15-20 mm. thick.; surmounted by pyramidal processes and traversed from the upper surface downwards by large cloacal spaces; color white, with a tinge of green.	900 x 320 µm (?)	32-36 m depth, bottom sand, mud, and shells, growing around a hydroid bush.	Arafura Sea.
***Amorphinopsis fenestrata* (Ridley, 1884) sensu Hooper et al., 1997 of "*Ciocalypta fenestrate*"**	Partially burrowing; subspherical, massive, buttressed base (50mm diameter,100 mm high), with small tapering fistules onapex (up to 30 mm long, 10 mm basal diameter) with basal portion buried beneath sediment and fistules protruding through sand; oscules up to 8mm diameter, on apex of fistules; color yellow-brown in life, pale brown in spirit; consistency compressible, harsh, easily torn; surface irregular, transparent and hispid.	**Ecto:** multispicular tracts of larger choanosomal styles, up to three spicules abreast, lying tangential to surface, and irregular bundles of smaller ectosomal styles arranged mostly paratangentially to surface as plumose brushes. Collagen present but light. **Choano:** disorganised halichondroid criss-cross of both unispicular and multispicular tracts, containing 5-10 spicules abreast, composed of larger choanosomal styles; in subectosomal region tracts becoming more wide-meshed, paratangential, producing cavernous subectosomal region; in fistules choanosomal tracts more compressed in central region, cavernous towards periphery; cavities at least as wide as spicule bundles, up to 400 µm in basal region, 1.5 mm in fistular region. Collagen moderately abundant in central region of choanosome, sparse in peripheral skeleton; no spongin fibres observed. **Oxeas:** large, in the choanosme, straight or slightly curved at centre, fusiform with sharp points or very slightly telescoped points (355-521.6-775 x 8-19.2-32) µm. **Styles:** smaller dispersed in the mesohyl, fusiform, sharply pointed with evenly rounded bases (153-246.5-330 x 6-9.1-12) µm.	Burrowing in sand, mud, coral rubble, shell grit substrates, 4-72 m depth range.	Darwin Harbour, Arafura Sea, Shoal Bay, NT; Low Isles, Mangrove Park, Great Barrier Reef, Qid.; Providence Reef, Amirante, Indian Ocean; Java and Lesser Sunda Islands, Indonesia.

***Amorphinopsis fenestrata* (Ridley, 1884) sensu Alvarez & Hooper, 2011** Species changed to *Amorphinopsis* because of its skeleton	Massive to subspherical, with tapering, hollow, rudimentary, subconical or volcano-shaped fistules protruding through substrate, up to 18 mm long and 30 mm diameter; basal portion buried beneath sediment; color alive yellow, brown or pale mauve; oscula large, up to 10 mm in diameter or, grouped on a terminal sieve-plate, on apex of fistules; consistency compressible, harsh, easily torn; surface irregular, rugose, translucid, hispid, marked in some specimens with longitudinal channels.	**Ecto:** detachable, supported by subectosomal multispicular tracts, formed by multispicular tracts of larger choanosomal styles, up to 3 spicules abreast, lying tangential to surface, directionless or criss-crossing, forming a nearly regular reticulation of polygonal meshes; and, irregular bundles of smaller ectosomal styles arranged mostly paratangential to surface as plumose brushes or tufts. **Choano:** disorganised, halichondroid criss-cross of both unispicular and multispicular tracts, containing 5–20 spicules abreast, with larger choanosomal styles mainly confined to central region; becoming more wide-meshed, paratangentially oriented and cavernous at subectosomal region. In fistules choanosomal tracts more compressed in central region, cavernous towards periphery. Styles: choanosomal styles and styloids (thicker in apical third and with basal ends narrower than the centre), slender, straight or slightly curved at centre, fusiform, in a great size range (163–895 x 3.3–17.4) µm. Smaller styles can be transitional to subtylostyles. Relative proportions of styles, styloids and subtylostyles vary among populations.		Northern Territory coast (Sahul Province), from Parry Shoals (NW of Darwin Harbour) to the Gulf of Carpentaria.
***Amorphinopsis filigrana* (Schmidt, 1862)**	Consistency very fragile, color yellowish/reddish	Skeleton consisting of a dense but almost transparent meshwork of loosely connected spicules. Two forms of these are present in almost equal quantities.		Muggia, Italy.
***Amorphinopsis fistulosa* (Vacelet, Vasseur & Lévi, 1976)**	Massive base partly embedded in the substrate; papillae tubular, reaching 5-1 cm, with walls 1 mm thick, color yellow in life, pale yellow to brownish in spirit.	**Choano:** very disordered, the wall of the papillae contains a network irregular and unclear with axes of various sizes and small styles. **Ecto:** styles in bouquets that are not very marked and never abundant. **Oxeas:** 230-800 x 4-15 µm. **Styles:** 200-350 x 4-7 µm		Grand Recif, Tulear, Madagascar.
***Amorphinopsis foetida* (Dendy, 1889) of "*Hymeniacidon foetida*"**	Massive, sessile, slightly lobose; 143 mm wide x 60 mm high; large oscula present on the summits of the low lobes; surface reticulate, hard and incompressible, in spirit a little softer, color grey when alive, dull blackish grey in spirit.	**Choano:** very dense irregular reticulation of large oxea, sometimes aggregated in thick strands or fibers; little to no spongin. **Ecto:** close reticulation of stout bands of spicules, with small and rounded meshes, the bands of spicules dividing them are irregular, composed principally of large oxea and scarce small styli arranged with their apices projecting at the surface of the sponge **Oxeas:** large, curved, gradually sharp-pointed (800 x 21) µm. **Styles:** small, slightly curved, smooth, evenly rounded off at the base and gradually sharp-pointed at the apex (200 x 7) µm.		Gulf of Manaar.
***Amorphinopsis foetida* (Dendy, 1889) sensu Thomas, 2002, of "*Prostylyssa foetida*"**	Irregularly tuberous and attached to the substratum by broad base; dimensions 8 x 4 cm; color brown when dry; consistency hard but brittle when dry; oscules scattered, with or without elevated rim, up to 3 mm wide	**Ecto:** oxeas tangentially placed in polygonal to irregular bands ornamented with small styles laterally. **Choano:** oxeas in loose irregular bands running to surface. **Oxeas:** Slightly curved and sharply pointed, size up to 1200 x 32 µm. **Styles:** up to 230 x 8 µm.		Indo-Australian.

Amorphinopsis foetida **(Dendy, 1889) sensu Hooper et al., 1997** Alvarez and Hooper 2011 refer to this specimen as *A. fenestrata*	Enlarged base burrowing into substrate with two subconical, low volcano-shaped fistules protruding above sediment; oscules up to 8 mm diameter, grouped on a terminal sieve-plate at the apex of each fistule; color yellow-beige when alive, white in spirit; consistency soft, compressible and easily torn; surface transparent, membranous, irregular, wrinkled and hispid.	**Ecto:** dense layer of larger choanosomal styles lying tangential to the surface, mostly in irregular multispicular bundles of 2-10 spicules, with smaller ectosomal styles producing tufts (`echinating') around spicule bundles bound together with small amounts of collagen. **Choano:** cavernous, reticulate, deeper multispicular tracts composed of larger styles, 20-50 spicules wide, mainly confined to central region of sponge (particularly in fistules). Peripheral skeleton with widely spaced multispicular radial tracts of styles arising perpendicular to central skeleton, becoming plumose in near surface, supporting tangential ectosomal skeleton; spicule tracts forming wide-meshed reticulate skeleton with very large cavernous meshes up to 2 mm diameter, particularly in fistular region; some collagenous material associated with spicule tracts but true fibres absent. **Styles:** choanosomal, long, slender, straight or slightly curved at centre, nearly hastate, occasionally slightly telescoped points, with evenly rounded bases (448-609.8-794 x 8-16.4-23) µm. Smaller ectosomal styles slender, straight, fusiform, with sharp points and evenly rounded bases (67-106.8-252 x 3-5.4-8) µm.	Sandy mud substrate with sparse seagrass cover.	Tuticorin, Gulf of Manaar, Sri Lanka; S. coast of Vietnam, South China Sea; Ambon and Ternate, Moluccas, Indonesia; Arafura Sea, Indonesia; Shoal Bay, Darwin region, NT.
Amorphinopsis foetida **(Dendy, 1889) sensu Lévi, 1961**	Encrusting; color whitish; thin, with flattened lobes; surface smooth with few small oscules, 300-700 um wide.	**Ecto:** oxeas arranged in irregular tangential bundles. **Choano:** confused.		Indo-Pacific.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A. (1986 [1980]) of “*Prostylissa foetida*”**	Tuberous with upright branches with oscules in the extremities (1-3 mm wide); color pale yellow; consistency friable when dry; surface smooth and microscopically hispid.	**Ecto:** oxeas in badly band not well defined with styles on their sides, meshes polygonal or triangular, with pores (210-620 µm). **Choano:** irregular reticulation of oxeas running towards the surface supporting the ectosome, oxeas may project out of the surface giving hispidity, spongin rare. **Oxeas:** slightly curved and sharply pointed, (283-623-1112 x 4-15-25) µm. **Styles**: slightly curved, greatest width at the central portion (113-182-227 x 5-7-11) µm.		Indian Ocean, Australian region.
Amorphinopsis foetida **(Dendy, 1889) sensu Vacelet, J. and Vasseur, P. 1965 of “*Prostylissa foetida*”**	Large and massive, rising in numerous blades or conical extensions more or less anastomosed, often ending in small oscula 1-1.5 mm wide; color greenish-yellow alive, orange-yellow in spirit; surface slightly hispid.	**Ecto:** bouquets of small styles make a short hispidation. **Choano:** very lacunous, bundles or large oxeas not very coherent, few styles sometimes in a bristling position. **Oxeas:** with median curvatureand sharp points (320-860 x 8-25) µm. **Styles:** almost straight, very slightly tapered head, 170-240 µm.	Pneumatophores of mangrove trees.	Indo-Pacific.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A. 1981, of “*Prostylissa foetida*”**	Massively encrusting; 80 x, 30 mm; surface with tubercular branches and conules 1-2 mm high; color pale yellow; consistency hard and friable; oscules terminal on branches, 1-3 mm in diameter and compound; pores minute, one per mesh, diameter up to 0.06 mm.	**Ecto:** irregular bands of oxeas forming polygonal, triangular or irregular meshes, often ornamented with small styles. **Choano:** irregular with bands of oxeas rather confused towards the outer part of the specimen, and some oxeas may even project out giving considerable hispidity to the surface, Spongin content is rather meagre and is colorless. **Oxeas:** slightly curved and sharply pointed, (311-567-1211 x 2-16-21) µm. **Styles**		Indian Ocean, Australian region.

		slightly curved with greatest width at the central part (113-182-223 x 4-6-10) µm		
Amorphinopsis foetida **(Dendy, 1889) sensu Pulitzer-Finali, G. 1993**	Incompressible; color dull green when alive.	**Oxeas:** (200-750 x 7-23) µm **Styles:** (130-190 x 4-7) µm		North Kenya Banks.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A. 1979, of “*Prostylissa foetida*”**	Body attached to substrate, repent branches fused forming a clathrous mass; later tubular branches up to a 24-40 mm long bear oscular openings; dimensions up to 180 x 130 x 60 mm, color light gray; consistency hard but friable; oscules scattered irregularly on the surface or on tubular branches; diameter 1-4 mm; surface minutely conulose and microscopically hispid.	**Ecto:** oxeas arranged in triangular or polygonal meshes ornamented at sides by small styles. **Choano:** oxeas arranged in an irregular reticulation. Spongin is slightly noted. The oxeas may project beyond the surface giving much bispidity to the surface. **Oxeas:** (211-0.628-1012 x 2-12-25) µm. **Styles:** (110-0.182-212 x 2-5-6) µm		Indian Ocean, Australian Region.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A., 1976, of “*Prostylissa foetida*”**	Thickly encrusting with tubular osculae bearing projections arising from the upper part; dimensions up to 35 × 20 × 25 mm; color pale grey when dry; consistency hard and fragile; oscules on papillae 1-2 mm in diameter and compound; subdermal canals prominent around oscular vicinity; surface microscopically hispid.	**Ecto:** large oxeas in bands ornamented by styles. Meshes polygonal and bear pores of 0.025 mm diameter. **Choano:** oxeas arranged in bands with negligible amount of spongin. Large oxeas may project out of the surface giving some hispidity to the latter. **Oxeas:** slightly curved and sharply pointed; size (250-631-1010 x 4-13-24) µm. **Styles:** slightly curved and sharply pointed; central portion wider than the rest; size (112-152-163 x 3-5-6) µm.		Indian Ocean and Australian region.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A., 1984, of “*Prostylissa foetida*”**	Body irregularly tuberous, size 8 x 5 x 4 cm and attached to the substratum at many points; upper part of the body, at places, with several papillar projections averaging to 10 mm (height) and 3 mm (diameter) ending blindly; color sandy grey; consistency friable when dry; oscules not visible; surface smooth where sand grains are not incorporated	**Ecto:** detachable, thickness about 0.8 mm when free of sand grains. Meshes polygonal or triangular at the dermal part; pores one per mesh and up to 0.07 mm in diameter. At places the dermal skeleton may assume an irregular arrangement with oxeas strewn irregularly. Styles are abundant at the dermal part ornamenting the dermal bands. **Choano:** rather irregular with scanty spongin binding the main spicular bands. **Oxeas:** uniformly curved and sharply pointed (200-680-1130 x 4-15-23) µm. **Styles:** slightly curved and sharply pointed, greatest width at the central part (160-170-250 x 4-5-6) µm.		Indo – Australia.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A., 2002 of “*Prostylissa foetida*”**	Irregularly tuberous and attached to the substratum by broad base; up to 8 x 4 cm; colour brown when dry; consistency hard but brittle when dry, oscules scattered, with or without elevated rim, diameter up to 3 mm.	**Ecto:** oxeas tangentially placed in polygonal to irregular bands ornamented with small styles laterally. **Choano:** oxeas in loose irregular bands running to surface **Oxeas**: Slightly curved and sharply pointed, size up to 1200 x 32 µm. **Styles:** size up to 230 x 8 µm.		Indo-Australian.
Amorphinopsis foetida **(Dendy, 1889) sensu Thomas, P.A. 1985**	Encrusting, massive or irregularly spherical; colour pale green externally and pale white internally when alive; consistency hard and	**Ecto:** oxeas in reticulation, dermal bands ornamented with small styles; meshes triangular or polygonal. **Choano:** dense reticulation of oxeas; and spongin content is sparse. Bands expand towards the outer part		Gulf of Mannar and Palk Bay.

of "*Prostylissa foetida*"	slightly compressible; oscules scattered, with or without oscular tubes, diameter 1-3 mm and compound; surface minutely hispid and reticulated	and support the ectossomal skeleton or add to the hispidity of the surface. **Oxeas.** (280-1010 x 2-25) µm. **Styles:** (113-226 x 3-10) µm.		
***Amorphinopsis foetida* (Dendy, 1889) sensu Lindgren, N.G., 1898, of "*Ciocalypta foetida*"** Considered by the author as identical to *A. excavans* holotype	Irregular shape, dimensions 10 x 10 x 10 mm	**Ecto:** oxeas lie tangentially in various directions. Styles are positioned vertically, with the tips slightly protruding above the surface. **Choano:** the oxeas are densely packed inside the sponge without any particular order. Near the surface, small columns of spicules arise, which support the dermal membrane along with its spicules. Large subdermal cavities are found between the columns. **Oxeas:** (900 x 32) µm. **Styles:** (192 x 8) µm		Chinese seas; Amboina; Mergui Archipelago; Maanarbusch.
***Amorphinopsis kempi* Kumar, 1925**	Basal plate-like portion attached to the ground, from which a number of free cylindrical processes rise vertically upwards and give off branches at irregular intervals; surface hispid; consistency compressible; color dark brown in spirit.	The skeleton consists of a number of parallel strands of spicule-fibres gradually curving outwards and echinating. The longitudinal strands of spicule-fibres are connected with each other by a number of transverse connections of a similar kind. **Oxeas:** scarce and curved (360-400 x 17 or 180-250 x 17) µm. **Styles:** curved or straight (500-660 x 17-23 or 260 x 3) µm.		Waltair, India.
***Amorphinopsis maculosa* (Pulitzer-Finali, 1996) of "*Topsentia maculosa*"**	Irregularly cushion shaped, 10 cm across x 2 cm thick; color cream to light brown in spirit, sand coloured alive; consistency tough and moderately compressible, but friable; surface appears smooth but is rough to the touch, oscules not visible.	**Choano:** spicules in confusion and in loose bundles intercrossing without any regularity or tracts. **Ecto:** spicules arranged tangentially. **Oxeas:** (650 x 25 to 950 x 37) µm, smaller ones are present, not abundant and not representing a separate category.	6 m depth.	Papua New Guinea.
***Amorphinopsis maculosa* (Pulitzer-Finali, 1996) sensu Alvarez & Hooper, 2011**	Thickly encrusting, following substrate with convoluted ridges and short projections, color light grey or yellow alive, yellow inside, beige in spirit, oscules inconspicuous, of different diameter, flushed and irregularly distributed or aggregated in top of the short projections; surface smooth, lumpy, with dermal skin of reticulated appearance, consistency firm but crumbly.	**Ecto:** tangential to paratangential crust, approx. 200–300 µm thick, supported by choanosomal tracts of spicules and with disorganised brushes of small styles with ends projecting through surface, forming a discontinuous palisade spaced roughly at regular distances. **Choano:** halichondroid, forming oval to round lacunae, 300–1000 µm in diameter, becoming compact towards surface, with very little collagen and abundant spicule content. Spicule tracts long and multispicular, running either towards surface or parallel to surface at the subectosomal area. **Oxeas**: (207–994 x 5–38) µm. **Styles:** small, ectosomal, and much less frequent (139–274 x 3–8) µm.	6–28 m depth.	Papua New Guinea (Eastern Coral Triangle Province), Gulf of Carpentaria and outer region of Shoal Bay (Sahul Shelf province) between Torres Strait, Northeastern Australian Province.
***Amorphinopsis maza* (de Laubenfels, 1954)** Holotype redescribed by Hooper & Van Soest, 2002	Amorphous, up to 15 cm in diameter, color yellow or green, interior yellow; surface smooth with soft texture; pores abundant, 50 - 100 µm in diameter and 60 - 160 µm apart, center to center; oscules fairly conspicuous, about 5 mm in diameter and 3 cm apart.	**Ecto:** conspicuously separable dermis, with abundant spicules tangentally arranged. **Choano:** cavernous with spicules in confusion around small chambers which are often as little as 100 µm in diameter but in some cases are much larger. **Styles:** about (12 x 540) µm predominating in the ectosome. **Strongyles**: (12 x 630) µm in diameter, found chiefly in the choanosome; but even here they are not quite as numerous as the styles.	Mangroves, in very shallow, darkly discolored water, at a depth of only 30 cm, substrate coral sand.	Western portion of the Truk lasroon south of Polle Islet.

Amorphinopsis megarrhaphea (Lendenfeld, 1888) of “_Reniera megarrhaphea_”	Massive, lobose, digitate, and erect, attached by a small base, up to 15 cm; the digitate processes generally coalesce for the greater part of their length, and taper towards their upper end; small and irregular oscules on their summits; surface smooth.	The skeleton consists of bundles of spicules, arranged somewhat in the fashion of a network, the meshes of which measure 15-200 µm. The spicules in the bundles are rather irregularly situated. Spongin cementing the spicules is not discernible. **Oxeas:** large, straight or slightly curved, (500 x 30) µm; or small, straight and pointed, densely packed, scattered more or less irregularly between the fibres, and participating in their formation (200 x 8) µm.		East coast of Australia : Port Jackson.
Amorphinopsis mollis Annandale, 1924	Almost spherical mass about 5 cm; a single oscula visible of oval form , 2 x 1.5 mm, situated on one side on a low, broad, rounded eminence; massive, cavernous; consistency soft an delicate.	The spicules agree closely with those of the typical form except that none of the styles are quite so large as the largest in that form.	Attached to fragments of pumice.	Lake on Verlaten Island, southern Java.
Amorphinopsis pallescens (Topsent, 1892) of “_Hymeniacidon pallescens_”	Encrusting, thin but long; color whitish.	Smooth oxeas excessively abundant and crisscrossing in all directions. **Styles:** smooth, a little curved (300 x 4) µm., numerous, scattered without apparent order. **Oxas:** smooth curved, sharp, uneven, 80 to 160 µm long, excessively abundant and crisscrossing in all directions. The spiculation are composed of styles and smooth edges.		South France.
Amorphinopsis pallescens (Topsent, 1892) sensu Gracia et al., 2005	Massive base from which profuse fistulas of different length, long and thin (2-3 mm in diameter), which anastomose, do not remain erect and usually ending in an oscule; color whitish in spirit; surface velvety to the touch, microhispida under the magnifying glass.	**Ecto:** easily separable from the choanosome, with external tangential spicules, disordered, crossed by axes loosely arranged perpendiculars. Fistulas present under the layer of tangential oxeas ascending poly-spiculate bundles that can anastomose. **Oxeas:** robust, fusiform, with very sharp, straight or slightly curved tips (345-450 x 10-16) µm. **Styles:** stout, slightly shorter and less abundant than oxas, sometimes with one slight dilatation at the base; very conical, straight, with the tip wider and shorter than oxeas (240-337 x 11-16) µm	In a cavity abundant in the first hundred meters .	Coll cave (Felanitx, Mallorca)
Amorphinopsis papillata (Baer, 1906)	Lumpy, dimensions 46-85 x 47 x 29 mm (long x wide x high); color yellowish; consistency very rough; surface uneven, rough and with short covered wart-shaped elevations, which flatten out in some places; pores 0.6 mm wide; oscules are present only in small numbers, 2 mm wide.	**Ecto:** oxeas lying very close together without any particular arrangement forming a very dense structure. **Choano:** oxeas not that close to each other, but also without a specific order, confused. **Oxeas:** (703-1242 x 11-30) µm, straight or curved, fusiform, thickest in the middle, complete towards the ends gradually and sharply tapered. **Styles:** (200-220) µm (by Lim et al., 2009).	Growing attached to stones.	Papeete, French Polynesia.
Amorphinopsis sacciformis (Thiele, 1900) of “_Ciocalypta sacciformis_”	Bag shape; the largest pieces over 3 cm long, color reddish in spirit.	**Oxeas:** fairly short points on both sides, (700 x 22) µm. **Small oxeas and styles:** ~ (360 x 8) µm.		Halmahera, Indonesia.

Amorphinopsis sacciformis **(Thiele, 1900) sensu Hooper et al., 1997** allocated to *A. excavans* by Alvarez & Hooper, 2011	Thinly encrusting up to 8 mm thick following contours of substrate; oscules not visible; color yellow-brown in life, brown in spirit; texture firm, compressible, harsh; surface hispid, not opaque.	**Ecto:** Indistinct, very thin surface peel with larger choanosomal oxeas lying tangential to surface and pointed ends of smaller ectosomal styles arranged paratangentially (`echinating') over larger spicules. **Choano:** confused halichondroid reticulation of larger choanosomal oxeas, packed densely and bound together by small amount of collagen, in uni- and paucispicular bundles. Skeletal meshes oval, usually compressed, and only few larger spaces (lacunae) visible in choanosomal or subectosomal regions. Subectosomal skeleton with more obliquely directed tracts supporting tangential ectosomal skeleton. **Oxeas:** straight or slightly curved at centre, with long tapering fusiform sharply pointed ends, in two size classes, (225-318.5-420 x 5-7.9-10) µm or (540-781.1-1105 x 11-20.3-35) µm. **Styles:** short, slender, fusiform, sharply pointed, with rounded or occasionally slightly subtylote bases (118-213.4-264 x 3-5.3-9) µm.	Intertidal rock and dead coral reef, frequently mud covered, encrusting under lateritere rock boulders and covering bivalve shells. 0-23 m depth.	Distribution. Moluccas, Arafura Sea; Palau, Is., central west Pacific; Motupore Island, Papua New Guinea; and Darwin Harbour.
Amorphinopsis sacciformis **(Thiele, 1900) sensu Laubenfels, 1954 of "*Ciocalapata sacciformis*"**	Irregular shape, 6 cm x 12 cm in diameter; color dirty white when alive, interior pale green; consistency crisp, without spongin, easily cut; surface level and punctiform with obvious skeletal pores, 300 um in diameter, about one for each square mm, covered with a thin membrane, which is pierced by about 4, 5, or 6 real pores, the latter being 60 to 80 um in diameter; no oscules visible.	**Ecto:** relatively enormous subdermal spaces with a roof held up above them by fascicular columns up to 500 µm high. Its roof, often more than 100 µm thick, is abundantly provided with tangential spicules and fleshy structures. **Choano:** crumb-of-bread type with many gross cavities, spicules in confusion, and very little protoplasm. **Oxeas:** great size range, up to (800 x 21) µm **Styles:** varying greatly in size, up to (220 x 6) µm. Both common in the ecto and the choano.	2 m deep, substrate dead coral.	Iwayama Bay, Palau island.
Amorphinopsis sacciformis **(Thiele, 1900) sensu Kelly-Borges, M.; Bergquist, P.R., 1988**	Small pencil-like fragments or massive base giving rise to tapering fistules 7 -11 mm at the base and 2 - 3 mm at the top, 50 mm in height but two-thirds is usually buried in the sand; cavernous; color alive is pale green in the surface, yellowish deeper in the choanosome, drab grey in spirit; texture crip and compressible; surface hispid irregularly lumpy with interlacing troughs running longitudinally down the fistules	**Ecto:** large subdermal spaces and a dense dermal skeleton of radiate projecting and tangential spicules. **Choano:** vague spicule tracts that follow the longitudinal axis of the turret and extend in a plumose fashion through the ectosome. **Strongyloxeas:** gently tapering from the centre to ends (380-613-900 x 8-17-27) µm. **Oxeas:** fusiform, finely pointed (375-478-575 x 6-8-11) µm or (120-169-230 x 2-2.5-4) µm. **Styles:** finely pointed and gently curved (162-175-212 x 5-6-8) µm	growing freely in the seagrass or erected in Montipora or Thalassia patches.	East Indies, West Central Pacific.
Amorphinopsis siamensis **(Topsent, 1925) sensu Hooper & Van Soest, 2002**	Mass of irregular thick anastoming branches, up to 2 cm in diameter; surface smooth but slightly conulose, displaying a few large openings, presumably oscules; consistency firm but friable.	**Ecto:** detachable due to some limited subectosomal vestibules. It consists of tangentially intercrossing tracts of large oxeas surrounded by small spicules, which are strewn irregularly or appear to 'echinate' the tracts. **Choano:** thick tracts of large oxeas and many single spicules. Smaller spicules concentrated at the periphery. **Oxeas:** large fusiform (980-1050 x 40) µm or smaller but similar (300 x 7-10) µm. **Styles:** small fusiform (180-300 x 7-10) µm		Golfe de Siam.

***Amorphinopsis subacerata* (Ridley & Dendy, 1886) of "*Hymeniacidon subacerata*"**	Massive, consisting of irregularly anastomosing trabeculae; color pale yellow, with a waxy translucent look, consistency rather brittle; surface uneven, subglabrous.	**Ecto:** thin sheet of spicules, also densely and irregularly reticulate, supporting numerous small outwardlyprojecting spicules. **Choano:** irregular reticulation. **Oxeas:** smooth fusiform, somewhat curved, apex finely and gradually sharp-pointed, base tapering, but evenly rounded off (1200 x 31) µm. **Styles (or oxeas):** straight, gradually sharp-pointed, smooth acuates or subspinulates (200 x 6.3) µm.		Philippine Islands.

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