### Impact and Range Extension of Invasive Foraminifera in the NW Mediterranean Sea

### Implications for Diversity and Ecosystem Functioning

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#### Abstract

Climate warming and the poleward widening of the tropical belt have induced range shifts in a variety of marine and terrestrial organisms. Among the key taxa that are rapidly expanding their latitudinal range are larger symbiont-bearing foraminifera of the genus *Amphistegina*. Amphisteginid foraminifera are abundant in tropical and subtropical reef and shelf regions of the world's oceans. As key carbonate producers, amphisteginids contribute significantly to carbonate substrate stability, growth of reefal structures, and habitat formation. The Mediterranean Sea represents the northernmost geographical extension of amphisteginid foraminifera. Fueled by substantial warming, the Mediterranean has been identified as one of the most severely affected areas. Analyses of foraminiferal faunas from new sites from the Ionian and Adriatic Sea show that amphisteginid foraminifera continue to expand their biogeographic range, rapidly outcompete all native species and represent the most abundant taxon at almost every site colonized.

This study documents for the first time that amphisteginid foraminifera have now crossed the Strait of Otranto and invaded the eastern Adriatic coast along southern Albania. Sampling on the opposite side along the southern part of the Italian boot shows, however, that amphisteginid foraminifera have not yet colonized the western coast of the Adriatic. The asymmetric invasion of the Adriatic displays spatial heterogeneity, where the progressive colonization follows the major surface currents with a northerly flow along the eastern coast and a southerly return along the western coastline. The observed recent rate of range expansion in *Amphistegina* is computed between 4.0 and 10 km/year-1 and provides strong support for current species model projections. Based on the new data, the range boundary shift is projected to lead to a total northward range expansion of  $5.2^{\circ}$  latitude in the year 2100. The latitudinal range extension computed for the Mediterranean is thus almost twice as large as those computed for the southern hemisphere.

The introduction and range expansion of *Amphistegina* puts significant pressure on local species, affects foraminiferal diversity and decreases species richness of associated biotas. Native species richness is reduced at all sites invaded by amphisteginids and correlates with the degree of infestation. Amphisteginids invasions specifically impact those species that share a similar microhabitat and include other larger symbiont-bearing foraminifera and numerous trochospiral species. The impact of *Amphistegina* on native biotas gradually increases from the range expansion front towards those sites where invasions commenced decades ago. High abundances may result in prolific monocultures of *Amphistegina* that modify the composition of sedimentary substrates and ultimately trigger changes in ecosystem functioning. Assemblage structures and patterns observed at the expansion front in modernday environments resemble amphisteginid invasions recorded in Miocene foraminiferal communities from the Vienna Basin and Poland. Miocene range shifts are among the largest biogeographic range expansions documented in earth history and highlight the magnitude of modern ocean range shifts.

The ongoing range extension into new areas of the Mediterranean Sea is shown to trigger changes in community structures with potential consequences for ecosystem functioning. Numerical abundances and impacts of invasive amphisteginids are greatest at shallow depths <20 m. Evidence is now accumulating that the invasion of amphisteginid foraminifera results in (1) a loss of benthic foraminiferal biodiversity, (2) alterations of foraminiferal community structures and (3) shifts in abundances of functional groups of foraminifera.

For comparison, benthic foraminiferal assemblages in human impacted and non-impacted areas were studied (also partly inhabited by amphisteginids). The study area is the seacoast of Albania, located along the north-eastern Ionian and southeastern Adriatic Sea. Its shallow waters provide a wide range of habitats for a large number of marine species. The composition and distribution of shallow-water benthic foraminiferal assemblages in relation to substrates, water depth and ecological conditions were documented. The samples collected show high species richness values (277 species, 112 Genera) with taxa known to be distributed in the Adriatic as well as in the eastern and western Mediterranean Sea. The performed hierarchical cluster analysis reveals the presence of two distinct clusters and biofacies characterized for the northern and southern coastline respectively. Increasing anthropogenic pressure accompanied with pollution from sewage, urban wastes, maritime traffic, and building activities lead to partly degrading conditions in the Gulf of Vlore and Sarande Bay. Darezeze e Re, Shengjin, Durres, and Diviaka show likewise increasing degradation rates traced back to human mediated impacts (urban and industrial sewages, hydrocarbon exploration, building activities) and natural forcing (river discharge, erosion rates). The presence of non-indigenous (NI) benthic foraminifera with Indo-Pacific origin in the samples sites off Albania is documented. The presence of NI benthic foraminiferal species of Indo-Pacific and Atlantic origin is mainly controlled by rising sea surface temperatures and the subsequent dispersal by currents. Ballast ship water is also considered to be a major source of nonnative species introductions. The invasive benthic foraminifera Amphistegina lobifera is currently the most abundant species, which continues to proliferate along the Albanian coastline with severe consequences on native biotas and ecosystem functioning.

#### Zusammenfassung

Klimaerwärmung und die Erweiterung des tropischen Gürtels in Richtung der Polregionen führt zur Ausbreitung vieler mariner und terrestrischer Organismen. Zu den Taxa, die ihr Verbreiterungsareal um mehrere Längengrade erweitern, gehören symbionten-tragende Foraminiferen der Gattung *Amphistegina*. Amphisteginen sind besonders häufig in tropischen und subtropischen Riffen und Schelfmeeren der Welt. Als Schlüsselproduzenten für Karbonat tragen sie erheblich zur Stabilität von karbonatischen Substraten, dem Wachstum von Riffstrukturen und Habitaten bei. Das Mittelmeer bildet die nördlichste geographische Erweiterung amphisteginer Foraminiferen. Das Mittelmeer gehört, angetrieben von der erheblichen (Klima)Erwärmung, zu den am schlimmsten betroffenen Gebieten der Welt. Analysen der Foraminiferenfauna von neuen Standorten innerhalb des Ionischen und Adriatischen Meeres zeigen, dass Amphisteginen kontinuierlich ihre biogeographische Ausdehnung erweitern und rapide native/heimische Arten auskonkurrieren und das häufigste Taxon in nahezu allen Bereichen bildet, die sie kolonisiert.

Diese Studie dokumentiert zum ersten Mal, dass Amphisteginen nun die Straße von Otranto passiert haben und die östliche Adria entlang der südlichen albanischen Küste besiedeln. Die Probennahmen auf der gegenüberliegenden Seite, entlang des südlichen Teils des italienischen Stiefelabsatzes zeigen, dass Amphisteginen noch nicht die südwestliche Küste der Adria besiedelt haben. Die asymmetrische Besiedelung der Adria zeigt, dass die progressive Kolonisierung der oberflächlichen Meeresströmung folgt, welche entlang der östlichen Adriaküste nach Norden verläuft und in der nördlichen Adria abbiegt und entlang der Westküste nach Süden fließt. Die Ausbreitungsgeschwindigkeit von *Amphistegina* wurde auf 4.0 bis 10km/Jahr berechnet und bestätigt gegenwärtige Ausbreitungsmodelle für diese Art. Basierend auf den neuen Daten, wird die zukünftige Arealextension im Jahr 2100 auf eine latitudinale Ausweitung von 5.2° projektiert. Die latitudinale Ausweitung, die für das Mittelmeer errechnet wurde ist demnach nahezu doppelt so hoch wie die Ausbreitungsmodelle für die südliche Hemisphäre voraussagen.

Die Invasion und Ausbreitung von Amphistegina erhöht signifikant den Druck auf die native Fauna, beeinflusst die Diversität der Foraminiferen, und minimiert die Artenvielfalt vergesellschafteter Faunen. Die natürliche Artenvielfalt ist in allen besiedelten Standorten verringert und korreliert mit dem Grad des Befalls. Die Invasion von Amphisteginen beeinträchtigt vor allem die Arten, welche dieselben Mikrohabitate besiedeln, wie andere symbionten-tragenden Foraminiferen und zahlreiche Arten mit trochospiraler Morphologie. Der Einfluss auf die natürliche Foraminiferenfauna verringert sich sukzessive von der Expansionsfront entgegen den Standorten an denen die Invasion vor Jahrzehnten begann. Massenhafte Vorkommen resultieren lokal in Monokulturen aus Amphistegina, welche die Zusammensetzung der Sedimente verändern und letztendlich Veränderung in der Funktion des Ökosystems hervorrufen. Die gegenwärtige Zusammensetzung der Foraminiferenvergesellschaftungen entlang der Expansionsfront ähnelt den Invasionen von Amphisteginen in Miozänen Foraminiferengemeinschaften aus dem Wiener Becken und Polen, welche bezeichnend für biogeographische Erweiterungen zu dieser Zeit sind. Die zunehmende Erweiterung der Expansionsfront im Mittelmeer zeigt, dass es zu Veränderungen in Foraminiferenvergesellschaftungen kommt und es zu weitreichenden Folgen für das Funktionieren des Ökosystems führen kann. Die Häufigkeit und der Impakt invasiver Amphisteginen resultiert demnach in (1) dem Rückgang der benthischen Foraminiferendiversität, (2) Veränderungen in den Strukturen nativer Foraminiferenvergesellschaftungen und (3) Veränderungen in der Häufigkeit funktionaler Foraminiferengruppierungen.

Darüber hinaus wurden benthische Foraminiferenvergesellschaftungen (ebenfalls von Amphisteginen besiedelt) in vom Menschen beeinflussten und nicht beeinflussten Gebieten innerhalb des Mittelmeeres untersucht, welche bis zu diesem Zeitpunkt überhaupt nicht untersucht wurden.

Die Lokation innerhalb des Mittelmeeres ist die Küste Albaniens, welche entlang des nordöstlichen Ionischen Meeres und entlang der südöstlichen Adria verläuft. Die Flachwassergebiete liefern ein weiträumiges Angebot an Habitaten, welche von zahlreichen marinen Arten besiedelt werden. Die Zusammensetzung und Verbreitung von benthischen Flachwasserforaminiferen wurde im Zusammenhang mit gegebenen Substraten und ökologischen Bedingungen dokumentiert. Die gesammelten Proben zeigen eine hohe Artendiversität (277 Arten, 112 Genera) und beinhalteten Taxa, die sowohl in der Adria, als auch im östlichen und westlichen Mittelmeer verbreitet sind. Die hierarchische Clusteranalyse zeigt zwei unterschiedliche Cluster und Biofazies, welche für die nördliche beziehungsweise südliche Küste charakteristisch sind. Das Vorkommen nicht indigener Arten mit Indo-Pazifischem Ursprung wurde ebenfalls dokumentiert. und ist hauptsächlich durch steigende Wasseroberflächentemperturen und der anhaltenden Verbreitung durch Meeresströmungen gesteuert. Ballastwasser von Schiffen wird ebenfalls zu einer der Hauptursachen für das Auftreten nicht-indigener Arten überlegt. Die invasive benthische Foraminiferenart Amphistegina lobifera ist gegenwärtig die häufigste Art, welche sich mit weitreichenden Folgen für native Foraminiferenvergesellschaftungen und dem Funktionieren des Ökosystems entlang der albanischen Küste ausweitet.

#### Acknowledgements

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#### **Background and Motivation of the thesis**

Climate change and biological invasions are key processes that modify biodiversity. One of the most severely affected areas of global change is the Mediterranean Sea, where global warming, the opening of the Suez Canal and increasing maritime traffic triggered a mass invasion of tropical taxa (especially of Indo-Pacific origin) into the Mediterranean territories. The Mediterranean Sea is acting as a transition area between subtropical and mid-latitudes. It is a climate change hot spot and as an enclosed miniature ocean it serves as natural laboratory for climate induced invasions and future changes.

Global warming and the extension of the tropical belt lead to a poleward range extension of tropical species. Among the key taxa that are rapidly expanding their latitudinal range are larger symbiontbearing benthic foraminifera. Range shifts and latitudinal expansions are most pronounced in species of the genus Amphistegina. The Mediterranean Sea represents the northernmost geographical extension of amphisteginid foraminifera. Here, they are particularly abundant and successful invaders. Their range expansion correlates with rising sea surface temperatures that mirror processes of global change. As ecosystem engineers (organisms that interact with the recipient environment and modify habitats), amphisteginids are among the most prominent foraminiferal species in tropical- to subtropical reef and shelf regions of the world's oceans, contributing significantly to shallow-water carbonate sediments. In the Mediterranean Sea, amphisteginid foraminifera are among the 100 worst invasive species, changing the habitat structures and altering species and sediment composition of coastal nearshore ecosystems. Given their prominent environmental role, rapid biogeographic range expansion, and impact on native ecosystems, amphisteginid range expansion and invasion into new territory are likely to trigger changes in future ecosystem functioning. Among the uncertainties, it is not known whether all parts of the Mediterranean Sea will be affected equally and to what extent amphisteginid invasions will impact native biotas. They are rapidly progressing northwestwards, closely approaching the Adriatic and Tyrrhenian Sea.

The present study uses amphisteginid foraminifera as model taxa and serves as baseline study to explore the effects of invasive amphisteginid foraminifera in native foraminiferal assemblages in the Mediterranean Sea. Expansion rates and effects of shifting community structures are explored including ecosystem functioning along the northwestern range expansion front and in areas that have been invaded by amphisteginids decades ago.

Furthermore, benthic foraminiferal assemblages in anthropogenic impacted and non-impacted areas (also partly inhabited by amphisteginids) within the Mediterranean Sea are documented. So far, some of the new study sites have not been investigated before. The study area is the seacoast of Albania, located along the north-eastern Ionian and southeastern Adriatic Sea.

The following general introduction gives an overview of the oceanographic setting and outlines ancient and recent biodiversity patterns in the Mediterranean Sea. Furthermore, it summarizes recent anthropogenic pressures on the Mediterranean Sea accompanied with climate warming trends and its consequences for native biotas. The introduction of non-indigenous (alien) and invasive species and the numbers of alien benthic foraminifera including the worst invasives are summarized at the end of the general introduction.

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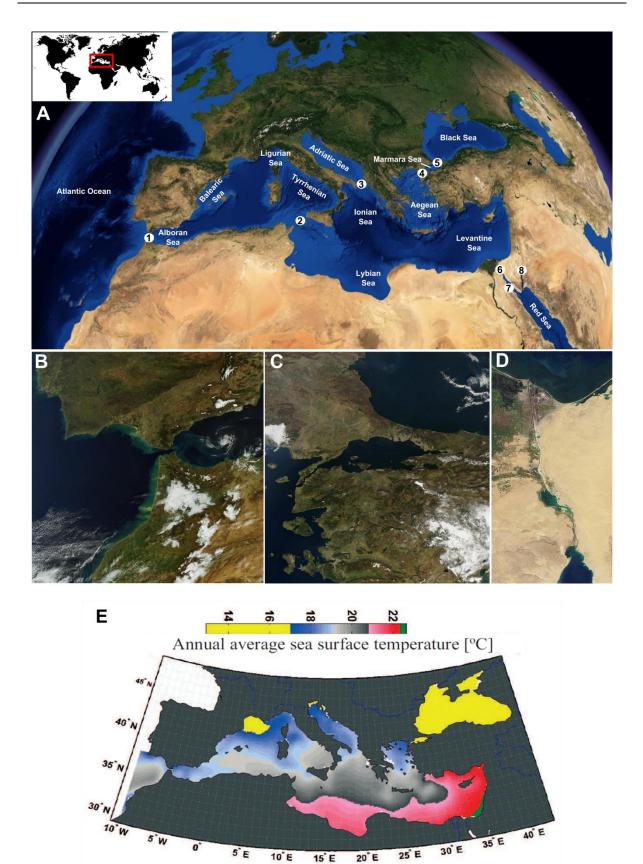
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#### Part 1 General Introduction

#### 1.1 The Mediterranean Sea

The Mediterranean Sea (Mare medi terraneum latin: "sea in the middle of land") is the largest (2.969.00 km2) and deepest (average 1.460m, maximum 5267m) enclosed sea on earth (Coll et al. 2010). As mid-latitude ( $30^{\circ}$  to  $46^{\circ}$  N and  $6^{\circ}$  to  $36^{\circ}$  E) enclosed 'miniature ocean', the Mediterranean Sea lies between Europe, Asia and Africa. The Mediterranean Sea covers an approximate surface area of  $2.5 \times 10^6$  km<sup>2</sup> (Pinte, 2003), which is 0.82% of the surface area of the world's oceans and 0.32% of the world water volume (Bianchi and Morri, 2000). It is characterized by shelf waters representing 20% of the total Mediterranean waters, compared to 7.6% of the world's oceans (Pinardi, 2006; Coll et al. 2010). The Sea is connected to (1) the Atlantic Ocean through the 14km wide and 320m deep Strait of Gibraltar in the West, to (2) the Sea of Marmara and the Black Sea, by the 70.1m deep Dardanelles and the 91.4m deep Bosporus respectively in the Northeast and to (3) the Red Sea via the 163km long man-made Suez Canal in the Southeast (Fig. 1B-D). The exchange with the Atlantic Sea in the west is essential as it plays an important role in the circulation and productivity of the Mediterranean Sea (Turley, 1999). On the other hand the very saline outflowing Mediterranean water also plays an important role for the deep circulation of the Atlantic and even the stability of the global thermohaline equilibrium state (Robinson et al. 2001; McCartney and Mauritzen, 2001; El-Geziry and Bryden, 2010). The Mediterranean circulation is forced by water exchange through the various straits, by wind stress, and by buoyancy flux at the surface due to freshwater and heat fluxes (Robinson et al. 2001). The Mediterranean Sea is known as a concentration basin, with a higher evaporation rate in the eastern basin, causing the water level to decrease and salinity to increase from west to east. The resulting pressure gradient pushes relatively cool, low-salinity and nutrient depleted water from the Atlantic across the Mediterranean basin, where it warms up to the east and becomes saltier and then sinks in the Levantine Sea before circulating west and exiting 80-100 years later through the Strait of Gibraltar (Turley, 1999; Coll et al. 2010; Fig. 2). There is a west-east gradient in ocean productivity, with increasing oligotrophy eastwards (Turley, 1999). The Mediterranean Sea is composed of two nearly equal sized basins, connected by the Strait of Sicily, which is a shallow ridge at 400m depth separating the Island of Sicily from the coast of Tunisia. The western Mediterranean sub-basin is around  $0.85 \times 10^6$ km<sup>2</sup> and is subdivided into the Alboran, the Balearic, the Ligurian and the Tyrrhenian Sea, whereas the eastern Mediterranean sub-basin is around  $1.65 \times 10^6$  km<sup>2</sup> large and is subdivided into the Ionian, the Levantine and the Aegean Sea. The Adriatic Sea is northernmost located sub-basin, and is seen as a separate area. The annual average sea surface temperature shows a high seasonality and important gradients from west to east and north to south (Hopkins, 1985) and is calculated to be 19.7 +/- 1.3°C (Fig. 1E). Much warmer water occurs over only 0.4% of the Mediterranean Sea, especially to the east of the Levantine sub-basin, and much colder water occurs over only 2.8% of the Mediterranean Sea, especially in the Gulf of Lions and in the north Adriatic Sea (Coll et al. 2010). The spatial pattern of the Mediterranean SST differs significantly from season to season, being 9.7–17.7°C in winter, 15.8– 22.1°C in spring, 20.8–28.3°C in summer and 15.1–23.4°C in autumn (Shaltout and Omstedt, 2014).



**Fig. 1A** Biogeographic areas in the Mediterranean Sea. 1=Strait of Gibraltar, 2=Strait of Sicily, 3= Strait of Messina, 4=Strait of Otranto, 5=Dardanelles, 6=Bosporus, 7=Suez Canal, 8= Gulf of Suez, 9=Gulf of Aqaba, **1B** Strait of Gibraltar, **1C** Dardanelles and Bosporus, **1D** Suez Canal, **1E** Spatial distribution of annual average SST means over the 1982-2012 period (Shaltout and Omstedt, 2014).

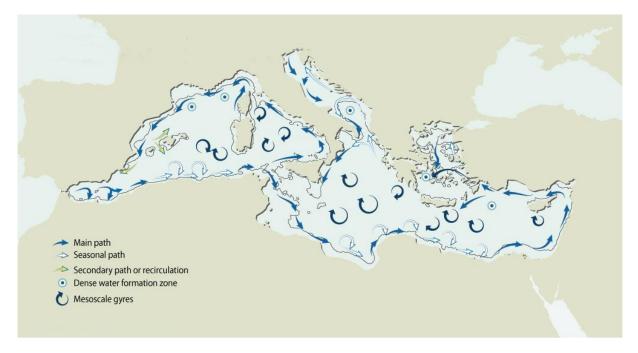


Fig. 2 Sea surface circulation in the Mediterranean Sea (after Millot and Taupier-Letage, 2005).

# **1.2** Mediterranean and Paratethys seaways influencing ancient and recent biodiversity traits in the Mediterranean Sea

The present shape of the Mediterranean Sea is the result of continuous interaction of complex geodynamic processes during the last 50-70 million years (Sohelme, 2005). The Mediterranean Sea is a remnant of the east-west oriented Tethys Ocean, a wedge-shaped eastward-open equatorial water body, which in the early Jurassic (200 million years ago) separated the two supercontinents Laurasia in the north and Gondwana in the South (Bianchi and Morri, 2000; Lejeusene et al. 2009). The final closure of the Tethys Ocean close to the Eocene/Oligocene boundary and the creation of the Mediterranean Sea at its western end as well as the intercontinental Paratethys Sea to the north were caused by a reorganization of the lithospheric plates (Rögl, 1999; Steininger and Wessley, 2000). This includes the northward movement of India and Australia, the beginning collision of India and Asia in the late Eocene, the northward movement and counterclockwise rotation of Africa from the Late Eocene onwards as well as the collision of Africa and its sub-plates (e.g. the Adriatic and Arabian subplate) with the Eurasian plate and subplates (Steininger and Wessley, 2000).

#### 1.2.1 Mediterranean and Paratethys seaways from late Eocene to early Pliocene

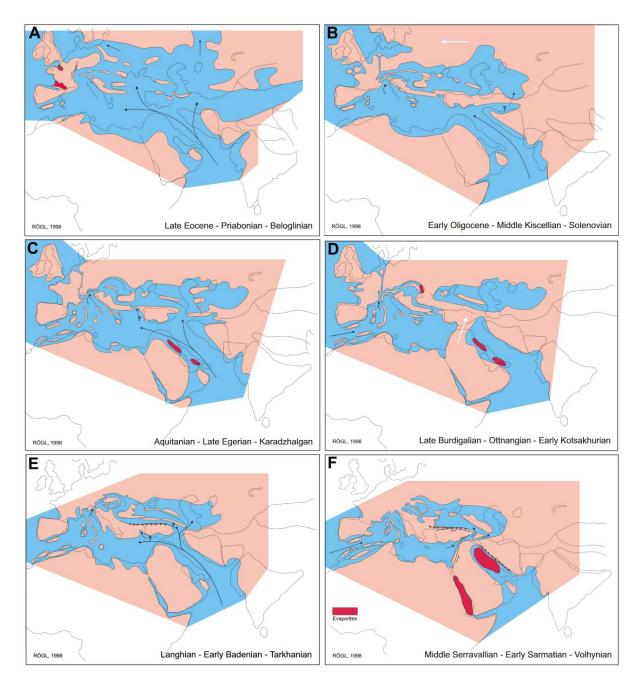
During the development of the Mediterranean basin, several seaways opened through lithospheric processes that connected this area with the Atlantic-, the Indo-Pacific- and the North Sea-realms. Through temporary connections to the Paratethys Sea, there have also been connections to the northern Polar Sea via the Turgai Strait during the Late Eocene. These seaways allowed marine faunal exchanges influencing the Mediterranean region until now. The following paragraph briefly summarizes the main seaways that developed during the late Eocene to early Pliocene times (Table 1, Fig. 3).

During the late Eocene the Mediterranean realm was characterized by an open marine connection with the Indo-Pacific and the Atlantic, as well as a connection with the North Sea via the "Danish-Polish trough. The Turgai Strait, a shallow water seaway, allowed for a faunal exchange of warm water

faunas of the Tethys towards the polar waters in the north (Rögl, 1998b; Steininger and Wessley, 2000, Fig.3A). From the Late Oligocene to early Miocene, horizons of tropical, larger foraminifera and molluscs are reported from the Mediterranean, the Paratethys and the Middle East (Adams, 1973, 1976, 1983; Baldi and Senes, 1975; McGowran, 1979, a, b; Popov et al. 1993; McCall et al. 1994). This is connected with a worldwide widening of the tropical belt in the marine realm at that time (Rögl, 1999). During the Oligocene the Mediterranean area was still connected with the Atlantic and the Indo-Pacific by a wide open seaway (Fig. 3B). A connection to the Paratethys was given through the Dinaride corridor and via the Molasse basin. The opening of the Rhine graben provided an active seaway from the Molasse Basin to the North Sea realms (Steininger and Wessley, 2000). In the early Miocene (Aquitanian to Early Burdigalian) the Arabian sub-plate moved in a counterclockwise direction and faster towards the northeast than the African plate, which caused the opening of the Red Sea. It also caused the beginning of evaporitic environments on the northeastern edge of the subplate and narrowed the Indo-Pacific seaway. The northward movement of the African plate system created the emerging Atlas and the Betic mountain chains, which narrowed the Atlantic seaway. A connection of the Paratethys to the Mediterranean Sea was present through the "Transtethyan Trench Corridor" from Slovenia via the Venetian Basin. This triggered the immigration of western Mediterranean faunal elements (bryozoan, Mollusca) into the western and central Paratethys. The connection of the Paratethys to the West and from here to the North via the Rhine Graben was not active anymore (3C, Steininger and Wessley, 2000). The progressive counterclockwise rotation of the Arabian sub-plate and its collision with the Anatolian plate accompanied with a sea level drop during the middle Burdigalian closed the Indo-Pacific/Mediterranean/Paratethyan seaway (Fig. 3D). In the Late Burdigalian the Eastern Paratethys became isolated with reduced salinity and an endemic fauna. The renewed seaway in the Alpine Foredeep was again connected to the North Sea by the Rhingraben (Rögl, 1998a, b). The Mediterranean was connected with the Atlantic Ocean and fed the western and central Paratethys. But the Mediterranean realm was also separated from the Indo-Pacific through the Arabian Peninsula, which collided with the Anatolian Plate establishing the "Gomphotherium" land bridge (Rögl, 1998a, b, 1999). The Mediterranean-Indo-Pacific seaway reopened during the beginning of the Middle Miocene, which is marked by a world-wide sea level high (TB 2.3 of Haq et al. 1988; between Bur5/Lan1 and Lan2/Ser1 of Hardenbol et al. 1998) corresponding to a global warming phase and widespread warm water elements (warm water planktonic foraminifera, mass occurrences of larger foraminifera of Indo-Pacific origin, tropical to subtropical corallinacea/coral reefs growing as far north as Krakow (Poland) and tropical mollusk faunas and fishes). This sea level rise also flooded the Eastern Paratethys transgressively, which was still linked to the Mediterranean by the "TransTethyan Trench Corridor" via the Venetian Basin to Slovenia and the Drava-Sava Basin respectively (Fig. 3E). Due to a regressive phase during the Servallian and in the middle Badenian-Karaganian respectively (TB 2.3/TB 2.4 sea level drop of Haq et al. 1988; between Lan2/Ser2 and Ser2/Ser3 of Hardenbol et al. 1998) the Indo-Pacific marine link with the Mediterranean and the Eastern Paratethys ceased and disconnected the Mediterranean and the Paratethys from the Indo-Pacific realm (see Rögl, 1999; Steininger and Wessley, 2000; 3F). The brief reopening and restoration of marine conditions through the Mesopotamian 'corridor' flooded the Eastern and Central Paratethys but did not reach the Mediterranean Sea. The movements along the Anatolian fault system, caused by the northward motion of the Arabian plate activating the Dead Sea fault system, opened a narrow marine connection from the Eastern Mediterranean towards the Eastern Paratethys and created a transgressive sequence (Fig. 3F). In the Tortonian the Aegean Sea opened and by this time another connection via the Dardanelles towards the Eastern Paratethys came into existence (Steininger and Wessley, 2000). Short living marine excursions are known to have occurred several times in the Late Miocene from the Aegean into the Eastern Paratethys (Rögl and Steininger, 1983) and the Maeotian Paratethys fauna migrated into the Aegean Sea (Papp et al. 1978). During the late Miocene (5.65.3 mya), the communication between the Mediterranean and Atlantic Ocean was interrupted on several occasions by events known as 'Messininan Salinity Crisis' (MSC) and the Mediterranean almost entirely dried out (Govers, 2009). The MSC and the following desiccation had a deep impact on the Mediterranean biota. The deep sea fauna became extinct (Bouchet and Taviani, 1992), whereas the shallow water biota may have survived in refuge areas through the Neogene (Stanley, 1990; Bellan-Santini et al. 1992; Myers, 1996). The interconnected Paratethyan water bodies became disconnected and evolved into fresh water lake systems, which were successively drained and began to dry up. The endemic Paratethys biofacies even invaded the Mediterranean region through the Aegean. Wide areas of the Mediterranean were populated by the 'Lago Mare' facies with brackish conditions overlaying the Messinian evaporates, whose origin is traced back to the Eastern Paratethys (Rögl and Steininger, 1983). The Mediterranean basin was flooded by the Zanclean flood in Early Pliocene times, so that the modern Mediterranean Sea came into existence through marine waters from the Atlantic. As such the biogeographic physiognomy of the Mediterranean Sea became that of an Atlantic province (Briggs, 1974). This transgression also reached the Eastern Paratethys (Taner, 1980, 1982) via the Dardanelles, went over the Aral Sea and probably reactivated the Turgai-Street over the Caspian Sea into the north (Vinodradov, 1967-1969; Semenenko, 1979). The Pannonian and Dacian basin in the central Paratethys silted up creating the modern Danube river drainage system (Fink, 1966). (Rögl and Steininger, 1983; Rögl, 1998a, b, 1999; Steininger and Wessley, 2000).

**Table 1** Stratigraphic correlation chart of the standard scale with Central Paratethys and Eastern Paratethys regional stage systems, and the planktonic foraminifera and calcareous nannoplankton biozonation (according to Berggren et al. 1995; Popov et al. 1993; Rögl 1996, 1998b).

	т							DNES & al. 1995
M.A.	EPOCH	AGE	CENTRAL PARATETHYS STAGES	EASTERN PARATETHYS STAGES		Planktonic Foraminifera		Calcareous Nannoplankton
5 —	PLIO- CENE	ZANCLEAN	ZANCLEAN DACIAN KIMMERIA		IERIAN	PL1 M14		NN13 NN12
-	5.3 BN	MESSINIAN	PONTIAN	PONTIAN				
- - 10—	LATE MIOCENE	TORTONIAN	PANNONIAN		OTIAN Khersonian	М13	b a	NN11 NN10 NN9b
-	<u>11.0</u>		SARMATIAN	Bess- arabian		M1 M1 M8	1-	NN9a/8 NN4
-	MIDDLE	SERRAVALLIAN		Kor Karag	Volhynian kian ganian yrakian	M7		NN6
15—	_ ≥ <u>∍</u> 16.4	LANGHIAN	BADENIAN	Tshokrakian TARKANIAN		M6 M5		NN5
-			KARPATIAN	KOTSAKHURIAN		M4		NN4
-		BURDIGALIAN	OTTNANGIAN			M3		NN3
20-			EGGENBURGIAN	SAKARAULIAN KARADZHALGAN KALMYKIAN		M2		NN2
-		AQUITANIAN				M1	b a	NN1
- 25— -	-	CHATTIAN	EGERIAN			P22		NP25
-	OLIGOCENE		KISCELLIAN	SOLENOVIAN		P21	b a	NP24
30— -		RUPELIAN				P19		NP23
-	33.7			PSHEKIAN		P18		NP22 NP21
- 35—						<u>P17 –</u> P16		NP 19-20
-	LATE EOCENE	PRIABONIAN PRIABONIAN		BELOGLINIAN		P15		NP18



**Fig. 3** Paleogeographic reconstruction of the Mediterranean and Paratethys region from Late Eocene (Priabonian) to Middle Miocene (Serravallian) (A)Lower Eocene (B) Early Oligocene (C) Aquitanian (D) Late Burdigalian (E) Langhian (F) Middle Serravallian, (Rögl, 1998b).

#### 1.2.2 Recent biogeography of the Mediterranean Sea

The alternations of the ice ages with warm interglacials during the whole Quaternary resulted in different immigration waves of Atlantic fauna of boreal and subtropical origin, respectively (Bianchi and Morri 2000). During low sea water temperatures of the glacial periods, the Mediterranean was invaded by cold water biota from the northern Atlantic, while during the last Interglacial (Eem~ 125.000-110.000 years ago), there are fossil proofs that the West African tropical fauna and faunal elements from the Canary, Madeira and Cap Verde Islands (altogether the so called 'Senegalese faunas') succeeded to overcome the cold Canaries current barrier and the temperature barrier in the Mediterranean and reach the Levant (Por, 2009).

The recent Mediterranean Sea is one of the world's biodiversity hot spots with approximately 17,000 marine species including high percentages of endemic taxa (Tortonese, 1985; Boudouresque, 2004; Coll et al. 2010; Lejeusne et al. 2010). However, the estimates of marine diversity are still incomplete, as for example the numbers of microbes are substantially underestimated and deep sea areas and portions of the southern and eastern region are still poorly known (Coll et al. 2010, 2012; Bianchi et al. 2012). Additionally, the invasion of alien species continues to change the biodiversity of the Mediterranean (chapter 1.5 and 1.6). The high biodiversity may be explained (1) by the geological history of the last 5 mya leading to the occurrence of distinct biogeographic areas (explained below), (2) by its variety of climatic and hydrological settings within a single basin with probably no equals in the world, as well as (3) by the fact that the Mediterranean Sea belongs to the best studied areas and therefore ranks among the best known regions in the world (Bianchi and Morri, 2000; Coll et al. 2010). Spatial patterns show a general decrease in biodiversity from northwestern to southeastern regions, while biodiversity is higher in coastal areas and the continental shelves, whereas it decreases with depth (Coll et al. 2010). The western Mediterranean Sea has a maximum of 391 species in a 10x10 km cell, compared to the Eastern Mediterranean Sea, where a minimum value of 84 species is mapped in a 10x10km cell (Katsanevakis et al. 2014b). The Mediterranean biota has historically been divided into three biogeographical provinces (the western and eastern basins, and the Adriatic Sea), each subdivided along latitudinal patterns (Fredi, 1972). The climate and hydrology of the Mediterranean Sea have contributed to the co-occurrence and survival of both temperate and subtropical species, with temperate species dominating the northern parts and subtropical species being more abundant in the southern parts of these provinces (Lejeusne et al. 2009; Coll et al. 2010). More recent studies demonstrate the presence of more than three biogeographical areas. Bianchi and Morri (2000) suggest ten biogeographical areas composed of species that tend to occur more or less abundantly in different parts of the Mediterranean: (i) a temperate Atlantic- Mediterranean background; (ii) cosmopolitan/panoceanic species; (iii) endemic elements, comprising both paleoendemic species (possibly of Tethyan origin) and neoendemic species (mainly of Pliocenic origin); (iv) subtropical Atlantic species (interglacial remnants, especially of the Tyrrhenian Stage); (v) boreal Atlantic species (ice-ages remnants, especially of the Würm glacial); (vi) Red Sea migrants (especially into the Levant Sea); (vii) eastern Atlantic migrants (especially into the Alboran Sea). After this biogeographic classification the most typical Mediterranean flora and fauna obviously occur in the central parts of the Sea and especially in the western basin, whereas the Alboran Sea exhibits stronger influence of Atlantic species, due to the continued penetration of Atlantic flora and fauna with the incoming flux of water from the Strait of Gibraltar (Harmelin and d'Hont, 1993). The Levantine Sea is experiencing an important influx of Red Sea species so that the south-eastern Mediterranean Sea has been proposed as a separate biogeographic province (Por, 1999). Nevertheless the western Mediterranean displays the highest species richness values, followed by the central Mediterranean, Adriatic and Aegean Sea that are areas of medium species richness, whereas the Levantine and the southeastern basin in general have the lowest species richness, due to unfavorable conditions prevailing in this area (Coll et al. 2010).

#### 1.3 Recent anthropogenic pressure on the Mediterranean Sea

The highly diverse ecosystems within the Mediterranean Sea are under threat due to human activities. There is growing evidence that human activities are directly or indirectly resulting in an impoverishment of the Mediterranean marine biota (Relini, 1992). Human activities that likely affect species diversity and ecodiversity (ecosystem diversity) are coastal development (unplanned urban development, reclamation, port facilities, habitat alienation, artificial beaches, groynes that alter sediment transport), dredging, dumping (solid waste), fishing (commercial fishing, trawling,

overfishing and amateur fishing) and pollution (nutrients, organic matter, heavy metals, turbidity, and aquaculture facilities) (Boudouresque et al. 2005). The main reservoir of biodiversity, the continental shelf and more particularly the subtidal zone (from sea level to 30-40m water depth) are mostly affected (Meinesz et al. 1981, 1982, 1991; Boudouresque, 2003; Boudouresque et al. 2005). A demographic aspect is given by increasing population rates especially along the coastal areas (particularly along the southern shores) which seem likely to result in eutrophication and an increased risk of pollution (Turley, 1999). Ocean warming caused by anthropogenic climate change is already starting to impact the marine biota, with possible consequences for ocean productivity and ecosystem services (Wohlers et al. 2009). Anthropogenic impacts are shown in changing N:Si and Si:P ratios due to surface inputs, which results in a shift from phytoplankton that is dominated by siliceous species (diatoms) to assemblages dominated by non-siliceous species (flagellates and dinoflagellates) (Bethoux et al. 2002). Changes in marine plankton may have consequences for biogeochemical cycles (such as oceanic carbon uptake by reducing efficiency of the biological pump), climate patterns, fisheries and the structure and function of marine ecosystems (Lewandowaska et al. 2014). A further anthropogenic factor resulting in hydrological imbalance in the Mediterranean Sea is damming. Reduced river flow from the Nile due to damming has been estimated to have a profound influence on the freshwater budget entering the Mediterranean (Rohling and Bryden, 1992; Bethoux and Gentili, 1996). Thus damming of the Nile may not only have deleteriously influenced the productivity, biogeochemistry and food web structure in the delta and Eastern Mediterranean, but also the hydrological functioning and structure of the whole of the Mediterranean which itself will influence the chemical and biological characteristics in a feedback loop (Turley, 1999). This hydrological imbalance in the Mediterranean Sea may also have far-reaching consequences in the circulation of deep water in the Atlantic, as the saline Mediterranean outflow water affects water formation processes in the Atlantic and even the stability of the global thermohaline equilibrium state (Robinson et al. 2001; El-Geziry and Bryden, 2010). Climate changes in Northern Europe similar to that seen during the last glaciations may also be linked to a hydrological deficit in the Mediterranean Sea resulting from a decline in the Nile outflow (Turley, 1999).

Increasing anthropogenic induced greenhouse gas emissions result in ocean acidification and warming of the world oceans. Global atmospheric carbon dioxide (CO<sub>2</sub>) has increased from a pre-industrial concentration of 280 ppm to a current concentration of ~400 ppm (Keeling et al. 2013). Current  $CO_2$ concentrations are nearly 40% above pre-industrial levels and are likely to double by the end of this century (Feely et al. 2009). Approximately one-third of the carbon dioxide produced by human activities have been absorbed by the oceans resulting in acidification of the surface layers of the oceans with a steady decrease of 0.02 pH units per decade over the past 30 years and an overall decrease since the pre-industrial period of 0.1 pH units (Doney et al. 2009; Hoegh-Guldberg and Bruno 2010). Open ocean pH values have decreased since the pre-industrial era from 8.2 to approximately 8.1 in 2014 and are predicted to decrease another 0.3 to 0.5 during the next 80 years (Cicerone et al. 2004; Orr et al. 2005). These decreases are associated with a substantial decline in the concentration of carbonate ions in the water with deleterious effects on many calcifying organisms (Fabry et al. 2008; Kroeker et al. 2010, 2013). These effects include lower calcification rates, lower development rates, lower fertilization success and decreased larval size (Kroeker et al. 2013). This may reduce the fitness of calcifiers and consequently result in decreased abundances and lower species richness (Bambach, 1983) through ecological replacement by non-carbonate producers (Kuffner et al. 2008; Busch et al. 2013; Fabricius et al. 2014). Reduced calcification rates and lower abundances may go along with a reduction of the contributions of calcifiers to the carbon budget and a reduction of marine carbonate sedimentation (Muller, 1974; Milliman, 1993). Long-term data series (over several decades) of changes in relative acidity of the Mediterranean Sea are scarce (Calvo et al. 2011; The MerMex Group, 2011) but recent re-analysis, however, has concluded that the pH of the Mediterranean waters has decreased by 0.05 to 0.14 pH units since the preindustrial period (Luchetta et al. 2010; Touratier and Govet, 2011). The Mediterranean Sea represents only 0.8% of the global oceanic surface and despite the general sparseness of water column CO<sub>2</sub> measurments (Alvarez, 2012) it has been identified as important anthropogenic carbon storage where the column inventory is much higher compared to the Atlantic or Pacific oceans (Schneider et al. 2010; Lee et al. 2010). It is not clear how increasing  $CO_2$  concentrations may affect ecosystem functioning in the future, because some calcifying and non-calcifying organisms, such as echinoids (Amphiura filiformis, Wood et al. coccolithophorids (Emiliani huxleyi, Iglesias-Rodriguez et al. 2008), frondose algae, 2008). seagrasses (Posidonia oceanica, Hall-Spencer et al. 2008) and some larger benthic foraminifera (Baculogypsina sphaerulata, Fujita et al. 2011), reacted to increased CO<sub>2</sub> partial pressures by increased rates of calcification, photosynthesis, and regeneration. The potential for marine organisms to adapt to increasing  $CO_2$  and broader implications for ocean ecosystems are not well known and need some long-term studies to observe chronic exposure to increased  $CO_2$  values, which (1) may have complex effects on the growth and reproductive success of calcareous organisms and (2) could induce possible adaptations that are not observed in short-term experiments (Doney et al. 2009). However, recent observations demonstrate that most of the calcifying organisms suffer under increased CO<sub>2</sub> concentrations. A great impact is expected on calcifying phytoplankton (coccolithophorids), which plays a significant role in the primary production of the generally oligotrophic Mediterranean Sea (Coll et al. 2010). Sessil calcifying benthic organisms such as calcareous red algae that provide important reef structure in the Mediterranean may also be severely impacted by increasing CO<sub>2</sub> concentrations (Kuffner et al. 2008) through lower calcification rates and dissolution, but also due to increasing sea surface temperatures. Studies in open-water marine conditions in the Mediterranean Sea show that low pH stations around volcanic vents emiting carbon dioxide from the sea floor at ambient seawater temperatures results in the disappearance or strong reduction of most of the calcifying organisms, such as the majority of Foraminifera, Bivalvia, many Gastropoda and all Spirorbidae polychaetes (Dias et al. 2010, Cigliano et al. 2012). This underlines how sensitive these organisms react on ocean acidification, which may cause significant changes in their assemblages (Dias et al. 2010) in future. Phototrophic marine calcifiers (such as coccolithophorids, foraminifera, calcareous algae and corals) strongly contribute to the cycling of carbon in the world's oceans, as part of the 'biological pumps' (Gattuso and Buddemeier, 2000; Riebesell et al. 2007; Ridgwell et al. 2009), so that by changes in ocean chemistry ocean acidification poses a direct threat to most calcifying organisms and consequently the biological pump (Doney et al. 2009; Fabry et al. 2008; Ries et al. 2009; Glas et al. 2012).

Global average temperatures have increased by  $0.2^{\circ}$ C per decade over the last 30 years due to rising atmospheric greenhouse concentrations (Hansen et al. 2006). Most of this CO<sub>2</sub> is absorbed by the world's oceans, so that the upper layers of the global oceans have increased by  $0.6^{\circ}$ C over the past 100 years (IPCC, 2007), with an increasing heat content of 14x1022 J since 1975 for the upper 700m (Levitus et al. 2009). The average global sea surface temperature for 2016 was the highest in the 137-year record, at 0.76°C above average, surpassing the previous record set in 2015 by  $0.03^{\circ}$ C (NOAA, 2016). Sea surface warming and its consequences for the Mediterranean Sea and its biota are commented on in the next sub-chapter.

#### **1.4 Climate warming in the Mediterranean Sea and consequences for marine biotas**

The Mediterranean Sea is vulnerable to increasing sea surface temperatures because it acts as a transition area between subtropical and mid-latitude climates, and as such it is a climate change hot spot (IPCC, 2007; Lionello et al. 2010). Data collected in the Mediterranean Sea show that sea surface temperatures (SST) over the last 30 years have raised at a much faster rate than documented for the time period between 1885 and 1976 (Bethoux et al. 1990, 1999; Prieur, 2002; Romano and Lugrezi, 2007; Vargas-Yanez et al. 2008; Theocharis, 2008; Coma et al. 2009; Nykjaer, 2009; Lejeusne et al. 2010). Sea surface temperatures from in situ measurements reveal the presence of a cooling trend in the upper 150m layers during the 1970's until the 1980's, before an extensive warming period began in approximately the 1980's respectively the mid- 1980's (Lelieveld et al. 2002; Rixen et al. 2005). Recent observations show that the annual trend distribution of the Mediterranean sea surface temperatures range from 0.017°C yr<sup>-1</sup> (in the mid-western Ionian sub-basin) to 0.05°C yr<sup>-1</sup> (north-east of the Levantine sub-basin), with average values of  $0.035\pm0.007$  °C yr<sup>-1</sup>. There is a significant seasonal warming trend over the Mediterranean Sea, ranging from 0.016±0.001°C yr<sup>-1</sup> in winter to  $0.038\pm0.109$  °C yr<sup>-1</sup> in spring. Similarly, the maximum warming trend displays seasonal behavior, being 0.04°C yr<sup>-1</sup> (in the northern Aegean sub-basin and south-east of Crete) in winter, 0.067°C yr<sup>-1</sup> (off the coasts of Mahdia, Tunisia and of Toulon, France) in spring, 0.058°C yr<sup>-1</sup> (southeast of Crete) in summer, and 0.061°C yr<sup>-1</sup> (north-east of the Levantine sub-basin) in autumn (Shaltout and Omstedt, 2014). Model simulations provide a comprehensive picture of substantial drying and warming of the Mediterranean region in the future, especially in summer, with average precipitation expected to decrease by 25-30% and temperatures expected to rise by 4°-5°C by the end of this century, approximately (Giorgi and Lionello, 2008; Lionello et al. 2010). Increased intensity in heat waves, dry spells and warmer and saltier water masses accompanied with changes in the mean sea surface circulation are expected to come along with the above mentioned changes. This may pose very serious problems to existing ecosystems and human societies within the Mediterranean in the future.

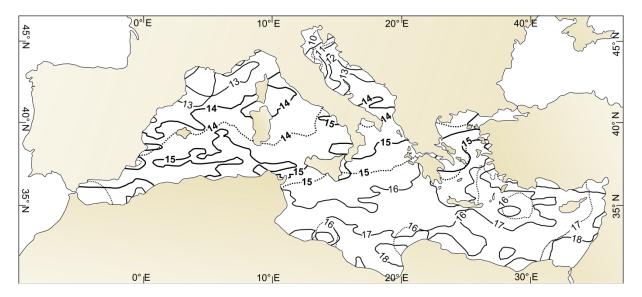
The Mediterranean region has been identified as one of the climate system's most responsive hotspots in the face of increased greenhouse gas forcing, particularly because of pronounced mean warming, large decreases in precipitation, and increases in inter-annual warm-season variability (Giorgi, 2006). Climate change accompanied by seawater warming is exerting a major effect on Mediterranean marine biodiversity (Bianchi, 1997, 2004; Schneider et al. 2007; Fowler, 2008; CIESM, 2008; Lejeusne et al. 2010). The relative shallowness of continental shelves makes them particularly vulnerable to warming (Harley et al. 2006). The increase in water temperature in the Mediterranean already alters population dynamics of marine species (e.g jellyfishes; Molinero et al. 2009) and may lead indirectly to fishing impacts (Coll et al. 2008). Analysis of the most recent 33-year temperature time series by Coma et al. (2009) demonstrated enhanced stratification in the Mediterranean Sea due to global warming, which produced a  $\approx 40\%$  lengthening of summer conditions. Warmer summer conditions coupled with reduced food resources may lead to increasing mass mortality events of important engineer species within the coralligenous community (Coma et al. 2009), which is one of the most diverse in the Mediterranean Sea with approximately 1,666 species (Ballesteros, 2006). Recent analyses have shown that changes in phytoplankton biomass and productivity correspond to ocean warming (Behrenfeld et al. 2006; Polovina et al. 2008; Boyce et al. 2010). This is essential as phytoplankton comprises between 14 and 30% of total oceanic primary production (Gattuso et al. 1998) and account for about 30% of oceanic respiration (Smith and Hollibaugh, 1993). Upper-ocean warming on vertical stratification indirectly affects phytoplankton by limiting nutrient supply rate and directly affects plankton metabolic rates (Lewandoweska et al. 2014). Nutrient limitation through warming of the surface waters results in reduction in phytoplankton biomass and a shift toward a phytoplankton

assemblage dominated by small phytoplankton (picophytoplankton) (Li et al. 2009; Moran et al. 2010). Size is a key property of phytoplankton, with far-reaching influences in the structure and functioning of pelagic food webs (Legendre and Le Fèvre, 1991; Cohen et al. 2003) and ultimately the biogeochemical fate of photosynthesized organic carbon (Falkowski et al. 1998) as it depend on phytoplankton size (Moran et al. 2010). The direct effect of warming on plankton manifests itself in increasing metabolic rates of both phytoplankton and zooplankton, and a growing imbalance between photosynthesis and respiration rates as temperatures increases (Lewandoweska et al. 2014). Heterotrophic processes are more sensitive to temperatures than autotrophic ones (Lopez-Urrutia et al. 2006; O'Connor et al. 2009), leading to higher grazing rates by zooplankton and a consequent reduction in phytoplankton biomass under warmer conditions (Sommer and Lengfellner 2008; O'Connor et al. 2009; Sommer and Lewandowska 2011). A study conducted in the Mediterranean Sea by Volpe et al. (2012) have shown that phytoplankton biomass and sea surface thermal stratification show a strong inverse relationship at seasonal and sub-basin scales. A gradual decline of phytoplankton biomass in the whole central Mediterranean Sea occurs with a delay of one year relative to the decrease of the cyclonic circulation in the eastern basin, and the northward shift of the Algerian current. Regionally, the phytoplankton biomass and the surface heat content anomalies associated with extreme atmospheric anomalies (such as the cold 1998-1999 winter and the summer 2003 heat wave) show as significant correlation with a ~5month time lag. One of the unexpected effects of warming observed in a study from the NW Mediterranean Sea about changes in the dinoflagellate genus *Ceratium* was the disappearance of species that are less tolerant to temperature change, rather than the appearance of warm water species. This caused a loss of biodiversity since it was not balanced with immigration of tropical species (Tunnin-Ley et al. 2009). On the other hand, the deepening of the stenothermic species may be considered as colonization over vertical dimension, a response to warming already observed for fish species (Perry et al. 2005) that is likely to occur for phytoplankton in future decades (Tunnin-Ley et al. 2009). Organisms for which population dynamics are mainly controlled by temperature, global warming may increase (production of an additional annual generation; Kiritani, 2006; Jönson et al. 2007) or decrease development (due to e.g lower fertilization rates or slower development). Climate warming thus plays an important role in triggering increases or decreases in population abundance and distribution of native and NI species (Walther et al. 2009).

Past changes and projected future increases in sea surface temperature in the Mediterranean Sea are shown in Figure 6. The 15°C isotherm, whose one-century climatological mean crosses the Straits of Sicily, may have moved northward in recent times, implying that a number of tropical Atlantic species that entered the Mediterranean during the last interglacial (125.000- 110.000 years ago) will reenter the Western Mediterranean in near future (Bianchi and Morri, 1993, 1994; Guidetti and Boero, 2001). In the meantime, in the Western Mediterranean, the "14°C divide" (Bianchi, 2007) the one-century climatological mean of the surface isotherm for February that coincides with a frontal system created by mesoscale eddies in the Algerian Basin (Millot, 2005) and that may act as a barrier to dispersal, has apparently moved northward in recent times (Fig. 4; Coll et al. 2010).

Rising temperatures and shifting of winter isotherms enlarges the pool of alien species that could establish themselves, enables the warm water species (native and alien) present in the sea to expand beyond their present distributions, and provides the thermophilic aliens with a distinct advantage over the native Mediterranean biota (Coll et al.2010). Numerous allochthonous species of tropical origin appearing in the Mediterranean Sea lead to the re-establishment of the Tethyan biota and the so called "tropicalization" of the Mediterranean Sea (Bianchi and Morri, 2003; Por, 2009).

It is uncertain what will happen to species of boreo-Atlantic origin established in colder parts of the Mediterranean Sea (Coll et al. 2010). They migrated into the Mediterranean during glacial periods but may dramatically decrease or even get extinct due to the impossibility to move (northwards). Warming stresses native dwellers adapted to lower seawater temperatures and facilitates the arrival and establishment of new arrivals, which is adding extra pressure on the ecosystem (Harris and Tyrell, 2001). There are also several unique, sensitive, endangered habitats (such as *Posidonia oceanica* meadows, coralligenous assemblages and vermited reefs built by the gastropod *Dendropoma patreum*) which may be affected due to increasing sea surface temperatures or the accompanied introduction of non-native species.



**Fig. 4** Recent northward shifting of February sea surface isotherms (°C) in the Mediterranean Sea (broken lines are the one-century climatological means, solid lines the means for 1985–2006: the 14°C and the 15°C "dividers" are highlighted by a thicker tract (modified after Coll et al. 2010).

# **1.5** Non-indigenous species in the Mediterranean Sea: status quo and main introduction pathways

The Mediterranean Sea is inhabited by an increasing rate of non-indigenous (NI/non-native, introduced or alien) species of tropical origin. The introduction of NI species is (beside a natural dispersal phenomena) almost primarily a human induced phenomenon through (1) the opening and enlargement of natural barriers (man-made canals), (2) increasing trade and maritime traffic on an international scale, (3) increasing warming rates triggered through increasing greenhouse gas emissions and it is directly influenced through (4) stressed coastal environments (polluted or physically degraded).

Abruptly rising sea surface temperatures since the end of the 1990's have modified the potential thermal habitats available for warm water species, facilitating their settlement at an unexpectedly rapid rate (Zenetos et al. 2012) and enables non-native species to migrate into the Mediterranean Sea. Winter temperatures, which are steadily increasing in recent times, are of great importance, since they must be above the lower tolerance limit of these species (Ben-Tuvia, 1966).

By transporting animals to habitats that they otherwise would never reach, humans have bridged the biological 'filter' imposed by geographic barriers (Simberloff, 1989; Williamson, 1989). Elton (1958) reported that invasions "most often come to cultivated land, or to land much modified by human practice." He expanded this view with the concept of biological resistance, wherein resistance by

established species against exotic species was greater in intact communities than those disrupted or disturbed by human activities (Lozon and MacIsaac, 1997). After White and Pickett (1985), disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. It has been shown that human activities are, furthermore, attributed with the establishment of NI (nonindigenous) species (animals and plants), while common mechanisms associated with the establishment included ballast water discharge, intentional releases, residential development (Lozon and MacIsaac, 1997) and ecosystem disturbance (Elton, 1958; Moyle, 1986; Orians, 1986; Hobbs, 1989; Mack, 1989; Rejmanek, 1989). The number of established non-native species is a function of both the supply of potential invaders, or propagule pressure, as well as susceptibility to invasion determined by both abiotic and biotic factors (Lonsdale, 1999; Lockwood et al. 2005). Studies in terrestrial and marine environments, however, demonstrated that polluted or degraded habitats favor invaders, independent of propagule pressure (Lozon and MacIsaac, 1997; Lonsdale, 1999; Stacowicz et al. 2002; Lockwood et al. 2005; Piola and Johnston, 2009; Olyarnik et al. 2009; Crooks et al. 2011). In general, within anthropogenically-modified systems, many non-native species may have advantages over natives (Dafforn et al. 2009; Johnston et al. 2009), as natives are now existing in conditions different than those in which they have evolved (Crooks et al. 2011). This has been called the "selection regime alteration" hypothesis, where non-natives are in essence 'preadapted' to conditions in recipient environments (Byers, 2002).

Western Mediterranean (WMED)	Central Mediterranean (CMED)	Adriatic (ADRIA)	Eastern Mediterranean (EMED)
Ligurian Sea	Greek Ionian Sea	Italian Adriatic Sea	Greek Aegean Sea
Monaco	Italian Ionian Sea	Slovenia	Turkish Aegean Sea
France	Albanian Ionian Sea	Croatia	Sea of Marmara
Corsica	South-easr Sicily	Montenegro	South Turkey
Sardinia	Malta	Albanian Adriatic Sea	Cyprus
Tyrrhenian Sea	Libya		Syria
Baleraic Islands	South Tunisia		Lebanon
Spain			Palestine Authority
Gibraltar			Israel
Morocco			Egypt
Algeria			
North Tunisia			
West Sicily			

**Table 2** Countries and coastal sectors included in the four sub-regions of the Mediterranean Sea (Zenetos et al. 2012).

To distinguish the abundance of alien species in the Mediterranean Sea, Zenetos et al. (2012) separate the Mediterranean into four sub-regions: The western, central and eastern sub-basin and the Adriatic Sea (Table 2). A total of 986 introduced species were reported from the Mediterranean Sea in the year 2012 and 2014 respectively, with 775 taxa in the Eastern Mediterranean (EMED), 249 in the central Mediterranean (CMED), 190 in the Adriatic Sea (ADRIA) and 308 in the western Mediterranean (WMED) (Zenetos et al. 2012, Fig. 5A-C). But the true numbers of introduced species are certainly downward biased, due to the exclusion of natural dispersed species, underestimation of microorganisms and lacking data about important and species-rich taxa (such as Porifera, Hydrozoa, Platyhelminthes, Nematoda, Acari, Harpacticoida, Ostracoda, Amphipoda; Por, 2009; Coll et al. 2010). But the high number of recorded introduced non-native species makes the Mediterranean Sea one of the most severely affected areas worldwide (Bourdouresque et al. 2005; Galil, 2007), with a

number of introductions that has doubled nearly every twenty years since the beginning of the 19<sup>th</sup> century (Ribera and Bourdouresque, 1995; Bourdouresque and Verlaque, 2002).

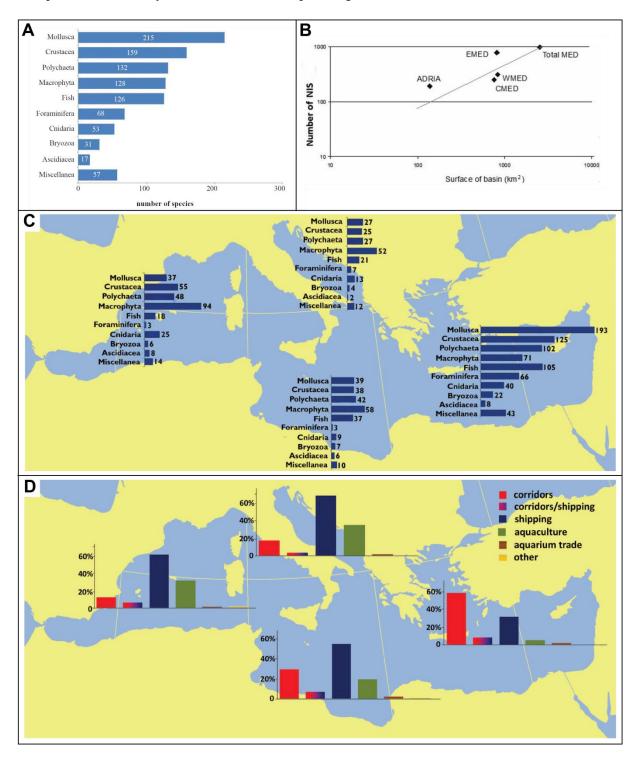
A great proportion of introduced species in the Mediterranean have the ability to become invasive. Invasive species are defined as (NI) species that act as key or engineer species within the recipient environment and which are therefore ecologically and/or economically harmful (Bourdouresque et al. 2005; Lejeusne et al. 2009; Walther et al. 2009). According to Jones et al. (1994, 1997) an ecosystem engineer refers to the process by which organisms interact with and modify habitats. They generate habitat changes without a concomitant increase in their own fitness. They may facilitate their own establishment and population expansion by reducing biotic resistance and modify local physical conditions in favour of enhanced recruitment of the invader within the new habitat (Willimason 1966; Davis et al. 2000), so that native species that were well adapted to the previous environmental regime no longer have a competitive advantage. The competitive advantage over native species allows invaders to spread rapidly and to conquer novel areas within the recipient ecosystem in which they become dominant (Valery et al. 2008).

Ben Rais Lasram and Mouillot (2009) consider that the currently warmer Mediterranean is acting increasingly as a "catchment basin" ("cul de sac") for southern species, with a (re-)colonization process, which is gaining speed and amplitude (Por, 2009). The increasing numbers of introduced species, especially in the eastern part of the Mediterranean Sea have paralleled a substantial warming initiated at the beginning of the 1980's and accelerating at the end of the 1990's, leading to a 150% increase in the annual species invasion rate (Raitsos et al. 2010). The Mediterranean is to date undergoing a rate of approximately one new entry every two weeks, while dominant groups are found among mollusks (215 species), crustaceans (159) and polychaetes (132) (Zenetos et al. 2012). Further species comprise Macrophyta, fishes, Foraminifera, Cnidaria, Bryozoa, Ascidiacea, Miscellanea (i.e. Chaetognatha, Ctenophora, Echinodermata, Nematoda, Platyhelminthes, Porifera, Pycnogonida, Sipuncula), parasites and several microorganisms. The introduction of thousands of tropical species into the Mediterranean is without doubt the most remarkable biogeographic phenomenon today (Por, 2009). The native provenance of introduced species in the Mediterranean was most commonly the Indo-Pacific respectively Indian Ocean (69%), while some species have pantropical or circumtropical distribution (19%), although the source populations of most non-indigenous species have not been assessed by molecular means (Coll et al. 2010).

The introduction pathways of tropical species in the Mediterranean are different (Fig. 5D). More than half (54%) were probably introduced via corridors (mainly Suez Canal), whereas shipping is blamed as second most important introduction pathway, followed by aquaculture and aquarium trade (Streftaris et al. 2005; Zenetos et al. 2012; Katsanevakis et al. 2013). Whereas some introductions have been facilitated by more than one vector, some introduction pathways are unknown or assumed. Those species, whose introduction pathways may not be assessed or species which have been recorded casually (1-2 times), are often called cryptogenic in literature, although Carlton (1996) defines a cryptogenic species solely as taxon that is not demonstrably native or introduced.

The introduction through the Suez Canal is termed Lessepsian migration after Ferdinand de Lesseps, the French engineer who constructed the Suez Canal (Por, 1978). The opening of the Suez Canal in 1869 created the first salt-water passage between the Mediterranean and the Red Sea, although migration of Red Sea species was blocked for decades through the hypersaline Bitter Lakes (Galil, 2007). The salinity in the Bitter Lakes gradually approached that of the Red Sea, so that colonization of Red Sea species into the Eastern Mediterranean Sea became possible. Species with Red Sea origin have advantages over Atlantic species in the Eastern Mediterranean Sea, because the Red Sea

conditions are more similar to the Eastern Mediterranean being generally saltier and more nutrientpoor than the Atlantic. The introduction through the 168 km long Suez Canal is possible by (1) the natural dispersal of adults or larvae, (2) the stepwise advance of active swimmers and it is further possible (3) through the increasing volume of maritime traffic passing through the canal. Species are transported continuously via ballast water or ship fouling.



**Fig. 5** (A) Contribution of marine alien taxa in the Mediterranean Sea (B) Species-area plot of the number of non-indigenous species (NIS) in the 4 Marine Strategy Framework Directive (MSFD) subregions of the Mediterranean Sea (C) Number of marine alien species per major groups in the MSFD subregions of the Mediterranean Sea (D) Percentages of marine NIS known or likely to be introduced by each of the main pathways by subregion. Percentages add to more than 100% as some species are linked to more than one pathway (all figures taken from Zenetos et al. 2012).

The unabated influx of Red Sea biota is rooted in the continuous enlargement of the Suez Canal that has altered its hydrography and hydrology, and enhanced its potential as a "corridor" allowing even a higher number of organisms through (Galil, 2007). Before the completion of the Aswan dam in 1964, Nile floodwater acted as barrier for larvae species sensitive to low salinities. The river's freshwater flow was cut by 10% through the completion of the damn, so that the numbers of Lessepsian migrations increases additionally (Katsanevakis et al. 2013).

The arrival of tropical species from the Atlantic has become noticeable in recent decades but plays only a minor part compared to the numbers of Lessepsian migrants (Atlantic invaders: 40, Lessepsian migrants: 343) (Streftaris et al. 2005). It is interesting to notice that 80% of the species entering the Mediterranean via Gibraltar are fishes, followed by phytobenthos (10%), Crustacea (7%) and Mollusca (3%), whereas introductions via the Suez Canal are Mollusca (33%), Crustacea (15%), Polychaeta (14%), followed by fish (17%), phytobenthos (9%), zooplankton (3%) and phytoplankton (1%), (Streftaris et al. 2005). But there are uncertainties about the status of some species with an Atlantic origin that were introduced via Gibraltar because (1) intense fishing and transport activities (goods, commercial passengers, tourists) occur between Africa and Spain or France (e.g. the ports of Algeciras, Malaga, Barcelona, Marseille), which represents a potential and continuous source of introduction of NIS, via ballast water and transfers of organisms attached to ship hulls as fouling or fishing discards, (2) the Strait of Gibraltar is a boundary more or less permeable to Atlantic species that naturally increase their distribution range, and (3) there is a limited knowledge on the biodiversity from North African littoral (Zenetos et al. 2012). The numbers of alien species in the Mediterranean Sea therefore has to be handled with care, as particularly many alien species inventory lists just include alien species that has been introduced by human activities (e.g. man-made canals, shipping and aquaculture) so that natural dispersal is often neglected, but should urgently be taken into consideration.

The highest estimated rate of the ratio of alien species to native species richness is observed in the eastern Mediterranean Sea (especially Levantine and eastern Aegean Sea) (Katsanevakis et al. 2014b), considering Lessepsian migration to be the most significant biogeographic changes currently underway worldwide (Bianchi et al. 2012). The center of alien invasions is therefore located in the Eastern Mediterranean Sea, with coastal areas along Israel (especially in the Haifa coastal area) and Turkey displaying the highest numbers and impacts of introduced species. Further hot spot areas are found in the Thau and Venice lagoon in the northwestern Mediterranean as well as in the Northern Adriatic Sea mainly due to aquaculture. Most of the recorded introduced species are shallow-water thermophilic demersal species and just a very few invasive alien species have been reported in offshore areas (Katsanevakis et al. 2014b). The dissimilarity among those data may be due to (1) the fact that all important introduction pathways respectively vectors (Suez Canal, shipping, aquaculture) operate in shallow waters (lagoons, estuars, harbours) assisting the introduction of shallow-water species (2) studies on the impacts of introduced species, which are generally restricted to coastal waters, whereas (3) there is reduced sampling effort offshore, causing a monitoring and reporting bias in favor of coastal areas (Danovaro et al. 2010; Katsanevakis et al. 2016).

Alien species richness is decreasing from the Southeast to the Northwest showing an opposite trend in relation to native biodiversity decreasing from northwestern to southeastern areas (Katsanevakis et al. 2014b). The southern sector is currently inhabited by a significant portion of thermophilic species of tropical origin, whereas the numbers in the northern sector are generally lower, so that the establishment of allochthonous species there more likely falls under the term 'meridionalization' than 'tropicalization' (Coll et al. 2010). But this may change at an unprecedented rate due to further range

expansions possible through substantial warming accompanied with the shifting of winter isotherms. This enables thermophilic species to expand into areas where they previously were kept in check by climate (Bianchi and Morri, 2004; Bianchi, 2007; Roques, 2008; Langer, 2008a; Raitsos et al. 2010; Zenetos et al. 2012).

There is considerable empirical and modeling evidence that, once a non-native population has established, proximity to a source of dispersing individuals will increase the likelihood that the invasive species will expand its geographical range (Rouget and Richardson, 2003; Bossenbroek et al. 2001). Tropical species that have entered the Mediterranean Sea either through the Suez Canal or via the Strait of Gibraltar used to remain in the eastern and western basin, respectively (Coll et al. 2010). But climate warming facilitates the longitudinal migration of established non-indigenous species into other Mediterranean sub-basins. Thus there are 63 new findings in the WMED, 90 in the CMED, 52 in the ADRIA and 182 in the EMED (Zenetos et al. 2012). The Strait of Sicily and Otranto became a crossroad for species of distinct tropical origins in the last two decades (Azzurro, 2008; Lejeusne et al. 2010; Coll et al. 2010).

Lessepsian migrants that crossed the Strait of Sicily include algae, seagrass, many invertebrates and fish (Klein et al. 2005; Gambi et al. 2008; Garibaldi et al. 2008; Galil, 2009), whereas (among others) fishes, mollusks, hydroids and urchins have travelled the opposite way to reach the Levantine basin (Yokes and Galil, 2006; Morri et al. 2009; Por, 2009). The Adriatic Sea is recently invaded by alien marine species (Macrophyta, Mollusca, Crustacea, fishes and foraminifera such as *Amphistegina*), which are already established in the Ionian Sea and whose northward expansion is facilitated through shifting of isotherms and sea surface currents (Kashta, 1992; 2005, 2007, 2010; Zenetos and Polychronidis, 2010; Zenetos et al. 2011; Katsanevakis et al. 2011; 2013). The Dardanelles as well as the Sea of Marmara, which is seen as Mediterranean Sea sub-basin, is likewise also affected by species invasions due to northeastward expansion of established Aegean Sea taxa (Kaminski et al. 2002; Meric et al. 2005, 2007, 2008a; Oral, 2011; Ozturk, 2013; Kirci-Elmas and Meric, 2016).

# **1.6** The impact of non-indigenous and invasive species in the Mediterranean Sea: Gain or loss?

It is often claimed that, in the course of or at the end of the expansion phase, the abundance of an introduced species will naturally decline (the "boom and bust" model - a population that repeatedly and regularly increases and decreases in size), but such a natural decline has proved to be a rather rare event or comes from a misinterpretation of natural fluctuations (Bourdouresque et al. 2005). It seems that the establishment of alien biota, and the concurrent adverse changes in the native communities, are irreversible and part of a catastrophic anthropogenic ecosystem shift in the Mediterranean Sea (Bourdouresque et al. 2005; Galil, 2007).

Introduced species encounter a suite of novel stresses and selection pressures (Novak, 2007), which consequently ends in a considerable potential for rapid adaptation, which is proposed to explain why some introduced species establish, proliferate, and become invasive in new environments (Bossdorf, et al. 2005; Laerne and Molofsky, 2007). Native species may become increasingly poorly adapted to the local environment due to changing environmental conditions (e.g. warming), whereas newcomers might be better adapted and more competitive under new and perhaps more suitable conditions. Changes in climatic conditions that result in prolonged growth and reproduction period often provide NI species with exploitable opportunities (Hemerik et al., 2004).

Little is known about the kaleidoscopic interspecific relationships of native and non-native biota in the Mediterranean Sea (Boudouresque et al. 2005). The biodiversity of the Mediterreanean is influenced by the introduction of non-native species (Streftaris et al. 2005; Zenetos et al. 2005, 2009; Galil, 2006, 2007; Streftaris and Zenetos, 2006; Galil et al. 2009; CIESM, 2009), which initially leads to increasing species richness values at the whole-basin scale (c-diversity), but it is not clear how the diversity on local scale (a-diversity) is influenced (Coll et al. 2010). Such mixed assemblages and the resulting 'novel ecosystems' (Occhipinti-Ambrogi, 2007) raise questions concerning future ecosystem functioning. Marine invasive species are responsible for local population loss (local metapopulation extinctions) worldwide, a phenomen so severe that it is regarded as the second biggest cause of biodiversity loss after habitat destruction (Breitenhaupt, 2003). Moving physiological barriers and inducing spatial overlap between native and non-native species may cause biotic homogenization ('replacement of local biotas with non-indigenous species'; McKinney and Lockwood, 1999) and lead to a decrease in the b-diversity (Olden and Poff, 2003). Studies have shown that species replacement (Morri and Bianchi, 2001; Chevaldonne and Lejeusne, 2003; Sabatés et al. 2006; Galil, 2007) has already taken place, though no extinction of native species has been recorded (Bourdouresque, 2004). Local population losses and niche contraction of native species may not induce immediate extirpation, but they indicate reduction of genetic diversity, loss of functions, processes, and habitat structure and increase the risk of population decline and extinction (Bourdouresque et al. 2005). The decline of natives within a community and the dominance of aliens may be a consequence of, rather than the driving force behind, ecosystem disturbance (Chabrerie et al. 2008), as some alien species can better tolerate disturbance due to their generalist ecology and phenotypic plasticity (Smith, 2009; Goodenough, 2010). Anthropogenic induced ecosystem disturbance including rising sea surface temperature is putting extra pressure on the Mediterranean Sea, which is highly sensitive to environmental changes. The Mediterranean is therefore among the most impacted eco-regions globally by cumulative pressure (Halpern et al. 2008; Micheli et al. 2013) and, as mentioned, constitutes one of the global biodiversity hotspots of biological invasions (Nunes et al. 2014; Galil et al. 2015; Katsanevakis et al. 2014b, 2016). It is not clear how species react to increasing migration rates, as some may be unable to undertake migrations and became extirpated, whereas others may acclimatize or even take advantage of new arriving species.

Among nearly 1000 introduced species only 60-100 species have been documented to have high and large-scale impacts on biodiversity and ecosystem services (Streftaris and Zenetos, 2006; Katsanevakis et al. 2014a), although there are probably more species, which have not been studied yet. A threat to native biodiversity and the modification of recipient communities and ecosystems is reported for a variety of marine organisms, whereas the worst invasive species in the Mediterranean are found among macrophytes, phytoplankton (dinoflagellates), fishes and invertebrates (mollusks, polychaetes, crustaceans, foraminifers, bryozoans, cnidarians, corals) (Streftaris and Zenetos, 2006, Galil, 2007b; Rilov and Galil, 2009; Zenetos et al. 2012).

It is not clear what characterizes a successful invader (Streftaris et al. 2005), so that Carlton and Geller (1996) introduced the term 'ecological roulette'. There is a general rule that 10% of the introduced species become invasive, although it is not clear, if that rule can be applied to aquatic ecosystems (Williamson and Fitter, 1996). Considering the number of invasive species in the Mediterranean (mentioned above) reveal 6-10%, so that the 10% rule by Williamson and Fitter can be applied for the Mediterranean 'miniature ocean'. Ehrlich (1989) suggested that successful invaders tend to have large native ranges, broad diets, short generation times, and high genetic variability, among other features. It also has been suggested that ecosystems vulnerable to invasion share common attributes. These features include climatic matches between host and source habitats, early successional states, absence

of predators, and low diversity of native species (Lozon and MacIsaac, 1997). Invasion success depends not only on the invader's advantage over potential native enemies and competitors but also on the environmental characteristics of the host ecosystem (primarily species richness and disturbance) and the level of stress that is already imposed on it (Simberloff, 1989; Ribera and Bourdouresque, 1995; Cohen and Carlton, 1998; Goodwin et al. 1999; Occhipinti Ambrogi, 2000; Keane and Crawley, 2002; Streftaris and Zenetos, 2006). In the Mediterranean, stressed environments (polluted or physically degraded) appear to be more prone to invasion than pristine sites (Ribera and Bourdouresque, 1995; Galil, 2000; Occhipinti Ambrogi, 2000; Occhipinti Ambrogi and Savini, 2003; Streftaris and Zenetos, 2006) although the relationship between the number of introductions, diversity of the host ecosystem and disturbance acting on the community is not studied considerably in this area.

Ecological impacts of invasive species range from single species interactions and reduction in individual fitness of native species to population declines, local extinctions, changes in community composition, and effects on the entire ecosystem function (Blackburn et al. 2014; Katsanevakis et al. 2014b). Ecosystem changes through invasive species are due to ecological interactions like e.g. competition for resources, including settling places and spawning grounds, grazing or predation, trophic cascading effects, or niche contraction (Wallentius and Nyberg, 2007). They are, furthermore, triggered by the mixing of exotic genes, and the loss of native genotypes (through species replacement), community structures changes, introduction of pathogenes, the affection of food-web properties and ecosystem processes impeding the provision of ecosystem services (Grosholz, 2002; Wallentius and Nyberg, 2007; Molnar et al. 2008; Vila et al. 2010; Katsanevakis et al. 2013). Established invasive species can modify habitats and change habitat suitability for native species by changing the habitat itself physically or chemically, through ecosystem engineering. The invasive species may indirectly or directly affect the substrate itself, alter habitat architecture, indirectly influencing water movements and quality, sediment accumulation and sedimentation rates, alter erosion rates, and light conditions. When invasive species more or less monopolize an area, it is more difficult for native inhabitants to flourish and survive, so that introduced species, which have profound architectural importance for the ecosystem structure (such as macrophytes, several sessile invertebrates and foraminifera) play a fundamental role especially when they establish themselves in high abundances (Wallentius and Nyberg, 2007).

The change of infralittoral communities and ecosystems through established invasive species is also accompanied by an impact on human health (due to e.g. pathogenes and toxic microalgae) and causes substantial economic damage and losses (e.g. fishing, tourism, accumulating costs to eradicate invasive species and accompanied implications). On the other hand many alien species have positive impacts on ecosystem services and biodiversity, e.g., by locally increasing species richness values, acting as ecosystem engineers and creating novel habitats and increasing spatial heterogenity, controlling other invasive species, providing food, and supporting ecosystem functioning in stressed or degraded ecosystems (Schlaepfer et al. 2011; Simberloff et al. 2013; Katsanevakis et al. 2014a). Introduced invasive species can modify the functioning pattern of ecosystems through their abundance, their biomass or role as key species and in addition to that they may upset the energy and nutrient flows, when they belong to a different functional group than that of native key species and/or ecosystem with potential consequences for ecosystem functioning and services may not just have serious impacts on many local, endangered and endemic species, but will also lead to a homogenization of the fauna over time.

#### 1.7 Non-indigenous and invasive benthic foraminifera in the Mediterranean Sea

Little attention has been paid to alien and invasive benthic foraminifera until the early 1990's but the number of publications have been increasing since then. The Mediterranean Sea is a classical area in terms of foraminiferal research and probably has the most intensively studied record with a particularly detailed history that goes back more than 200 years (e.g. Cimerman and Langer, 1991; and references therein; Langer, 2008a). This allows baseline studies and the comparison of ancient and recent faunal changes in the Mediterranean realm. Fortunately foraminifera are among those microorganisms, which are generally well studied in terms of Mediterranean invasion ecology. This may be due to a good knowledge on their ecology and distribution, due to high (fossil) preservation rates of their tests and high abundances in the sediments and may be due to a relatively easy way to prepare and identify the organisms on species level.

The modern benthic foraminiferal fauna of the Mediterranean Sea is mainly of Atlantic origin although it shares a common Tethyan history with the Red Sea (Langer, 2008a). Separate biogeographic provinces are characterized by highly diverse faunas, which assemblages differ significantly in their composition of species (Langer, 2008a). To date, the Mediterranean Sea is affected by the introduction of a high number of foraminifera of tropical origin. Most of the introduced species are Lessepsian migrants and are distributed and established in the Eastern Mediterranean Sea. The numbers of Atlantic invaders is small but also difficult to assess, due to a lesser rate of publications present for the Western Mediterranean area.

In the present study it was differentiated between introduced foraminifera (non-indigenous/NI or aliens), cryptogenic foraminifera (after the sense of Carlton, 1996: a taxon that is not demonstrably native), invasive foraminifera (non-native and cryptogenic species with a certain impact on biodiversity or ecosystem functioning) and successful returnees (foraminiferal taxa, which occurred in the fossil record and return/ed recently). Literature data, gathering the numbers and distribution of introduced benthic foraminifera, shows an increasing rate of introductions since the warming phase at the end of the 1990's. Fewer than 8% of the alien foraminifera were reported before the 1950's in the Adriatic Sea, whereas the majority of the species (42%) was reported in the 1990's and 33% since 2000 (Zenetos et al. 2012). Whereas in the year 2005, the numbers of detected introduced benthic for aminifera was around 7, this increased 5-6 fold in the year 2008. Langer (2008a) estimated around 30 introduced species and 23 Genera (referred to Hyams et al. 2008), for the eastern Mediterranean Sea and a further publication in the same year dealing with alien species in the Mediterranean Sea (Zenetos et al. 2008) report of 45 alien foraminiferal taxa (34 genera). This elevated number is due to increasing introduction rates along the coast of Israel and Turkey. Zenetos et al. (2010) mentioned 50 alien foraminiferal species within 39 genera for the entire Mediterranean Sea. Eleven foraminiferal taxa formerly identified as aliens have been found to be present in the fossil record and were therefore excluded from the alien species list in 2012 (Appendix 7.7), whereas an additional 29 foraminifera have been included due to new references. Thus, the number of introduced benthic foraminifera increased to 68 taxa within 22 genera in the year 2012, so that foraminifera are therefore ranking among the 6<sup>th</sup> most introduced organisms in the Mediterranean realm (Zenetos et al. 2012). EASIN (European alien species information network) reveals the presence of 78 shallow-water benthic foraminfera out of 55 genera in the year 2016.

Shallow-water sites off Israel, Lebanon, Cyprus, Egypt, Libya, Tunisia, the Maltese Islands, the Pelagian Islands (Linosa and Lampedusa), Turkey, Greece, Italy, Croatia and France are affected by distinct numbers of introduced and/or invasive species. The highest numbers of introductions to date

are found along Israel (49 species within 36 genera; Yalcin et al. 2006; Hyams et al. 2002, 2008, 2009; Almogi-Labin and Hyams-Kaphzan, 2012) and Turkey (66 species out of 50 genera; Avsar et al. 2001; Oflaz 2006; Meric et al. 2001, 2004; 2007; 2008a, b,c, 2010; Yokes and Meric, 2004, 2009), which makes the Levantine Sea the center of foraminiferal invasion within the Mediterranean Sea. The numbers of introduced benthic foraminifera along the North African coast west of the Nile Delta (Egypt; Lybia, Tunisia) decrease to 18 taxa and 12 genera in Egypt (Samir and El-Din, 2001; Samir et al. 2003), 3 taxa within 3 genera in Lybia (Blanc-Vernet et al. 1979; Langer, 2008a; Bazairi et al. 2013) and 6 species and genera in Tunisia (Blanc-Vernet at al. 1979; Aloulou et al. 2012). The Pelagian Islands (Lampedusa and Linosa) reveal 6 species within 5 genera of tropical origin (Caruso and Cosentino, 2014), whereas Maltese Island is just migrated through 1 introduced foraminiferal taxon and genus (Yokes and Meric, 2007). There is 1 species present in Lebanon (Moncharmont-Zei, 1968), whereas the Island of Cyprus is inhabited by 3 introduced species within 3 genera (Abu Tair and Langer, 2010) and Greece and its surrounding Islands exhibit 9 species belonging to 9 genera (Emery and Neev, 1960; Hollaus and Hottinger, 1997; Debenay et al. 2005; Koukousioura et al. 2010; Zenetos et al. 2011; Triantaphyllou et al. 2009; 2010a; 2012; Siokou et al. 2013). Croatia reveal 12 introduced foraminiferal species and 9 genera although some species were casually observed and never been reported as established or mentioned again (Dezelic, 1896; Schaudinn, 1911; Wiesner, 1911a,b; 1913; Vatova, 1928; Alfirevic, 1964; 1998; von Daniels 1970a, b; Cimerman and Langer, 1991; Vanicek 2000; Cosovic et al. 2002; Vidovic et al. 2016). Italy is inhabited by 8 species and genera (Blanc-Vernet, 1969; Sgarrella and Moncharmont Zei, 1993; Cimerman and Langer, 1991; Romano et al. 2008; Caruso and Cosentino, 2014), and France is to date affected by 1 species (Bouchet et al. 2007). The numbers of introduced benthic foraminifera present off Lebanon, Cyprus, Tunisia and Maltese Island, Italy and France are most probably underestimated due to a lower rate of investigations and publications dealing with alien foraminifera from these areas.

Among the detected species only 5 have been classified as cryptogenic (*Amphistegina lobifera*, *Archaias angulatus*, *Coscinospira hemprichii*, *Planogypsina acervalis*, *Euuvigerina* sp.), whereas all other taxa have been assessed as aliens (Appendix 7.6). Most of the NI foraminifera are established aliens or cryptogenics (rare and frequent abundances), whereas some taxa that are just observed casually and some are locally highly frequent and invasive (e.g *Amphistegina lobifera*, *Amphisorus hemprichii*, Chapter 1.8).

As mentioned in the former chapter the introduction of tropical species into the Mediterranean Sea is a human induced as well as a natural phenomenon. Foraminifera migrate into the Mediterranean Sea through the man-made Suez Canal or through the Strait of Gibraltar. The dispersal is most probably indirectly facilitated by the migration of propagules through sea surface currents, than through active migration through the 168 km long Suez Canal or the 60 km long Strait of Gibraltar as foraminifera are known to actively move only over short distances (Schafer and Young, 1977; Kitazato, 1988; Wettmore, 1988; Weinberg, 1991; Hemleben and Kitazato, 1995; Bornhalm et al. 1997). However, the introduction of foraminiferal taxa through active migration of several generations over time is possible and in terms of the Suez Canal recently facilitated by the discontinuation of the chemical barrier formerly induced by the hypersaline Bitter Lakes (Galil, 2007; Coll et al. 2010) and also due to the Awsan dam, reducing freshwater influx of the Nile into the Mediterranean Sea (Rilov and Galil, 2009). Further likely introduction pathways comprise shipping and the transportation of foraminiferal propagules and living foraminifera via ballast water. Transportation of foraminiferal propagules or living species via ballast ship water is (globally) assumed several times (Witte, 1994; McGann and Sloan, 2000; McGann et al. 2001; Calvo-Marcilese and Langer 2010; Schweizer et al. 2011; Asteman and Schönfeld, 2015) and already documented for foraminiferal species (Galil and Hülsmann, 1997;

Chu et al. 1997; Lavoie et al. 1999; Radziejewska et al. 2006; Bouchet et al. 2007). The introduction via ship ballast water is also assumed for several other introduced taxa (e.g crustaceans, polychaeta, fishes), as their occurrences is often locally limited (e.g. harbors), but this definitely requires further examinations and studies.

The distribution of generalist and opportunistic warm-water tropical foraminiferal species is strongly constrained by water temperature (Langer, 2008a), so that a rapid distribution into the western Mediterranean was previously limited by temperature as physical barrier for introduced thermophilic benthic foraminifera due to colder water currents by the Atlantic (Langer and Hottinger, 2000). Temperature has long been considered the primary factor limiting the distribution of larger symbiontbearing foraminifera (Langer and Hottinger, 2000 and references therein). However, specific temperature limitations of smaller non-symbiont bearing foraminifera suggest that in the absence of endosymbionts, many tropical foraminifera exhibit distribution limitations which are also governed by temperature alone, pointing to the host as the primary driver that is limited by temperature (Langer, 2008a). Sea surface warming enables and facilitates the settlement of introduced benthic foraminifera and is thus responsible for an increasing rate of introduced non-native species like it is observed for miscellaneous thermophilic tropical species that enter the Mediterranean Sea. But increasing sea surface temperatures due to climate warming enable established introduced foraminiferal species and propagules, furthermore, to expand their distribution range and migrate into new environments to establish and proliferate likewise. Climate warming is definitely increasing the rate of foraminiferal introductions, but the increasing numbers may also be due to a sharp increase in reports of foraminifera partially related to the increasing awareness of foraminiferal specialists and to the publication of the Atlas of Recent Foraminifera from the Gulf of Aquaba, Red Sea by Hottinger et al. (1993) (Zenetos et al. 2012).

The distribution of introduced warm-water tropical foraminifera generally follows the counterclockwise longshore circulation pattern present in the eastern Mediterranean Levantine basin (Chapter 1.1, Fig. 2), whereas some species also trespassed the eutrophic Nile Delta barrier and migrated along the northern African coast in an anti-clockwise circulation pattern (Langer, 2008a). They also migrated in shallow-waters towards more offshore located islands such as Malta and the Pelagian Islands (Yokes and Meric, 2007; Caruso and Cosentino, 2014). Larger-symbiont-bearing species are observed to primarily follow carbonate-rich sedimentary belts along the continental shelf off the Levantine, Aegean and Ionian Sea coasts (Israel, Turkey, Pelagian Islands, Greece) and, furthermore, are correlated with warm winter temperatures or natural induced higher average sea surface temperatures, clear waters and extreme oligotrophy (Hyams et al. 2002; Langer, 2008a). Hot submarine springs located off the west coast of Turkey may act as a stepping stone for the further migration in the northwestern direction (Bianchi *et al.*, in press).

The invasion of Lessepsian migrants into the Mediterranean appears to be increasing and recently some have become prominent contributors to the local carbonate budget in some areas (Hyams et al. 2002; Langer, 2008a). Introduced benthic foraminifera are usually relatively rare (1-10 individuals/5 g sediment; Meric et al. 2008a), whereas some proliferate locally especially in the centre of invasion (shallow-waters off Israel, Turkey and Cyprus), but also to the west (Egypt, Tunisia, Pelagian Islands, Maltese Island) and northwestwards (Greece). Among those taxa are *Amphistegina lobifera*, *Amphisorus hemprichii, Amphistegina lessonii, Coscinospira hemprichii, Spiroloculina* cf. *S. angulata, Spiroloculina antillarum, Hauerina diversa, Heterostegina depressa, Haddonia* spp., *Peneroplis arietinus, Sorites orbiculus, Sorites variabilis, Pararotalia calcariformata* (Meric et al. 2008a). The high ratio of tests in the sediment results in large amounts of calcareous sand formation

with up to3.75g tests/5 g sediment and more (Meric et al. 2008a). Macro- and microhabitats former inhabited by native epifauna, especially around Israel and Turkey are now occupied by alien and cryptogenic species.

#### 1.8 The most invasive benthic foraminifera in the Mediterranean Sea

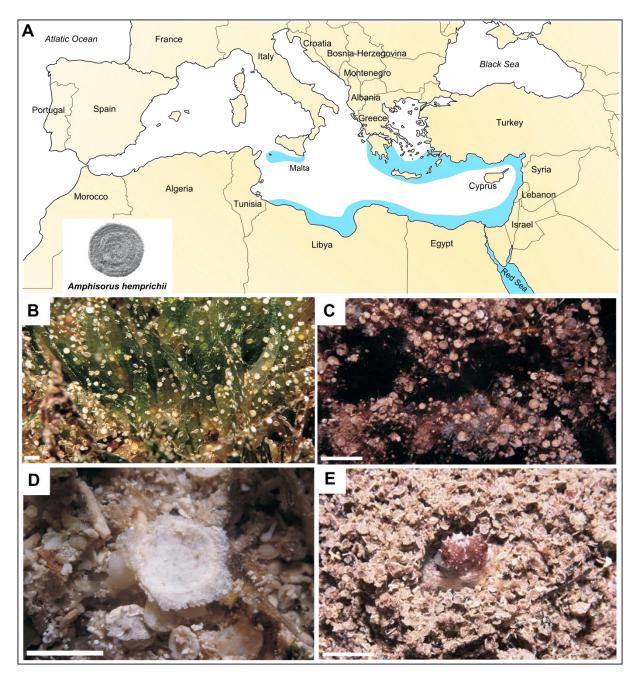
Among all alien, cryptogenic and successful returnees *Amphisorus hemprichii* and *Amphistegina lobifera* are the only species with a tendency to become invasive (locally).

#### 1.8.1 Amphisorus hemprichii

*Amphisorus hemprichii* is a porcelaneous larger symbiont-bearing taxa, which recently is distributed widely in the Indo-Pacific, Pacific and southeastern Atlantic. Like all other soritid foraminifera *Amphisorus* possesses dinoflagellate endosymbionts (Langer and Hottinger, 2000). In the Mediterranean, *Amphisorus hemprichii* was first observed by Hollaus and Hottinger (1997) in shallow waters off Greece. It is assumed to be a Lessepsian migrant, although the transportation via ballast ship water from the Atlantic cannot be excluded. *Amphisorus hemprichii* currently follows the counterclockwise circulation pattern in the Mediterranean Sea (present in shallow-waters off Israel, Cyprus, Turkey, Greece), but it is also (frequently) distributed along the northern coast of Africa excluding Tunisia (Egypt: Samir et al. 2001, 2003; Lybia, Langer, 2008a), as well as around Linosa (Pelagian Islands) and the southeastern coast of Sicily (Caruso and Cosentino, 2014, see Fig. 6A).

Introduced *Amphisorus hemprichii* specimens (most probably Lessepsian migrants) reveal dense populations around submarine springs in Turkey (between Kalkan and Kekova), where high frequencies and great test sizes (0.5-2mm) of the specimens in shallow waters off Turkey results in an extensive deposition of calcium carbonate in the sediment (Figs. 6B-E; Meric et al. 2008d).

If population expansion occurs in the future, this may lead to a much higher deposition of calcium carbonate due to large test sizes of this species. Yokes and Meric (2009) mention that *A. hemprichii* covered more than 100 km of coastline only two years after its introduction and form dense populations on the benthos. *Amphisorus hemprichii* is a shallow-water dwelling species, which is found on calcareous coarse grained soft substrates or even on pyhtal (seagrass and algae) and hard substrates. Around Turkey, *Amphisorus* is found between 3-24m, whereas most of the individuals are found in 8-18m water depth on *Posidonia oceanica* and *Halophila stipulacea* meadows or on every kind of substrate, even on themselves (Yokes and Meric, 2009, Fig 6E). Other locations inhabited by *Amphisorus* are between 1-30m water depth. The frequency of *Amphisorus hemprichii* decreases from shallow-waters off Turkey and Israel to the west and northwest, so that populations around the Pelagian Islands and southeastern Sicily are only rare (<1% of the assemblage) and it is absent from the northern Aegean Sea. This may be due to the temperature dependence (16-34°C) and lower SST present in this area in. winter.



**Fig. 6** (A) Biogeographic distribution of *Amphisorus hemprichii* in the Mediterranean and Red Sea, (B) *Amphisorus hemprichii* population on *Halophila stipulacea* Ascherson, Kas -Antalya, depth 26 m, scale bar = 6mm (Meric et al. 2014), (C) *Amphisorus hemprichii* population on *Cystoseira* sp., Kas - Antalya, depth 12m, scale bar = 2mm (Meric et al. 2014), (D) *Amphisorus hemprichii* individuals on the sea bottom, scale bar = 0.85, (E) dense *A. hemprichii* population on hard substrates, serving as a hiding place for a young individual of *Octopus vulgaris*, scale bar = 6mm (Photo: Baki Yokes; source: Cinar et al. 2010).

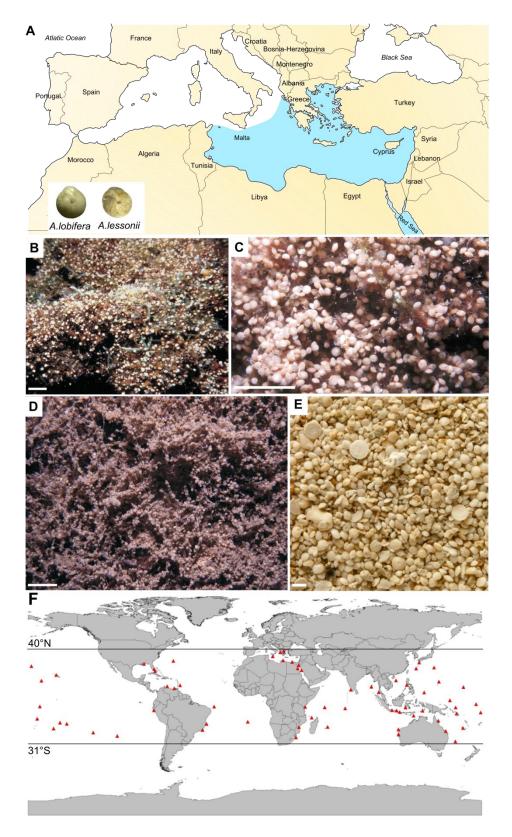
#### 1.8.2 Amphistegina spp.

Among the most successful invaders are symbiont-bearing foraminifera of the genus *Amphistegina* spp., which commonly comprise two species in the Mediterranean, *Amphistegina lobifera* Larsen, 1976 and *Amphistegina lessonii* d'Orbigny, 1826 and two ecomorphotypes *A*. cf. *A. lessonii* and *A. cf. A. papillosa*, although there might be more ecomorphotypes present (Hyams et al. 2002 mentioned biconvex *A. lessonii* types which may be hard substrate phenotypes and rarely occurring spiro-convex forms, considered to be sandy substrate morphotypes of *A. lessonii*). Another 3 taxa comprise *A*.

*radiata*, *A. papillosa*? and *A. bicirculata* all documented in historical samples from the National History Museum (NHM) in Israel (Benjamini and Almogi-Labin, 2008) and Egypt (Alexandria, Samir and El-Din, 2001, *A. radiata*). *Amphistegina madagascariensis* was documented from shallow-waters of Egypt (Samir et al. 2003) and Tunisia (Gulf of Gabes, Blanc-Vernet et al. 1979).

Amphisteginid foraminifera are among the most prolific and ubiquitous foraminifera on coral reefs and tropical carbonate shelves hosting diatom endosymbionts. As key carbonate producers they have often been referred to as living sands (Lee, 1995) and contribute substantially to substrate stability, the growth of reefal structures and the deposition of coastal sediments (McKee et al. 1959; Hallock, 1981; Langer and Hottinger, 2000; Langer, 2008a, b; Langer et al. 2012, 2013). They are circumtropically distributed, where they thrive in warm, clear, nutrient-poor, carbonate-rich, shallow-shelf environments (Todd, 1976; Hallock, 1988, 1999; Langer and Hottinger, 2000). *Amphistegina lobifera,* which is the most abundant and successful amphistegnid foraminifera in the Mediterranean, is a major carbonate producer in shallow shelf and reef environments of the tropical realm, precipitating up to 2kg/m<sup>2</sup>/year (Langer et al. 1997). In the Mediterranean Sea, *A. lobifera* is listed among the 100 worst invasive species (Zenetos et al. 2005).

The genus Amphistegina occupies a dominating position in many foraminiferal assemblages in tropical realms, particularly in the Pacific, and is found as a common to abundant constituent of foraminiferal faunas in the Cenozoic in both the eastern and western hemisphere (Todd, 1976). In modern oceans, amphisteginid foraminifera have been found as far North as 39° and 31° South displaying some of the widest latitudinal extensions among larger-benthic foraminifera analyzed to date (Langer and Hottinger 2000; Langer, 2008a; Fig. 7F). The Mediterranean Sea represents the northernmost range front of amphisteginids. In the Mediterranean Sea several amphisteginid species are known from Eocene to Pliocene in Amphistegina-rich levels. Amphistegina is the most important rotaliine larger foraminiferal genus which survived the Late Miocene Salinity Crisis attaining a widespread distribution throughout the Mediterranean in Early to Middle Pliocene times (Di Bella et al. 2005). Concrete data about the paleo-temperature in the Mediterranean are supplied by the presence of the symbiont-bearing foraminifera Amphistegina in the Tyrrhenian Sea, and the absence of Porites reefs (Checconi et al. 2007; Por, 2009). It is assumed (although not proved) that the genus became extinct in the western Mediterranean in Late Pliocene-Early Pleistocene times, whereas it may have survived in the Eastern Mediterranean (Reiss and Hottinger, 1984). Alternatively, it may have re-colonized more recently the Mediterranean along with other larger foraminifera as Lessepsian immigrant from the Indian Ocean (Reiss and Hottinger, 1984). Amphistegina lessonii has been reported from Miocene (e.g. Menorca; Mateau-Vicens et al. 2009) and Pleistocene deposits (Parker et al. 2012; Meric et al. 2015) so that it is classified as native Mediterranean species. The examination of historical collections at the NHM for symbiont-bearing foraminifera revealed (among others) the presence of A. lessonii, A. radiata, A. papillosa (?) and A. bicirculata in material collected from shore sands and dredging taken in the 1850's off Tunisia, Malta, Italy and Crete (Benjamini and Almogi-Labin, 2008). These foraminifera cannot have entered the Mediterranean via the Suez Canal, suggesting some warm water refugia during the Messinian Salinity Crisis for larger symbiont-bearing species, located on the arch between the Western Mediterranean and Levantine basins (Benjamini and Almogi-Labin, 2008). Amphistegina madagascariensis has been documented in shallow-waters off Tunisia (Blanc-Vernet et al. 1979) and Egypt (Samir et al 2003) and is considered to be a Lessepsian migrant or introduced via ship ballast water. Amphistegina lobifera has not been reported as early as Pleistocene (Parker et al. 2012) and is therefore classified as a cryptogenic taxon.



**Fig. 7** (A) Biogeographic distribution of *Amphistegina* spp. in the Mediterranean Sea, Red Sea and the Sea of Marmara. (B) *Amphistegina lobifera* population on a rock substrate, Üçadalar, Antalya, Mediterranean, 6.00m, scale bar = 20mm (Meric et al. 2014), (C) *Amphistegina lobifera* population on *Cystoseira* sp., Bodrum, Mugla, Aegean Sea, 9.00m, scale bar = 15mm (Meric et al. 2014), (D) *Amphistegina lobifera* population on algal mat, Arsuz, Iskenderun, Hatay, 8.00m, scale bar = 20mm. (Meric et al. 2014), (E) High accumulation rate of *A. lobifera* tests in shallow-waters off Cyprus, scale bar = 2mm, (F) global biogeographic distribution of amphisteginid foraminifera ranging from 40°N to 31°S (Weinmann, unpubl. data).

Amphisteginid foraminifera in the Mediterranean have the greatest spatial distribution among all alien and cryptogenic foraminifera and were locally shown to occur at abundances of up to 350 individuals/g sediment or up to 700 per g dry algae (Gruber et al. 2007; Meric et al. 2008a; Yokes and Meric, 2009). The Mediterranean range expansion front of amphisteginid foraminifera runs from the North African coast off Tunisia to the Pelagian Islands, Malta, the southeastern coast of Sicily and Corfu in northwestern Greece (Yokes et al. 2007; Triantaphyllou et al. 2009, 2012; Zenetos et al. 2010; Langer et al. 2012; Weinmann et al. 2013b; Fig 8A). Amphistegina radiata occurs in moderate percent abundances (0.3-2.9) in shallow-waters of Egpyt (Samir et al. 2001) and is, furthermore, solely documented in the historical samples investigated by Benjamini and Almogi-Labin in 2008. Amphistegina papillosa? (except of the ecomorphotype A. cf. papillosa) and A. bicirculata (only documented in the NHM historical samples) have never been reported again within the Mediterranean, pointing to an extirpation of these taxa, an established small population in shallow-waters off Tunisia, Malta, Italy and Crete or it is a question of synonymy. Its validity definitely requires further examinations. Amphistegina lobifera and A. lessonii show the greatest spatial distribution among Mediterranean amphisteginids, whereas the two ecomorphotypes A. cf. lessonii and A. cf. papillosa where only described from the Pelagian Islands (Caruso and Cosentino, 2014).

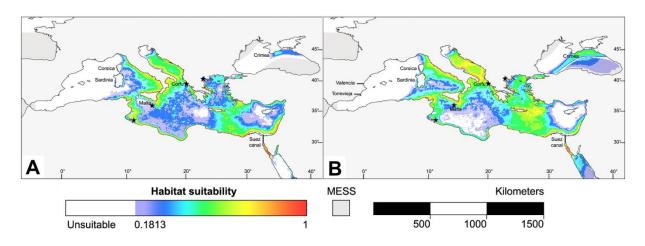
At several sites in the eastern Mediterranean Sea, amphisteginid foraminifera were recently reported to constitute up to 97% of the sediment (Hyams et al. 2002; Gruber et al. 2007; Abu Tair and Langer, 2010; Abu Tair, 2011; Triantaphyllou et al. 2012; Langer et al. 2012; Caruso and Cosentino, 2014; see also Fig. 7E). Like their counterparts in the tropics, amphisteginids in the Mediterranean (especially A. *lobifera*) preferentially live on hard substrates covered by macroalgae and algae mats, but are also distributed on carbonate rich coarse to medium grained soft substrates (Hallock, 1981, 1988, 1999; Hohenegger, 1994; Hohenegger et al. 1999; Renema and Trolestra, 2001). Amphistegina lobifera is the shallowest dwelling of the extant members of the genus thriving in high-energy hydrodynamic conditions (Hallock, 1981; Hallock et al. 1986), where it prefers mid-to high light conditions in 1-5m water depth (Hallock 1981, 1984; Hallock et al. 1986). Although A. lessonii also belongs to the shallow dwelling amphisteginids (generally in 5-20m water depth, Hallock, 1984; Hallock and Hansen, 1979), it seems to be excluded from high energy environments (Hallock, 1984) and can be inhibited by light intensities close to full sunlight (Hallock, 1981). Tropical A. lessonii are also distributed in greater water depth in deep-lagoonal and outer slope settings (Todd, 1976). In the Mediterranean Sea, A. lobifera and A. lessonii, may be found in the same depth range although A. *lessonii* is generally also found in greater water depths (>20-70m) and is truncated by the thermocline (16°C) occurring between 60 and 70m (Hollaus and Hottinger, 1997). Considering the abundance and distribution within the Mediterranean, A. lobifera is much more frequent and show a greater spatial distribution than A. lessonii. Whereas A. lobifera becomes dominant and invasive in nearly every habitat colonized, A. lessonii is distributed in shallow waters off Israel (less abundant than A. lobifera; Hyams et al. 2002), Turkey (rarely distributed; Meric et al. 2010), Egypt (frequently; Parker et al. 2012); Linosa (frequently; Pelagian islands; Caruso and Cosentino, 2014), Greece (frequently; Hollaus and Hottinger, 1997; Triantaphyllou et al. 2003, 2005) and southeastern Sicily (rarely; Caruso and Cosentino, 2014). The ecomorphotype A. cf. A. lessonii is found in 2-42m water depth around Linosa (4.4-25%) and A. cf. A. papillosa is distributed in 8-11m water depth around Linosa and Lampedusa (0.9-10%), (Caruso and Cosentino, 2014). Amphistegina lobifera shows especially high frequencies in the center of invasion (Israel and Turkey), although it may also occur in high frequencies along the range expansion front (up tp 97% around the Pelagian Islands/Caruso and Cosentino, 2014 and >50% around Greece/Aegean Sea/Triantaphyllou et al. 2005). Living A. lobifera individuals may reach a density of 230.000-310.000 individuals/m<sup>2</sup> on rocky substrate and 3.75g/5g sediment around Turkey, indicating a deposition rate of 2-4.5cm/year (Meric et al. 2008a; Yokes and Meric, 2009; Fig. 7B-D).

Along the coast of Turkey, invasions of amphisteginids resulted in sedimentary layers of 60-80 cm of pure amphisteginid, carbonate creating an immense ecological problem by changing the whole habitat structure and altering species composition of the coastal ecosystem (Meric et al. 2008a; Yokes and Meric, 2009). Waves carry amphisteginid tests to the shores, where they accumulate in small bays, thus changing gravelly shores to sandy beaches, with profound implications for native biotas and ecosystems (Yokes and Meric, 2009). Along the Israel rocky coast, Amphistegina lobifera is by far the most common species in shelf areas, taking over the local foraminiferal assemblage by occurring throughout the year, with a frequency of 180 individuals/g sediment (Hyams et al. 2002) and a contribution of 200g CaCO<sub>3</sub>m<sup>2</sup>yr<sup>-1</sup> (Gruber et al. 2007). In the Aegean Sea, it is the dominant foraminiferal species in southern and central regions, sometimes exceeding 50% of the assemblages (Triantaphyllou et al. 2009; Koukouisoura et al. 2010, 2011). As a result of the massive deposition of tests, A. lobifera is altering habitats and shorelines along the eastern Mediterranean Sea by the deposition of large amounts of sand-sized (0.5-2mm) soft substrates (Yokes and Meric, 2009; Streftaris and Zenetos, 2006; Hyams et al. 2002, 2008). The average Mediterranean carbonate production by corals and other bioconstructors has been reported to be approximately 1 kg of CaCO<sub>3</sub> per m<sup>2</sup> per vear (Bianchi, 2007). Amphistegina spp. is therefore currently contributing a significant portion of the local carbonate budget, and due to its abundance, ubiquity and appearance in monocultures can be considered true ecosystem engineers (Langer et al. 2012; Weinmann et al. 2013b, Thissen and Langer, 2017) in the sense of Jones et al. (1994, 1997).

According to Langer and Hottinger (2000) amphisteginid foraminifera are delimited by the 14°C winter isotherm, and laboratory experiments showed that *Amphistegina* only ceased all movement below 12°C (Zmiri et al. 1974). It's presence in the northern Aegean Sea and in the eastern Sea of Marmara, however, indicates an adaptation to lower water temperatures (Yokes and Meric, 2009 Triantaphyllou et al. 2012). The upper temperature limits of amphisteginid foraminifera are currently not known but vital populations thriving in tidal pools of eastern Africa and Raja Ampat indicate temperatures far beyond 30 °C (Langer unpubl. data; Weinmann et al. 2013b).

Since the reintroduction of *Amphistegina* spp. in the Mediterranean Sea to the eastern Mediterranean, ~ 140 years ago, it has crossed a total distance of approximately 1750km suggesting a dispersal rate of 12.5km/year (Langer et al. 2012; Weinmann et al. 2013b). Applied species distribution modeling for this taxon suggests a potential latitudinal expansion of *Amphistegina* spp. ranging between 515km in 2050 and 525 km in 2100, so that they are expected to migrate into the Adriatic Sea by the year 2050 and migrate west of Corsica and Sardinia by the year 2100 with an average dispersal rate of ~ 13.82km and ~ 11.76km per year respectively (Fig. 8; Weinmann et al. 2013b). Environmental factors such as calcite, nitrate and minimum and maximum temperature are the most important predictors for the model (Weinmann et al. 2013b).

The establishment and proliferating of foraminifera with a tendency to build monocultures may affect rates of carbonate production and may negatively impact the relationship between biodiversity and ecosystem functioning, resulting in biotic communities that are functionally more susceptible to environmental stress (Wallentius and Nyberg, 2007; Weinmann et al. 2013b). Although most of the introduced foraminifera are integrated in small proportions within native foraminiferal assemblages, some migrants have locally become dominant. Invasive species rapidly adapt to new environments, acting as consumers, prey, competitors, or disturbers, and provide evidence for biotic homogenization of foraminiferal faunal assemblages due to human-mediated breaching of biogeographic barriers (Calvo-Marclese and Langer, 2010). Therefore, their impact requires monitoring and detailed consideration, as newly established tropical benthic foraminifera will define a new Mediterranean geological phase for the future paleoecologists (Por, 2009).



**Fig. 8** (A) Species Distribution Models (SDM's) for *Amphistegina* spp. under current and future climates as projected by Maxent (modified after Weinmann et al. 2013b). Probability of presence is indicated by habitat suitability values ranging from high (1, red areas) to very low (0.1813, light blue areas). Black stars indicate currently known distribution limits of *Amphistegina* spp. in Tunisia, Malta, Corfu and the northern Aegean Sea. Gray hatched areas indicate areas of possible extrapolation of the model due to predictor values being outside the training range (MESS). (B) Species Distribution Model under climate conditions projected for 2050. Note the ongoing range expansion into the western Mediterranean. Habitat suitability is increasing around Italy. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of Weinmann et al. 2013b).

#### 1.9 Outline of this thesis: Aims and approaches

The Mediterranean Sea is facing increasing rates of biological invasions referable to global warming and increasing sea surface temperatures. The accelerating rate of introductions may lead to the so called 'tropicalization' (Bianchi and Morri, 2003) of the Mediterranean Sea with severe consequences on native species richness and ecosystem functioning. Amphisteginid foraminifera are among the most successful invaders in the Mediterranean Sea as they change coastal structures and native foraminiferal assemblages. As mentioned in "Background and Motivation of this thesis", the main goal of this study was to study the ecological, environmental and biotic impact of amphisteginid invasions along the NW range expansion front in the Mediterranean Sea. Furthermore, unknown 'foraminiferal territories' partly inhabited by amphisteginids were examined within the Mediterranean Sea. The study area along the coastline of Albania represents the current range expansion front of amphisteginid foraminifers and is of particular interest to study the impact of invasive species on native biotas.

The analysis of amphisteginid invasions addresses several key objectives along the current NW range front in the Mediterranean Sea. Among these objectives were to 1) identify amphisteginid species that occur along the NW range front and determine their percent abundances among the foraminiferal fauna, 2) explore the impact on native foraminiferal assemblages and communities, 3) detect alterations in community structures/ecosystem functioning, 4) compute current dispersal rates of amphisteginid foraminifera, 5) compare the range front data in locations that have been invaded by amphisteginids since decades.

To address these aims, several independent studies were conducted. In Part 2 of this thesis, we document the effect of amphisteginid invasions on established foraminiferal biotas along the front of the expanding range margin.

Part 2.1 deals with material collected from sites off northwestern Greece (Ithaka and Lefkada Islands, Ionian Sea). Recently invaded sample sites (Ithaka, Lefkada) were compared to sites of invasions where amphisteginids have been established since decades (Cyprus). The nature of these recent biotic exchanges and their consequences on the structure of communities (selected groups of benthic foraminifera), their composition and the diversity of assemblages for perspectives on the consequences of the mixing of biotas were explored.

Part 2.2 is a continuation of the NW range expansion study, monitoring amphisteginid foraminifera at the range front at the Strait of Otranto. This part of the thesis, report on the progressive invasion of amphisteginid foraminifera from the southern entrance into the Adriatic Sea (samples sites located in shallow-waters of Corfu, southern Albania and the southern boot of Italy). The impact of invasive amphisteginids on species richness of native biotas and on selected groups of benthic foraminifera (elphidiids, peneroplids, other larger benthic foraminifera, trochospiral, planispiral, smaller miliolids and epiphytes) was assessed. Recent range expansion rates for perspectives on the consequences altering native biotas were, furthermore, explored.

Part 3 deals with unknown foraminiferal assemblages in impacted and non-impacted sites within the Mediterranean Sea. Part 3.1 is the first survey of shallow-water benthic foraminiferal assemblages along nearly the entire coast of Albania. Investigated were the structure, composition, distribution and diversity of benthic foraminiferal assemblages in impacted and non-impacted sites along the coast. Non-indigenous benthic foraminifera that have invaded shallow-water sites off Albania and their introduction pathways have been assessed. All identified benthic foraminifera have been illustrated in a catalogue attached at the end of the chapter. (The systamtic of Albanian foraminiferal assemblages is included in Appendix 7.8).

All results of the individual studies are presented and discussed within the respective chapters.

Part 4 of this thesis provides a summary of the major findings and conclusions of the studies as well as a comprehensive discussion.

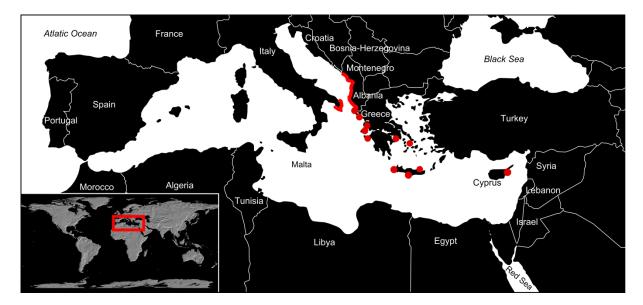


Fig. 10 Map showing Mediterranean sample site locations (red lines and dots) investigated in this thesis.

Part 2 Invasion and impact of amphistegind foraminifera in the NW Mediterranean Sea: Insights of the expanding range front

# <u>Part 2 Invasion and impact of amphistegind foraminifera in the NW Mediterranean</u> Sea: Insights of the expanding range front

# **2.1** At the front of expanding ranges: Shifting community structures at amphisteginid species range margins in the Mediterranean Sea

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## 2.1.2 Abstract

Climate warming and the poleward widening of the tropical belt have induced range shifts in a variety of marine and terrestrial organisms. Among the key taxa that are rapidly expanding their latitudinal range are symbiont-bearing foraminifera of the genus Amphistegina. Analyses of foraminiferal faunas from new sites in the western Ionian Sea (Ithaka and Lefkada Islands) show that amphisteginid for a minifera continue to expand their biogeographic range rapidly outcompete all native species and represent the most abundant taxon at almost every site colonized. The introduction and range expansion of Amphistegina puts significant pressure on local species, affects foraminiferal diversity and decreases species richness of associated biotas. Native species richness is reduced at all sites invaded by amphisteginids and correlates with the degree of infestation. Amphisteginids invasions specifically impact those species that share a similar microhabitat and include other larger symbiontbearing foraminifera and numerous trochospiral species. The impact of Amphistegina on native biotas gradually increases from the range expansion front towards those sites where invasions commenced decades ago. High abundances may result in prolific monocultures of Amphistegina that modify the composition of sedimentary substrates and ultimately trigger changes in ecosystem functioning. Assemblage structures and patterns observed at the expansion front in recent examples resemble amphisteginid invasions recorded in Miocene foraminiferal communities from the Vienna Basin and Poland, these latter being indicative of shifts in biogeographic ranges at that time. The assemblages thus preserve environmental information that is useful in paleoecologic and paleobiogeographic interpretations to evaluate the extent and magnitude of shifts along the front of expanding species ranges.

# **2.1.3 Introduction**

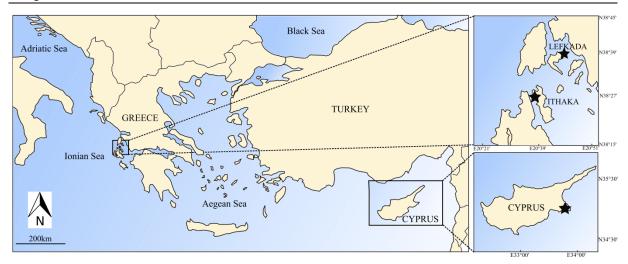
Amphisteginid foraminifera are among the most prolific and ubiquitous foraminifera on coral reefs and tropical carbonate shelves. They are indicative of warm tropical waters and their latitudinal range is strongly governed by water temperature. As key carbonate producers they have often been referred to as living sands (Lee, 1995) and contribute substantially to substrate stability and the growth of reefal structures (Hallock, 1981; Langer, 2008a; b Langer et al. 2012, 2013a, b). Climate change and the warming of the planet have induced a widening of the tropic belt including a poleward range expansion of amphisteginid foraminifera (Langer et al. 2012, 2013a; Weinmann et al. 2013b). One of the most severely affected areas of global change is the Mediterranean Sea, where global warming and the opening of the Suez Canal in 1869 triggered a mass invasion of tropical Red Sea taxa into Mediterranean territories (Boudouresque et al. 2005; Galil, 2007; Lejeusne et al. 2010). The "Red-to-Med" invasion of amphisteginid foraminifera has proceeded in a northwest direction and has generally followed the counterclockwise current pattern of the eastern Mediterranean Sea (Langer,

2008a). The Mediterranean range expansion front of amphisteginid foraminifera currently runs from the North African coast off Tunisia to the Pelagian Islands, Malta, the southeastern coast of Sicily and Corfu in northwestern Greece (Yokes et al. 2007; Triantaphyllou et al. 2009, 2012; Zenetos et al. 2010; Langer et al. 2012; Weinmann et al. 2013b). The invasion and continuing northwestern range expansion of *Amphistegina* spp. is historically well documented and samples collected in the 1960s show them to be mostly absent or present at low numbers at many sites along the range margin (Langer, unpubl. data). This would suggest the northwestern range expansion is a relatively recent event that proceeds at rates of 12.5 km/year (Langer et al. 2012; Weinmann et al. 2013b).

Recent studies have documented that the invasion and rapid proliferation continues at unprecedented rates and amphisteginid foraminifera have become extremely abundant locally. The successful invasion is not only reflected in numerical abundances but also in thick amphisteginid sediment layers that reflect the proliferation and continuing impact of the invasive taxa. At many eastern Mediterranean sites amphisteginid foraminifera were reported to represent between 30 and 70% or even more than 90% of the total faunal assemblage and, thus, they have the potential to modify the structure of habitats and ecosystems (Yokes and Meric, 2004; Meric, 2008a; Abu Tair and Langer, 2010; Triantaphyllou et al. 2012). Because of their abundance and ubiquity, and given that they are prominent producers of calcium carbonate, amphisteginid foraminifera were considered ecosystem engineers. However, the resilience of ecosystems to the disruptive forces of key invaders and the impact on native faunal communities remains to be determined. Given their prominent environmental role, rapid biogeographic range expansion and their impact on native ecosystems, amphisteginid range expansions and invasions into new territory are likely to trigger changes in community structures and ecosystem functioning. In addition, the relatively high rates of immigrants can lead to competitive exclusion (displacement) of native taxa and pose potential threats to established biotas. We have collected new material from sites off northwestern Greece (Ithaka and Lefkada islands, Ionian Sea) and Cyprus to document the effect of amphisteginid invasions on established foraminiferal biotas along the front of the expanding range margin. We also review sites of invasions where amphisteginids have been established for decades. We explore the nature of these recent biotic exchanges and their consequences on the structure of communities, their composition and the diversity of assemblages for perspectives on the consequences of the mixing of biotas.

# 2.1.4 Material and Methods

Sediment samples for foraminiferal assemblage analysis were collected from shallow waters off the Greek islands of Ithaka and Lefkada (Mediterranean Sea, see Fig. 1, 2 and Table 1) in July 2012. The islands are part of the Ionian Island region and are situated between  $38^{\circ} 26' 07.73''$  N to  $38^{\circ} 39'$  54.82" N and  $20^{\circ} 38' 21.39''$  E to  $20^{\circ} 48' 00.94''$  E. The samples cover a depth gradient between 12 and 20m. Samples were taken by SCUBA diving, filling plastic bags with substrata from the top 2 cm with subsequent transported to the laboratory. All samples were washed over 63 µm sieves, dried in the oven at  $50^{\circ}$  C and at least 300 specimens were then picked from each. Live foraminifera were grouped with dead tests and provide a time-averaged means to assess the structure of foraminiferal biotas. All specimens were identified to species level. For identification of species, our taxonomic and systematic arrangement follows the arrangement of Cimerman and Langer (1991). All samples are stored in the micropaleontological collection of the Steinmann Institute at the University of Bonn.



**Fig. 1** Location of the collection areas in the eastern Mediterranean Sea with insets showing the position of the sampling sites at Ithaka, Lefkada and Cyprus (for details see Table 1).



Fig. 2 Selected sample site locations (A) Ithaka, (B) Lefkada, (C) Aiya Thekla Beach (Cyprus), (D) Aegina Beach (Greece).

**Table 1** Sample site information for new collection locations from Ithaka, Lefkada and Cyprus (Mediterranean Sea).

Collection Site	Sample No.	Water depth (m)	Latitude	Longitude	Date
Ithaka 1	101/2012 12	12	38° 26' 07.73" N	20° 38' 21.39" E	12/July/2012
Ithaka 2	102/2012	20	38° 26' 07.73" N	20° 38' 21.39" E	12/July/2012
Lefkada	103/2012	15	38° 39' 54.82" N	$20^{\circ}$ 48' 00.94" E	13/July/2012
Cyprus 1	80/2009	2	34° 58' 36.59" N	33° 55' 22.61" E	9/March/2009
Cyprus 2	81/2009	3	34° 58' 36.59" N	33° 55' 22.61" E	9/March/2009

To determine the structure in our foraminiferal dataset and to assess the impact of *Amphistegina* on native foraminiferal biotas we analyzed percent abundances of symbiont- and non-symbiont-bearing taxa and wall structural types (including miliolid, perforate and agglutinated foraminifera). Species richness of individual assemblages was determined at each site, and diversity indices including Fisher  $\alpha$  and Shannon (H) were computed (Fisher et al. 1943; Shannon, 1948). Percent abundances of amphisteginid foraminifera were compared to numerical abundances of other foraminiferal species and to percent abundances of smaller miliolid, perforate, trochospiral and all other symbiont-bearing taxa (Fig. 3A-F). Elphidiid species, known to sequester diatom plastids, were recorded separately. Foraminiferal faunal data and diversity index values were then compared to other sites along the amphisteginid range expansion front in order to identify shifting community patterns in areas where amphisteginids have successfully invaded new territory.

## 2.1.5 Results

Quantitative faunal analysis and species level identification of the foraminiferal assemblages from Ithaka and Lefkada revealed the following results (Tables 1-2; Fig. 3A-F): A total of 987 individuals were recovered from the sediment samples belonging to 29 Genera and 54 species of benthic foraminifera. Perforate foraminifera are most abundant (53.8-62.6%) followed by miliolids (36.1-32.2%) and agglutinated individuals (1.3-3.9%, see Table 2). Fisher  $\alpha$  diversity indices range between 14.41 and 17.89 in individual samples. Shannon (H) values vary between 3.225 and 3.501 and dominance values range between 0.04775 and 0.05881.

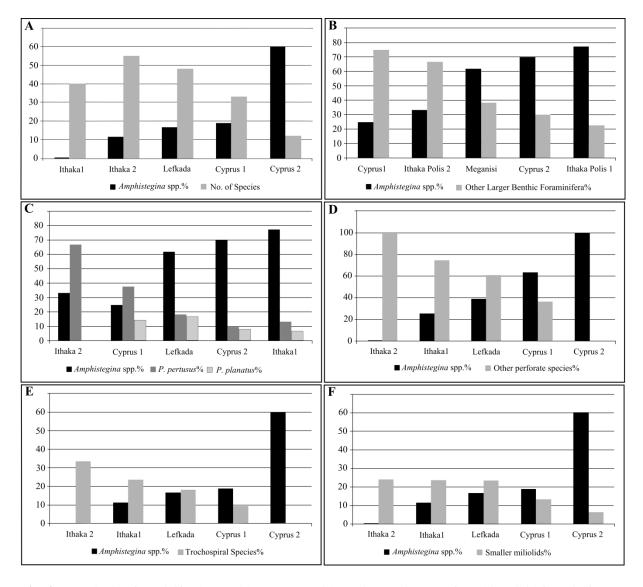
Percent abundances of symbiont-bearing foraminifera were found to range between 3.5-39.5% (excluding elphidiid taxa). Symbiont-bearing taxa include *Amphistegina* spp., *Peneroplis pertusus* (13.3-66.7%), *P. planatus* (6.7-16.8%) and *Sorites orbiculus* (0-3.1%). Elphidiid foraminifera, known to sequester diatom plastids, attain percent abundances of between 2.2 and 5.5%. The highest values are observed at depths of between 12 and 15 meters at both Ithaka and Lefkada. Non-symbiont-bearing porcellaneous taxa were found to occur in similar abundances at all of the sampled sites, ranging between 23.3 and 23.9%.

Amphisteginid foraminifera are the most frequent recorded species, attaining numerical abundance values of up to 21% of the entire foraminiferal assemblage at the new collection sites at Ithaka 1 and Lefkada Island. Once again, the highest values are observed at depths of between 12 and 15 meters. Considering all of the symbiont-bearing foraminifera, *Amphistegina* spp. represent between 33.3 and 77.3%, followed by *Peneroplis pertusus* (13.3-66.7%), *P. planatus* (6.7-16.8%) and *Sorites orbiculus* (0-3.1%) while in terms of the perforate benthic foraminifera, *Amphistegina* constitutes between 0.7 and 39.1%.

The sediment samples collected from the shallow-water sites of Cyprus was found to contain between 12 and 33 species of foraminifera. These contain between 9 and 12 genera. Fisher  $\alpha$  and Shannon (H) index values are low in these samples and range from 2.50 to 9.61 (Fisher- $\alpha$ ) and 1.47 to 2.42 (H). Specimens of non-symbiont-bearing miliolid (M), hyaline perforate (P) and agglutinated foraminifera (A) constitute between 32.2-70.1% (M), 29.5-60.1% (P), and 0.3-7.6% (A). The sediment samples off Cyprus are dominated by larger symbiont-bearing taxa (Amphisteginidae, Peneroplidae, Soritidae, elphidiids) and contribute between 75.7 and 86.0% to the total number of specimens of the foraminiferal biota. The species most frequently recorded include *Amphistegina lobifera* (18.9-60.1%), *Peneroplis pertusus* (8.3-21.1%), *P. planatus* (7.0-10.8%), *Coscinospira hemprichii* (6.6-7.0%), and *Sorites orbiculus* (4.0-10.5%).

Among the hyaline perforate larger symbiont-bearing foraminifera, specimens of amphisteginids represent the vast majority of taxa and make up between 63.5 and 100% at Cyprus (Fig. 3D). Among the symbiont-bearing foraminifera, the numerical abundance of *Amphistegina* varies between 24.8 and 69.9%, followed by *Peneroplis pertusus* (9.7-37.2%), *P. planatus* (8.1-14.2%), *S. orbiculus* (4.6-13.8%), *C. hemprichii* (7.7-9.2%), and *Elphidium* spp. (0.9%).

A comparison of species richness values and amphisteginid percent abundances shows that the high abundance values of *Amphistegina* (>50%) correlate with low species richness, while a higher species richness can be correlated with low percent abundances of amphisteginid foraminifera (Fig. 3A). Similarly, high numbers of amphisteginids correlate with low percent abundances of trochospiral taxa and samples rich in trochospiral individuals are characterized by low amounts of amphisteginid foraminifera (Fig. 3E). Smaller miliolid foraminifera, in turn, are least abundant in areas where numerical abundances of *Amphistegina* are >60% (Fig. 3F).



**Fig. 3.** Quantitative foraminiferal assemblage analyses illustrating the impact of amphisteginid foraminifera on selected groups at shallow-water sites off Ithaka and Lefkada. A negative correlation exists between (A) amphisteginid percent abundances and total diversity (species richness) of associated benthic foraminifera, (B) percent abundances of other symbiont-bearing foraminifera, (C) abundance values (%) of peneroplid taxa among all LBF' s, (D) percent abundances of other hyaline perforate benthic taxa, (E) occurrence values (%) of other trochspiral species, and (F) the amount of smaller non symbiont-bearing miliolid foraminifera.

**Table 2** Quantitative faunal analyses of foraminiferal assemblages from Ithaka and Lefkada, Greece (Mediterranean Sea). Numerical data include percent abundances of miliolid, hyaline and agglutinated foraminiferal specimens, relative amount of elphidiid and larger symbiont-bearing taxa (%) among foraminiferal biotas and other LBF's, and diversity and dominance indices of individual samples.

	Ithaka 1	Ithaka 2	Lefkada	Cyprus1	Cyprus2
	(12 m)	(20 m)	(15 m)	(2m)	(3 m)
Miliolid	36.5	36.1	42.3	70.1	32.2
Hyaline	60.8	62.6	53.8	29.5	60.1
Agglutinated	2.7	1.3	3.9	0.3	7.6
Number of species	54	39	47	33	12
Number of genera	29	27	26	22	9
Amphistegina %	15.5	0.4	21.0	18.9	60.1
Percent abundances of Amphistegina spp. among hyaline	25.4	0.7	39.1	63.5	100
taxa					
Percent abundance of smaller miliolids	23.5	23.9	23.3	14.0	6.3
Fisher a	17.98	14.41	14.61	9.614	2.501
Shannon (H)	3.501	3.225	3.326	2.424	1.47
Dominance	0.04775	0.05511	0.05881	0.146	0.3864
Percent abundance of symbiont-bearing foraminifera	20.0	1.3	34.0	75.7	86.0
(individuals) among all specimens					
Percent abundance of Amphistegina among symbiont-	77.3	33.3	61.8	25.0	69.9
bearing foraminifera (individuals)					
Percent abundance of Peneroplis pertusus among	13.3	66.7	18.3	37.5	9.7
symbiontbearing					
foraminifera (individuals)					
Percent abundance of Peneroplis planatus among	6.7	0.0	16.8	14.4	8.1
symbiontbearing					
foraminifera (individuals)					
Percent abundance of Sorites orbiculus among symbiont-	2.7	0.0	3.1	13.9	4.6
bearing					
foraminifera (individuals)					
Percent abundance of C. hemprichii among symbiont-	0.0	0.0	0.0	9.3	7.7
bearing					
foraminifera (individuals)					
Percent abundance of <i>Elphidium</i> spp.	4.0	1.5	4.3	0.9	0.0

## 2.1.6 Discussion

Assessing the impact of invasive species is a primary research focus of invasion biology (Didham et al. 2005; Rilov et al. 2012). Given the unprecedented rate at which species now traverse the globe, invasion biology has become a rapidly expanding field. Recently, Mediterranean amphisteginid foraminifera were shown to rapidly expand their biogeographic range and have become extremely abundant at many sites (Langer et al. 2012; Weinmann et al. 2013b). Their range shift has locally led to the establishment of amphisteginid monocultures (Abu Tair and Langer, 2010), the accumulation of thick sandy layers (30-60 cm; Meric et al. 2008b) ultimately leads to the displacement of previously established foraminiferal biotas (Abu Tair and Langer, 2010). The distribution and range expansion of amphisteginids is historically well documented and as such they are a particularly well suited genus to explore the scale, magnitude and impact of an invasion on the mixing of biotas. Of particular interest are the effects along the range expansion front in terms of changes in diversity (species richness) and ecosystem function. The latter reflects the collective life activities of organisms and the effects they have on the physical structure of the ecosystem itself.

Reports of amphisteginid invasions along the range expansions include a multitude of studies from the eastern Mediterranean Sea. Off the North African coast of Tunisia amphisteginids were reported as early as 1979 (Blanc-Vernet et al. 1979) where they represent up to 14% of the assemblage. Further to the east, Samir et al. (2003) noted abundances of up to 73% at shallow sites off the Nile Delta. Here, *Amphistegina* was reported to be the most frequent species, and often dominant in many of the samples. Similar observations were made by Hyams et al. (2002) and Gruber et al. (2007) along the continental shelf off Israel where *Amphistegina* was reported to occur in abundances of up to 700 specimens per gram of dry algae or 178 individuals/gram sediment.

Along the southwestern coast of Turkey, Yokes and Meric (2004) recorded up to 310000 individuals of *Amphistegina* per square meter resulting in the formation of large amounts of so called "living sand" and thus fundamentally changing the habitat type. Along the western range expansion front, Yokes et al. (2007) observed amphisteginids in the sediment and on phytal substrates at Malta Island and recorded low numbers of associated species of other foraminifera. Along the coast of Antalya (Turkey), Meric (2008) found thick sediment layers of *Amphistegina* that constitute more than 70% of the 0.5-1 mm size fraction.

Along the NW range expansion front in the Aegean Sea Triantaphyllou et al. (2005) and Koukousioura et al. (2010) reported amphisteginid occurrences that frequently made up 30 to 50% of the foraminiferal faunal assemblage. A comparison to samples collected in the 1960' s from the Aegean Sea and from Malta reveals that amphisteginids were either not present (Malta; Langer, 2008a, Langer et al. 2012) or, as in the Aegean Sea (Aegina), only present in low numbers (<2%, Langer, unpublished data). This clearly demonstrates that over the last 50 years amphisteginid foraminifera have become well established constituents in eastern Mediterranean ecosystems and are rapidly progressing to the northwest, approaching the Tyrrhenian and Adriatic seas. Langer et al. (2012) have identified the ongoing warming trend as the most likely agent facilitating the current range expansion.

#### Effect on ecosystems and biotas

To what extent climate-induced range shifts will affect biotic ecosystems are not yet fully understood. A perusal of data from eastern Mediterranean sites, however, provides further insight into the effects and consequences of the amphisteginid invasion along the range expansion front. Among the unresolved key issues of the rapidly progressing amphisteginid invasions is their impact on native for a miniferal biotas and assemblage diversity. Figure 4 shows a compilation of data from 71 sites from the eastern Mediterranean, where percent abundances of amphisteginids and species richness of foraminiferal assemblages have been reported (Samir and El-Din, 2001; Samir et al. 2003; Triantaphyllou et al. 2005). There is a clear correlation between the diversity of species present in foraminiferal biotas and the percent abundance of amphisteginid foraminifera (Fig. 4). High percentage values of Amphistegina (>50%) generally correlate with low species numbers (<25 species on average), whereas low amphisteginid abundance values (<10%) correlate with a significantly larger species richness (Fig. 4). Thus existing data corroborate the findings from the new sites (Fig. 3A), indicating that the percent abundances of the invader and species richness are closely related. This would suggest that the species richness of foraminiferal biotas and the numerical abundances of invasive species are intimately linked, and ultimately lead to the displacement of associated taxa. On average, overall foraminiferal diversity was reduced by more than 30% when amphisteginid percentages attain values of more than 25%. It should be noted, however, that while Amphistegina appears to exclude some native species from the invaded areas, the natives may persist in nearby uninvaded areas (Blanc-Vernet et al. 1979).

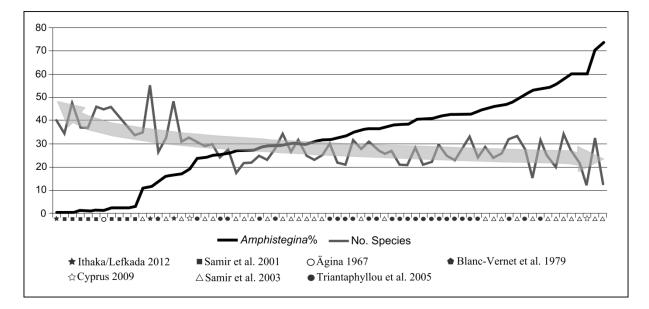
Among the taxa that appear to be directly affected by the invasion of *Amphistegina* spp. are other perforate trochospiral species including *Rosalina, Discorbina, Asterigerinata, Ammonia, Lobatula, Eponides, Cibicides,* and *Patellina.* Fig. 3E demonstrates that high values of amphisteginid percentages strongly correlate with low values of other trochospiral taxa. As epiphytes, amphisteginid and other trochospiral taxa share similar microhabitats, apparently leading to competitive exclusion and displacement by the invader. Smaller non-symbiont-bearing miliolids appear to be less affected by amphisteginid invasions. However, when *Amphistegina* reaches values of above 60% of the foraminiferal assemblage, miliolid foraminfera are reduced to less than 15%. Apparently the larger range of microhabitats occupied by miliolid foraminifera (infaunal, epifaunal, epiphytic) prevents a rapid decline of this group subsequent to an invasion.

The impact of *Amphistegina* on native biotas appears to differ between sites along the range expansion front (Ithaka and Lefkada) when compared to those where *Amphistegina* has been established for decades (Cyprus; Fig. 3A-F). In Cyprus, *Amphistegina* represents 60 to 100% of all hyaline individuals while in Greece their abundance remains at below 40%. The selective impact of the invader would support the observation that amphisteginids have a pronounced impact on those species that share a similar microhabitat (see above). Amphisteginid invasions also seem to have a selective impact on other larger symbiont-bearing taxa (LBF' s) where high percent abundances correlate with low percentages of other LBF' s (Fig. 3B). Among the LBF' s that appear to be most affected are *Peneroplis pertusus* and *P. planatus*. Both species of *Peneroplis* preferentially dwell on phytal habitats and thus share the same microhabitat preferences as the invasive amphisteginids. Apparently, an overlap of niche space, reduced room and resources, causes the drastic reduction of peneroplids once *Amphistegina* reaches threshold values of 40% (Fig. 3C).

Recently published studies indicate that native biotas throughout the eastern Mediterranean are exceptionally vulnerable to the invasion of Amphistegina (Langer, 2008a; Langer et al. 2012; Weinmann et al. 2013b) and that shallow-water foraminiferal communities show little resistance to this invasion. Furthermore, our data would suggest that, contrary to classic theory, where highly diverse assemblages are relatively resistant to invasion, both low and high diversity assemblages of native foraminiferal assemblages are equally vulnerable to amphisteginid invasions. Invasions along the range margin commonly begin low numerical abundances of amphisteginid individuals as indicated by the findings at Corfu, Aegina, Sicily or Tunisia (Blanc-Vernet et al. 1979; Langer, unpubl. data). Community invasibility then increases over time and Amphistegina rapidly becomes the most abundant taxon. At those sites where Amphistegina has been established for one or two decades, invisibility of foraminiferal communities intensifies and percent abundances of amphisteginids attain values that generally range between 10 and 50%. Fig. 4 shows that invasions at this level are accompanied by perceptible reductions in native species richness. Our compilation of data would suggest that the effect on native species richness is a gradual process (Figs. 3A, 4). The effect on diversity is even more pronounced in those for aminiferal communities where amphisteginids make up more than 60% of the assemblage, leading to competitive exclusions of primarily those taxa that inhabit the same microhabitats.

Fossil occurrences indicate that *Amphistegina* had a considerably wider latidudinal distribution during Eocene and the Miocene times (Todd, 1976). Eocene records were reported as far north as the Olympic Peninsula in Washington (48° N) and south to New Zealand (36° S). During the Miocene, amphisteginids were present in the Vienna Basin and were also found in sediments from Poland (48- $50^{\circ}$  N). At some of the Miocene localities amphisteginids formed thick amphisteginid marls similar to the amphisteginid sediments reported by Meric (2008a) from Antalya and by Abu Tair and Langer

from Cyprus (2010). At other Middle Miocene localities from the Weissenegg Quarry (Styrian Basin, Austria), amphisteginid foraminifera were reported to represent between 8 and 24% of all benthic foraminifera (Hansen et al. 1987). These values are comparable to the percent abundance records of modern amphisteginids at Ithaka and Lefkada. In addition, associated foraminiferal faunal elements (elphidiids and various trochospiral taxa) indicate a faunal structure that is similar to modern range front assemblages. Percent abundances and faunal similarities of the Miocene records from Austria and Poland thus suggest a position that represents the northernmost range expansion front of amphisteginid foraminifera (see also Langer and Hottinger, 2000). The assemblages thus retain information that is useful in paleobiogeographic interpretations to assess the extent and magnitude of range shifts along the expansion front.



**Fig. 4.** Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in selected samples from the central and eastern Mediterranean Sea. Note the negative correlation and the decrease in species richness with increasing abundances of amphisteginid foraminifera.

## 2.1.7 Conclusion

The numerical abundance and biogeographic range of the invasive foraminifer *Amphistegina* continues to increase in the eastern Mediterranean Sea. Analysis of foraminiferal assemblages along the range margin and from sites where *Amphistegina* has long been established has lead to the following conclusions:

1. Amphisteginids are continuously expanding their biogeographic range in the eastern and central Mediterranean Sea and have become the most abundant taxon at almost every site.

2. Native species richness is reduced at all sites invaded by amphisteginids and correlates with the degree of infestation. Indeed, there is a negative correlation between amphisteginid increase and reduced Fisher  $\alpha$  and Shannon (H) indices.

3. Amphisteginid invasions selectively affect associated taxa of infested foraminiferal assemblages and specifically target those epiphytic species that share a similar microhabitat. *Amphistegina* preferentially impacts other larger symbiont-bearing foraminifera (e.g. *Peneroplis pertusus*, *P*.

planatus) but also trochospiral taxa like Rosalina, Asterigerinata, Ammonia, Discorbis, Lobatula, Cibicides, Eponides, and Patellina.

4. The impact of *Amphistegina* on native biotas gradually increases from the range expansion front towards those sites where infestations took place some decades ago. The state of impact is thus closely linked to the amount of time over which *Amphistegina* has been active.

5. Amphisteginid invasions negatively impact the relationship between biodiversity and ecosystem functioning, resulting in biotic communities that are functionally more susceptible to environmental stress.

6. Amphisteginids are prolific producers of calcium carbonate and have substrate modifying capabilities. High abundances are thus likely to trigger changes in ecosystem functioning and will require careful monitoring studies in order to assess the impact on future ecosystems.

7. The diversity, assemblage structure and percent abundances of taxa may contain useful information for inferring the biogeographic course (i.e. shifting of the range expansion front) in species which are moving into new habitats as a result of changes, for example, climate conditions.

#### 2.2 Invasion of amphisteginid foraminifera in the Adriatic Sea

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#### 2.2.1 Abstract

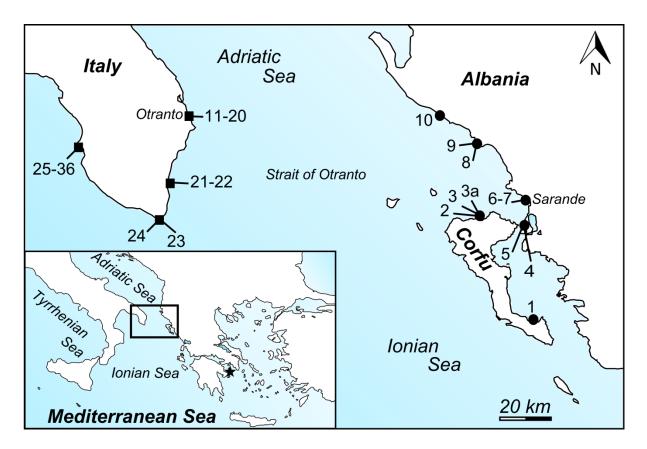
Amphisteginid foraminifera are larger symbiont-bearing foraminifera that are abundant in tropical and subtropical reef and shelf regions of the world's oceans. There is now unequivocal evidence that climate change has led to an expansion of tropical belts. As temperatures rise, surface isotherms are shifting poleward and habitat ranges are moving towards higher latitudes. Fueled by substantial warming, the Mediterranean has been identified as one of the most severely affected areas. This study documents for the first time that amphisteginid foraminifera have now crossed the Strait of Otranto and invaded the eastern Adriatic coast along southern Albania. Sampling on the opposite side along the southern part of the Italian boot shows, however, that amphisteginid foraminifera have not yet colonized the western coast of the Adriatic. The asymmetric invasion of the Adriatic displays spatial heterogeneity, where the progressive colonization follows the major surface currents with a northerly flow along the eastern coast and a southerly return along the western coastline. Previous sampling along Ionian Sea sample sites provides a baseline chronology allowing computations of range expansion rates. The observed recent rate of range expansion in Amphistegina is computed between 4.0 and 10 km/year-1 and provides strong support for current species model projections. Based on the new data, the range boundary shift is projected to lead to a total northward range expansion of 5.2°C latitude in the year 2100. The latitudinal range extension computed for the Mediterranean is thus almost twice as large as those computed for the southern hemisphere. The ongoing range extension into new areas of the Mediterranean Sea is shown to trigger changes in community structures with potential consequences for ecosystem functioning. Numerical abundances and impacts of invasive amphisteginids are greatest at shallow depths/20 m. Evidence is now accumulating that the invasion of amphisteginid foraminifera results in (1) a loss of benthic foraminiferal biodiversity, (2) alterations of foraminiferal community structures and (3) shifts in abundances of functional groups of foraminifera.

## **2.2.2 Introduction**

Climate-driven range expansions of species and organismal communities are considered the "next frontier" in marine ecosystem research. Larger benthic foraminifera of the genus *Amphistegina* were recently shown to rapidly expand their range to higher latitudes with far reaching consequences on ecosystem functioning, species diversity, carbonate production and impact on native biota (Langer et al. 2012, 2013a, b; Mouanga and Langer, 2014). Amphisteginid foraminifera are among the most conspicuous and ubiquitous foraminifera on coral reefs and tropical carbonate shelves, where they often have been referred to as living sands (Lee, 1995). As key carbonate producers, amphisteginids contribute significantly to carbonate substrate stability, growth of reefal structures, and habitat formation.

Larger symbiont-bearing foraminifera (LBF) are indicative of warm tropical and subtropical waters and their latitudinal distribution is strongly regulated by water temperatures. They have evolved to live in environments with particular temperature ranges (Langer and Hottinger, 2000), but those ranges are moving. Instead of being associated with particular latitudes, average temperatures are now shifting polewards (Seidel et al. 2008; Loarie et al. 2009). Paleontological evidence indicates that amphisteginids and other larger foraminifera cope particularly well with rising water temperatures and responded with range extensions and mass abundances during periods of increased atmospheric  $CO_2$  (Todd, 1976; Hallock, 1985; Goldbeck and Langer, 2009; Langer et al. 2013a; Weinmann et al. 2013b). Range shifts of these important protists are likely to impact native biotas and to induce changes in ecosystem functioning. Monitoring rates of range expansions in a group of beneficiaries of climate-driven temperature changes not only is a fingerprint of global change but also vital for effective management and conservation.

The Mediterranean Sea is currently undergoing a massive and unprecedented range expansion of amphisteginid foraminifera with severe consequences on ecosystem functioning (Langer et al. 2012). They are rapidly progressing northwestward, closely approaching the Adriatic and the Tyrrhenian Sea (Mouanga and Langer, 2014). The shift in range locally leads to profound ecological changes where amphisteginids have become the dominant species along entire stretches of coastline (Hyams et al. 2002; Gruber et al. 2007; Meric et al. 2008a, b; Yokes and Meric, 2009; Weinmann et al. 2013b). Hyperabundances and mass occurrences of amphisteginids reflect an increased carbonate production and reduced assemblage diversity, and these are likely to trigger major changes in ecosystem functioning. It is anticipated that the ongoing warming trend will convey the northwestward migration of amphisteginid foraminifers. This study is a continuation of previous research in the Mediterranean to monitor range expansion rates of amphisteginid foraminifera and to record the magnitude and impact of amphisteginid invasions along the range expansion front.

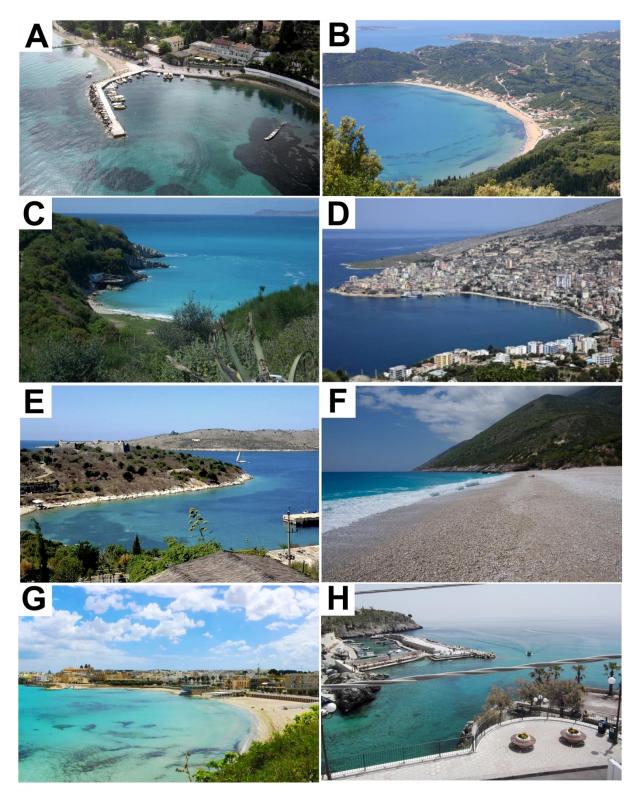


**Fig. 1** Location of the collection areas in the central Mediterranean and Adriatic Sea with insets showing the position of sampling sites in the northern Ionian, and southern Adriatic Sea at Corfu, Albania (black dots) and along the Salento Peninsula/Italy (squares, for details see Table 1). Star symbol shows the location of the sampling site from Aegina. Dashed line represents the range expansion front of amphisteginid foraminifera until summer 2010.

The current range expansion front of amphisteginid foraminifera was previously identified to run from the North African coast off Tunisia to the Pelagian Islands, Malta, and the southeastern coast of Sicily to Corfu in northwestern Greece (Fig. 1). Living amphisteginid foraminifera from the Adriatic Sea and the coast of Albania have never been reported (v. Daniels, 1970; Jorissen, 1987; Cimerman and Langer, 1991; Guelorget et al. 2000; Rada and Milat, 2002; Cosovic et al. 2006, 2011; Frontalini and Coccioni, 2008; Vidovic et al. 2010; Maiorano et al. 2011; Katsanevakis et al. 2011; Pecarevic et al. 2013; Popadic et al. 2013). Species distribution modeling has prognosticated that climate-driven range expansions will likely shift the current boundary towards the Adriatic and the Tyrrhenian Sea via the Straits of Otranto, Sicily and Messina (Langer et al. 2012). This study focuses on the invasion of amphisteginid foraminifers in the southern Adriatic Sea, a region that was previously identified by Species Distribution Modeling (SDM) to undergo future invasions of this taxon. To assess whether the amphisteginid invasion has taken place as prognosticated by SDM and whether the invasion in the Adriatic Sea progresses simultaneously along the western and eastern coast, sampling was conducted along the southern coast of Albania and the Salento peninsula (Italy, see Fig. 1; Table 1). New material from Corfu in addition to material from Aegina (northern Greece) and Gallipoli (S-Italy) was also studied to provide a baseline for comparison to compute the progress of invasion along both the Albanian and Italian coast. We have also analyzed numerous samples collected around the harbor of Otranto, a seaport that may serve as a potential settling site for organisms that underwent transcontinental transportation via ship ballast water (Fig. 1; Table 1; Calvo-Marcilese and Langer, 2010).

Mediterranean amphisteginids currently comprise two species: *Amphistegina lessonii* d'Orbigny and *Amphistegina lobifera* Larsen. In addition, two morphotypes of uncertain taxonomic status were recently reported from the Pelagian Islands (central Mediterranean Sea, Caruso and Cosentino, 2014). In modern oceans, amphisteginids have been found as far as 40°N and 31°S (Langer and Hottinger, 2000; Langer et al. 2012). Their biogeographic ranges are strongly controlled by water temperature and their distributional range is delimited by the 13.7°C winter isotherm (Zmiri et al. 1974; Hollaus and Hottinger, 1997; Langer and Hottinger, 2000). The upper temperature limits of amphisteginid foraminifers are currently not known but vital populations thriving in tidal pools of eastern Africa and Raja Ampat indicate temperatures far beyond 30 °C (Langer unpubl. data; Weinmann et al. 2013b).

Climate-driven range extensions of invasive amphisteginid foraminifers put significant pressure on local species impacting the structure, species richness and composition of native assemblages (Mouanga and Langer, 2014). In addition, evidence accumulates that the high abundances of immigrants can lead to competitive exclusion (displacement) and poses potential threats to established biotas and ecosystem functioning. Here we report on the progressive invasion of amphisteginid foraminifera from the southern entrance of the Adriatic Sea and document their effect on established foraminiferal biotas along the range expansion front. We assess the impact of invasive amphisteginids on the species richness of native biotas and on selected groups of benthic foraminifera (elphidiids, peneroplids, other larger benthic foraminifera, trochospiral, planispiral, smaller miliolids and epiphytes; for details see Langer, 1993 and Mouanga and Langer, 2014). We also explore recent range expansion rates for perspectives on the consequences of the mixing of biotas.



**Fig. 2** Selected sample site locations (A) Mpoukaris (Corfu), (B) Agnos Beach (Corfu), (C) Monastiri Bay (Albania), (D) Sarande Bay (Albania), (E) Porto Palermo (Albania), (F) Dermi Beach (Albania), (G) Otranto (Italy), (H) Tricase (Italy).

#### **2.2.3 Material and Methods**

Our sampling strategy for monitoring the extent and range of amphisteginid invasions targeted those coastal areas in the Adriatic Sea that displayed highest suitability for future invasions (Langer et al. 2012; Weinmann et al. 2013b). The Adriatic Sea is the northernmost arm of the Mediterranean and ranges from the Strait of Otranto in the south to the Gulf of Venice in the north. Sediment samples for foraminiferal analysis were collected in September 2014 along the southern coast of Albania (7 samples) and from sites northwest of Corfu Island (Ionian Sea, Greece - 3 samples, see Fig. 1-2; Tables 1, 2 for details). Samples from the shallow waters off Albania (Ionian Sea), are situated between 40°8'12.06"N and 39°46'28.92"N and 19°38'19.16"E and 19°59'59.87"E. For comparative analyses additional samples were studied from Corfu and Aegina Island (NW Greece) collected in 2010 and 1961 respectively. To monitor whether the amphisteginid invasion in the Adriatic Sea progresses simultaneously along the southeastern side of the Italian boot, intensive sampling was also conducted in 2013 along the Salento peninsula between 40°09'08.8"N and 40°02'43.7"N and 18°29'52.7"E and 18°00'24.08"E (see Fig. 1; Table 1). The sample sites studied also included the harbors of Otranto as potential settling sites of foraminiferal propagules transported by ships and ballast water. Additional material collected in the 1990s at Rada di Galippoli (Fig. 1; Table 1) was also studied to compare the progress of invasion along the southern Italian coast.

Samples were collected by Scuba-diving or a Van Veen grab covering a depth range between 1 and 30 m. Sediment collection and foraminiferal analyses followed a standard micropaleontological procedure where samples were filled into plastic bags, transported to the laboratory and then washed over 63 µm sieves and dried in the oven at 50 °C. A total of at least 300 specimens were then picked from each sample and identified to species level. Species identification follows the atlases of Mediterranean and Red Sea foraminifera (Cimerman and Langer 1991; Hottinger et al. 1993). In all analysis live foraminifera were grouped with dead tests to provide a time-averaged means to assess the structure of foraminiferal biotas. A portion of the amphisteginid foraminifera present were checked for the presence of vital protoplasm to assure that a fraction of the taxa were alive at the time of the collection. All samples are stored in the micropaleontological collection of the Steinmann Institute at the University of Bonn. To determine the structure in our foraminiferal dataset and to assess the impact of Amphistegina on native foraminiferal biotas we analyzed percent abundances of (a) wall structural types (porcellaneous, perforate and agglutinated foraminifera), and (b) symbiont- and nonsymbiont-bearing taxa. Species richness of individual assemblages was determined at each site and compared to percent abundances of amphisteginid foraminifers to (c) identify shifting community patterns in areas where amphisteginids have successfully invaded new territory in the Adriatic Sea and (d) to assess the invasive threat to the structure of native foraminiferal communities (here termed structural invasion). To identify the pathways of structural invasions and to determine whether amphisteginid invaders specifically displace selected groups or species of native benthic taxa, percent abundances were recorded for LBF's, individual morphotypes (trochospiral, planispiral, miliolids) and selected groups (ephiphytes, elphidiids) that share the niche of shallow water amphisteginid foraminifera. To place the new amphisteginid range expansion data in perspective, foraminiferal faunal and percent abundance data were then compared to other sites within the Mediterranean Sea.

Sample #	Countr y	Collection Site	Sample Number	Water Depth (m)	Latitude	Longitude	Collection Date	Amphistegina present
1	Greece	Corfu 2/ Mpoukaris	1	8	39°27'40.75"N	19°58'51.79"E	9/2014	yes
2	Greece	Corfu 1/ Ágnos	2	8	39°27'40.50"N	19°58'58.08"E	9/2014	yes
3	Greece	Corfu 3/ Agnos	3	10	39°47'58. 02"N	19°46'39. 65" E	9/2014	yes
4	Greece	Corfu 3/ Agnos	3a	5-10	39°47'58. 02"N	19°46'39. 65" E	5/2010	yes
5	Albania	Gjiri Monastiri Bay	4	5	39°48'49.79"N	20° 00'36.49"E	10/2014	yes
6	Albania	Gjiri Monastiri	5	30	39°48'51.71"N	20° 00'34.89"E	10/2014	yes
7	Albania	Sarande Bay	6	5	39°52'23.04"N	20°00'29.19"E	10/2014	yes
8	Albania	Sarande Bay	7	30	39°52'20.82"N	20°00'28.16"E	10/2014	No
9	Albania	Porto Palermo	8	5	40°03′51.14"N	19°47′33.98"E	10/2014	yes
10	Albania	Porto Palermo	9	30	40°03'51.30"N	19°47'31.89"E	10/2014	No
11	Albania	Kondraq/Dermi	10	5	40°08'38.48"N	19°37'41.08"E	10/2014	yes
12	Italy	Otranto	11	10-11	40°09'25.01"N	18°29'25.01"E	5/2013	No
13	Italy	Otranto	12	23	40°09'08.08"N	18°29'52.07"E	5/2013	No
14	Italy	Otranto	13	26	40°09'24.07"N	18°30'02.01"E	5/2013	No
15	Italy	Otranto	14	28	40°09'19.02"N	18°29'58.08"E	5/2013	No
16	Italy	Otranto	15	10	40°09'25.00"N	18°29'250.9"E	5/2013	No
17	Italy	Otranto	16	10	40°09'22.09"N	18°29'27.15"E	5/2013	No
18	Italy	Otranto	17	10	40°09'25.83"N	18°29'23.50"E	5/2013	No
19	Italy	Otranto	18	11	40°09'23.77"N	18°29'23.60"E	5/2013	No
20	Italy	Otranto	19	11	40°09'27.24"N	18°29'24.66"E	5/2013	No
21	Italy	Otranto	20	11	40°09'25.00" N	18°29'250.9"E	5/2013	No
22	Italy	Tricase /Porto di Gallipoli	21	1	39°55'49.01"N	18°23'42.42"E	5/2013	No
23	Italy	Tricase / Porto di Gallipoli	22	2-3	39°55'48.90"N	18°23'43.32"E	5/2013	No
24	Italy	Porto Santa Maria di Leuca	23	5-6	39°47'40.49"N	18°21'39.44"E	5/2013	No
25	Italy	Porto Santa Maria di Leuca	24	3	39°47'41.80"N	18°21'43.31"E	5/2013	No
26	Italy	Baia Verde (Gallipoli)	25	4	40°02'43.07"N	18°00'24.08"E	5/2013	No
27	Italy	Baia Verde (Gallipoli)	26	5	40°02'43.07"N	18°00'24.7"E	5/2013	No
28	Italy	Rada di Gallipoli	27	2	40°03'22.45"N	17°58'27.08"E	8/1990	No
29	Italy	Rada di Gallipoli	28	2	40°03'23.32"N	17°03'27.32"E	8/1990	No
30	Italy	Rada di Gallipoli	29	2	40°03'22.95"N	17°58'27.09"E	8/1990	No
31	Italy	Rada di Gallipoli	30	3	40°03'18.19"N	17°58'11.34"E	8/1990	No
32	Italy	Rada di Gallipoli	31	3	40°03'19.32"N	17°58'24.89"E	8/1990	No
33	Italy	Rada di Gallipoli	32	3	40°03'17.67"N	17°58'11.33"E	8/1990	No
34	Italy	Rada di Gallipoli	33	4	40°03'16.94"N	17°58'12.28"E	8/1990	No
35	Italy	Rada di Gallipoli	34	4	40°03'20.44"N	17°58'25.94"E	8/1990	No
36	Italy	Rada di Gallipoli	35	4	40°03'21.17"N	17°58'26.73"E	8/1990	No
37	Italy	Rada di Gallipoli	36	4	40°03'20.21"N	17°58'26.34"E	8/1990	No
38	Greece	Aegina	37	0.5	37°44'28.74"N	23°32'08.06"N	10/1967	yes

**Table 1** Sample site information for collection locations from Albania, Greece (Corfu, Aegina) and Italy (Mediterranean Sea).

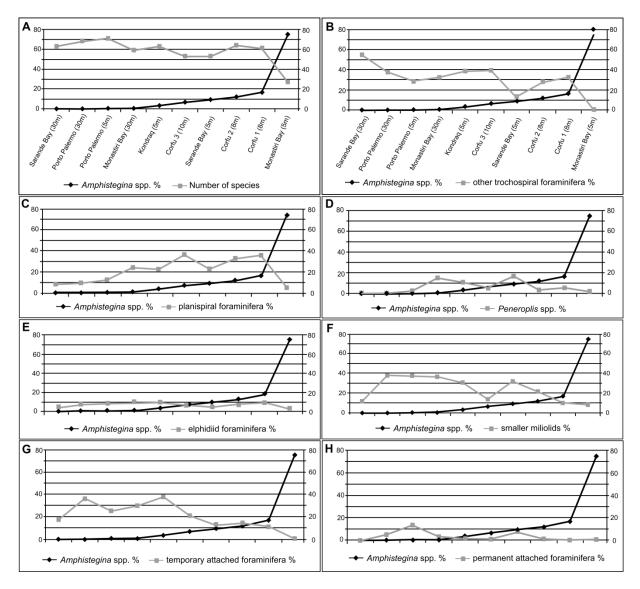
#### 2.2.4 Results

Quantitative faunal analysis and species level identification of the foraminiferal assemblages from Albania, Greece and the Salento Peninsula in southern Italy revealed the following results (Tables 1, 2; Fig. 3A–H): A total of 5057 individuals were recovered from the sediment samples belonging to 36 genera and 71 species of benthic foraminifera. Species richness ranges between 27 and 71 for samples from Albania, and between 53 and 64 and 41 and 65 for samples from Greece and Italy respectively (see Table 2). Perforate foraminifera are most abundant (35.1–61.8 %) followed by miliolids (11.0–52.8 %) and agglutinated individuals (0.3–42.1 %, see Table 2). Fisher  $\alpha$  diversity indices range between 7.191 and 28.71 in individual samples. Shannon (H) values vary between 1.23 and 3.80 and dominance values range between 0.032 and 0.11. Percent abundances of symbiont-bearing foraminifera were found to range between 0.3-77.4 % (excluding elphidiid taxa). Symbiont-bearing taxa include *Amphistegina* spp. (0–75.0 %), peneroplids (0.3–44.4 %), *Sorites orbiculus* (0.0–2.6 %) and *Coscinospira hemprichii* (0.4–7.2 %).

**Table 2** Numerical data include percent abundances of miliolid, hyaline and agglutinated foraminiferal specimens, number of species and genera, diversity and dominance indices, the relative amount of larger symbiont-bearing benthic foraminifera (including *Amphistegina* spp., *Peneroplis* spp., *Sorites* spp. and *Coscinospira hemprichii*), percent abundance values of *Amphistegina* spp. among LBF, abundance values (%) of symbiont-bearing foraminifera and *Amphistegina* spp. among symbiont-bearing taxa, percent abundance values of elphidiid, smaller non symbiont-bearing taxa, the relative amount of trochospiral and planispiral foraminifera as well as percent abundance values of temporary and permanent attached epiphytic species of individual samples.

	Albania Kondraq	Albania Porto Palermo	Albania Porto Palermo	Albania Sarande Bay	Albania Sarande Bay	Albania/Giri Monastiri	Albania/Giri Monastiri	Corfu 1 Mpoukaris	Corfu 2 Mpoukaris	Corfu Agnos
	(5 m)	(5 m)	( <b>30 m</b> )	(5 m)	(30 m)	(5 m)	( <b>30</b> m)	( <b>8 m</b> )	(8 m)	( <b>10 m</b> )
Miliolid %	43.0	52.1	40.3	52.8	13.1	11.0	41.0	33.0	42.7	36.9
Hyaline %	55.7	45.5	56.5	35.1	44.8	78.3	57.3	61.8	56.6	61.8
Agglutinated %	1.2	2.4	3.2	12.2	42.1	10.7	1.7	0.3	0.7	1.3
Number of species	63	59	68	53	63	27	71	61	64	52
Number of genera	28	26	33	26	33	13	35	31	33	36
Fisher a	23.37	20.8	28.71	19.69	23.48	7.191	29.37	18.07	25.11	23.48
Shannon (H)	3.485	3.44	3.716	3.181	3.149	1.234	3.809	3.063	3.465	3.409
Dominance	0.05	0.04	0.03	0.06	0.11	0.56	0.03	0.08	0.05	0.05
Amphistegina spp. %	3.4	0.6	0	9.2	0	75.0	0.3	16.7	11.9	6.6
Peneroplis spp. %	12.1	15.9	0.4	17.3	2.3	2.7	0	23.2	21.2	23.3
Sorites spp. %	0.3	0	0	2.6	0	0	0	0	0	0
Coscinospira spp. %	0	0	0	0	0	0	0	7.2	6.6	6.3
LBF in %	15.8	16.5	0.4	29.2	0.3	77.3	3.0	55.6	47.7	46.5
Amphistegina % among LBF	21.6	3.6	0	31.6	0	97.0	11.1	28.2	30.6	35.7
LBF in %	25.1	24.9	7.2	33.6	3.6	79.7	10.1	64.4	54.6	52.5
Amphistegina % among LBF (incl. elphidiid forams)	13.6	2.4	0	27.5	0	94.1	3.1	25.9	21.8	12.7
Elphidium spp. %	9.3	8.4	6.8	4.4	3.3	2.3	7.7	8.8	7.0	6.0
Smaller miliolids	30.7	36.2	37.8	32.1	11.9	8.7	37.3	9.8	21.5	13.6
Trochospiral foraminifera %	41.8	32.2	37.8	22.5	54.6	75.3	29.0	49.0	39.7	45.8
Amphistegina % among trochospiral foraminifera	8.1	1.8	0	41.0	0	99.6	1.1	34.0	30.0	14.5
Planispiral	22.3	24.3	9.0	22.5	8.1	4.7	11.7	36.3	32.8	36.5
Epiphytic forams % (temp. attached) %	37.5	29.6	36.3	12.9	17.6	0.3	25.3	11.1	14.6	20.9
Epiphytic forams % (perm. attached)	1.9	3.0	5.0	7.7	0	0.7	13.7	0.3	1.0	0.3
Epiphytes forams (temp. & perm.) %	39.4	32.6	41.3	20.6	17.6	1.0	39.0	11.4	15.6	21.2
Substrate type	coarse sand	coarse sand	mud	coarse sand	mud	coarse sand	sandy mud	medium grained sand	coarse sand	medium grained sand

Among all symbiont-bearing taxa, amphisteginid foraminifera represent up to 97 % (Table 2). Elphidiid foraminifera, known to sequester diatom plastids, attain percent abundances between 2.3 and 57.5 %. The highest values of symbiont-bearing foraminifera were recorded at shallow depths of\10 m at both Corfu and Monastiri Bay (Albania; Table 2). Amphisteginid foraminifers were recorded at almost all new sites located on the southeastern Adriatic coastline off Albania. No amphisteginid foraminifera were found along the southern Italian coastline off the Salento Peninsula including the harbor of Otranto. Amphisteginids were also absent from all samples collected between the tip of the Italian boot at Capo de Leuca and Gallipolli (see Fig. 1).



**Fig. 3** Quantitative foraminiferal assemblage analyses illustrating the impact of amphisteginid foraminifera on selected groups at shallow-water sites off Corfu and Albania. Locations listed in diagram **A**, **B** are identical for **C–H** A negative correlation exists between a amphisteginid percent abundances and species richness of associated benthic foraminifera, **B** percent abundances of other trochospiral foraminifera, **C** abundance values (%) of planispiral species, **D** percent abundances of peneroplid foraminifera, **E** occurrence values (%) of other elphidiid taxa, **F** the amount of smaller non symbiont-bearing miliolid foraminifera, **G** percent abundance values of temporary attached and **H** permanent attached epiphytic species.

Amphisteginid foraminifera were among the most frequently recorded species, attaining numerical abundance values of up to 75 % of the entire foraminiferal assemblage (Table 2). Percent abundances of this taxon off Albania were consistently higher at shallow sites (5 m, 0.6–75.0 %) compared to deeper reference sites from the same locations at 30 m (0.0–0.3 %). Moderate percent abundances ranging between 6.6 and 16.7 % were recorded at the sites off Corfu Island at depth between 8 and 10 m. A comparison of species richness values and amphisteginid percent abundances at the new collection sites off Albania and Corfu shows that the high abundance values of *Amphistegina* correlate with low species richness, while higher species richness correlates with low percent abundances of amphisteginid foraminifera (Fig. 3A). Similarly, high percent occurrences of amphisteginids correlate with low percent abundances of other trochospiral and planispiral taxa (Fig. 3A, B). Percent comparisons between amphisteginid, peneroplid, elphidiid, and smaller miliolid foraminifera are less

indicative but reveal a consistent impact when particularly high percentages ( $\geq$ 75 %) of amphisteginids occur (Fig. 3D-F).

A comparison of percent abundances of amphisteginids and epiphytic foraminifera shows, however, that ephiphytic foraminifera and in particular temporarily attached epiphytes decrease when percent abundance values of *Amphistegina* spp. are >9 % (Fig.3G, H; Table 2). Non-symbiont-bearing smaller miliolid taxa were found to occur with abundances ranging from 8.7 to 37.8 %. They are least abundant in areas where numerical abundances of *Amphistegina* attain values >16 % (Fig. 3E).

# 2.2.5 Discussion

Global warming and the extension of climate belts are likely to alter the range of suitable habitation areas for many species (Hoegh-Guldenberg and Bruno, 2010; Tittensor et al. 2010). To what extent climate induced range shifts will affect biotic ecosystems is considered the next frontier in climate change research (Kinitsch, 2008) but remains yet to be explored. One of the most severely affected areas in the world is the Mediterranean Sea, where range shifts are fueled by substantial warming and invasions of allochthonous species through the Suez Canal (Bianchi and Morri, 1994; Langer, 2008a; Langer et al. 2012). The opening of the Suez Canal in 1869 triggered a massive migration of Red Sea taxa (Lessepsian migrants), a predominantly unidirectional "Red-to-Med" dispersal (Por, 1971, 1978, 2009; Langer, 2008a; Merkado et al. 2012, 2013).

We have established a global biogeographic data base that covers the global occurrence records of amphisteginid foraminifera in modern oceans (Langer and Hottinger, 2000; Weinmann et al. 2013a, b). Our Mediterranean Sea occurrence records now comprise more than 200 sites and were used to document recent range shifts and the position of the range expansion front of amphisteginid foraminifers (Langer and Hottinger, 2000; Langer, 2008a; Langer et al. 2012; Weinmann et al. 2013b; Mouanga and Langer, 2014; see also Caruso and Cosentino, 2014). Based on our comprehensive data sets, we have previously located the Mediterranean extension of the current range expansion front to run from the North African coast off Tunisia to the Pelagian Islands, Malta, and the southeastern coast of Sicily to Corfu in northwestern Greece (Mouanga and Langer, 2014). Our new material collected from shallow-water sites off Albania now provide the first evidence that amphisteginid foraminifera have extended their range into the Adriatic Sea by crossing the Strait of Otranto (Fig. 1; Table 2). The new findings of amphisteginids migrating into the Adriatic Sea represent the northwesternmost occurrence record reported in the Mediterranean to date (at 40.08°N).

Amphisteginid foraminifera were previously identified to range among the 100 worst invasive species in the Mediterranean Sea (Streftaris and Zenetos, 2006; Zenetos et al. 2008). A range expansion of amphisteginid foraminifera in northwestern direction towards the Adriatic Sea was recently prognosticated by species distribution modelling (Langer et al. 2012; Weinmann et al. 2013b), as a consequence of dramatically risen sea surface temperatures. Temperature has been identified as a key variable controlling the spatial distribution of symbiont-bearing amphisteginids (Zimiri et al. 1974; Langer and Hottinger, 2000; Langer et al. 2012).

The species distribution model applied to amphisteginids is based on currently recognized ecological niche constraints to identify potentially suitable and future habitats within the Mediterranean Sea (for details see Langer et al. 2012; Weinmann et al. 2013b). Winter minimum sea surface temperature (SST) was identified to be among the main agents controlling the latitudinal distribution of this taxon. Recent studies from northern Greece indicate that amphisteginid foraminifera tolerate temperatures as low as 13.8 °C (Triantaphyllou et al. 2012) or even lower (Meric et al. 2001, 2005). For the latter,

however, minimum winter temperatures were not documented. The Species Distribution Model applied showed that *Amphistegina* spp. have the potential to expand their current biogeographic range towards the Adriatic and the Tyrrhenian Sea and that future climate warming will facilitate a range extension towards higher latitudes (Langer et al. 2012). Weinmann et al. (2013a, b) prognosticated that the average range expansion rate till the year 2100 will be approximately 12.5 km per year (for the Mediterranean Sea). The new occurrence records document a range extension along the coast of Albania into the Adriatic Sea and thus provide strong support for the scenarios prognosticated by Species Distribution Modeling (Langer et al. 2012; Weinmann et al. 2013b).

Previous research and extensive sampling on foraminifera from this area provides a baseline chronology illustrating the ongoing range expansion of amphisteginids in the Central Mediterranean Sea (Cimerman et al. 1988; Daniels v., 1970; Cimerman and Langer, 1991; Langer and Hottinger, 2000; Langer, 2008a, Mouanga and Langer, 2014 and references therein). The new occurrences document a realized expansion and exceed previously known distribution records by ~40 km (Corfu  $\leftrightarrow$  Albania, Langer in Zenetos et al. 2012) and 202.92 km (Ithaka  $\leftrightarrow$  Albania; Mouanga and Langer, 2014). The northwestern range extension and invasion of the Adriatic Sea is therefore a relatively recent event that corroborates amphisteginid expansion rates computed by Weinmann et al. (2013b). The potential biogeographic range expansion for amphisteginids in the Adriatic Sea was predicted to expand to the coast of Croatia (45.1°N) in the year 2100 (Langer et al. 2012; Weinmann et al. 2013b). This is equivalent to an average range shift of 8.5 km per year when compared to the latest record published from Corfu in NW Greece (Langer in Zenetos et al. 2012). The new records from Albania indicate a northwestward range shift of approximately 40 km for the last 4 years (compared to Corfu). This results in a current range shift rate of 10 km per year, slightly lower than the average range shift rate computed for the entire Mediterranean (12.5 km/year<sup>-1</sup>, Langer et al. 2012), but faster than previously prognosticated for the Adriatic Sea (~8.2 km/year<sup>-1</sup>; Weinmann et al. 2013b). This suggests that either the recent range expansion rate of 10.0 km per year has slightly increased over the last years or that computations of the previous range expansion calculations were too conservative. However, if the historical sample material from the Greek Island of Aegina is taken as a reference point, than the average range shift is computed to be at around ~4 km per year (Aegina  $\leftarrow \rightarrow$  Albania).

The range expansion along the coast of Albania is in line with recent SST increases and isotherm shifts recorded in the Mediterranean Sea (Francour et al. 1994, 2010; Coll et al. 2010; Lejeusne et al. 2010; Bianchi et al. 2013). Data from shallow-water sites in the Mediterranean in addition to satellite data show that Mediterranean waters have warmed by ~1.0 °C and that SST rise over the last 30 years is at a much faster rate than that documented for the time period between 1885 and 1967 (Prieur, 2002; Romano and Lugrezi, 2007; Vargas-Yanez et al. 2008; Coma et al. 2009; Lejeusne et al. 2010). As outline above, temperature has been invoked as the major factor controlling the latitudinal extension of amphisteginid foraminifera (Zmiri et al. 1974; Langer and Hottinger, 2000; Langer et al. 2012, 2013a). Northward shifts of surface isotherms, due to climate warming, facilitates the expansions of warmwater species and allows the penetration of the Adriatic sub-basin through the Strait of Otranto. The finding that amphisteginid foraminifera are currently expanding their distributional range agrees with multiple observations that numerous invertebrate and vertebrate species greatly expanded their territory northwestwards in the Mediterranean (Bianchi and Morri, 1994; Astraldi et al. 1995; Vacchi et al. 2001; Bianchi et al. 2013).

Surprisingly, however, no amphisteginid foraminifera were yet detected along the SE coast of the Italian boot. The occurrence records collected to date therefore indicate that the invasion of amphisteginids progresses along the eastern side of the Adriatic Sea from the northern region around the island of Corfu (Greece) into Albania. The biogeographic range extension thus follows the major

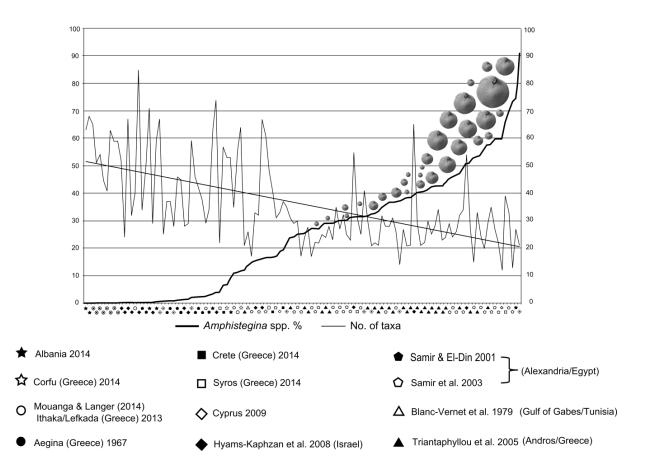
current system that transports warm water northwards into the Adriatic along the eastern coastlines and colder water southward along the eastern side of the Italian boot (see Fig. 1 and Reference Poulain, 1999, 2001; Artegiani et al. 1996, 1997). In addition, SST distribution shows that warmer waters are present on the eastern side of the Adriatic Sea driven by the inflow of a warm eastern current that originates in the Ionian Sea (Artegiani, 1997; Orlic et al. 1992; Poulain, 1999, 2001). The nonuniform colonization of the Adriatic thus provides further evidence that SST is a key environmental predictor driving the range extensions of symbiont-bearing amphisteginid foraminifera. The absence along the Adriatic coast of southern Italy also demonstrates amphisteginid foraminifera did not yet underwent transportation via ship ballast water in this region.

Amphististeginid foraminifera are among the key invasive species currently extending their ranges and have locally become extremely abundant. At numerous eastern and central Mediterranean sites they represent up to 70 % or more of the foraminiferal fauna (Langer et al. 2012; Caruso and Cosentino, 2014; Meric et al. 2008a;b; Samir et al. 2003; Yokes and Meric, 2009; Abu Tair and Langer, 2010; Arielie et al. 2011; Mouanga and Langer, 2014; Lazar, 2007). The new findings from the expansion front off Albania and Corfu show that amphisteginids are particularly successful invaders in shallow-water habitats <20 m (Table 1). These sites are characterized by medium to coarse grained calcareous/siliceous sediments or by hard substrates/rocky shores that are densely covered by macroalgae. Percent abundances of *Amphistegina* spp. at those sites ranges between 6.6 and 75 % (with two exceptions, Table 2). The proliferation of amphisteginid foraminifers in shallow-water sites agrees well with previous records from the eastern and central Mediterranean Sea (Samir and El-Din 2001; Hyams et al. 2002; Samir et al. 2003; Triantaphyllou et al. 2005; Gruber et al. 2007; Yokes et al. 2007; Lazar, 2007; Meric et al. 2008a, b; Hyams-Kaphzan et al. 2008; Yokes and Meric, 2009; Triantaphyllou et al. 2012; Mouanga and Langer, 2014; Caruso and Cosentino, 2014).

Recently published studies indicate that Mediterranean ecosystems and native biotas are exceptionally vulnerable to the invasion of *Amphistegina* (Mouanga and Langer, 2014 and references therein). The invasion and prolific occurrences indicate that the amphisteginid invaders successfully fill an open niche that obviously is providing ideal conditions. In the Mediterranean, shallow-water environments ( $\leq 20$  m) appear to have the highest susceptibility to colonization and establishment of individuals (Langer et al. 2012; Mouanga and Langer, 2014; see above). Here, the percent abundance of invasive *Amphistegina* spp. often exceeds abundance values of all other foraminiferal species. Extreme forms of ecosystem invisibility have been reported from several shallow Mediterranean sites, where foraminiferal assemblages resemble monocultures of *Amphistegina* (Hyams et al. 2002; Gruber et al. 2007; Langer et al. 2012; Caruso and Cosentino 2014; Mouanga and Langer 2014; Yokes and Meric, 2004; Abu Tair and Langer, 2010; Samir et al. 2003). Amphisteginids are prolific producers of calcium carbonate and have substrate modifying capabilities (Hallock, 1981; Langer et al. 1997; Yokes and Meric, 2004). At some sites extreme abundances of amphisteginid invaders were shown to result in the formation of large amounts of "living sands" (Meric et al. 2008a, b; Yokes and Meric, 2009; Abu Tair and Langer, 2010; Langer et al. 2012).

While the immediate impact of such changes appears to be obvious, the resilience of key invaders remains to be determined. Mouanga and Langer (2014) have demonstrated that massive invasions of amphisteginids result in the homogenization of the foraminiferal faunas. They also showed a clear correlation between the diversity of foraminiferal biotas and percent abundances of amphisteginid invaders. The data from Albania and Corfu provide additional support for this conclusion. The correlation of reduced species richness with ascending percent abundances of amphisteginid invaders is even more prominent when sample sites from the eastern and central Mediterranean sites are

compiled. Figure 4 shows a compilation of new data from a total of 124 sites (modified and extended from Mouanga and Langer, 2014) illustrating the negative correlation between species richness and increasing abundances of amphisteginids. This would suggest that the species richness of foraminiferal biotas and the numerical abundances of invasive species are intimately linked and ultimately leads to the displacement of associated taxa. Amphisteginid invasions selectively affect associated taxa of infested foraminiferal assemblages. Among the taxa that are primarily impacted are other perforate trochospiral and planispiral species of foraminifera (Fig. 3, Table 2). They appear to share the same microhabitat as *A. lessonii* and *A.lobifera*, which were reported as epifaunal and epiphytic constituents from shallow water ecosystems (Langer, 1993; Hallock, 1981; Hallock et al. 1988, 1999; Hohenegger, 1994; Hohenegger et al. 1999). The displacement of taxa from similar microhabitats suggests that competitive exclusion is a major driving force regulating species richness in invaded communities. Smaller non-symbiont bearing miliolid foraminifera appear to be less affected by amphisteginid invasions apparently due to their wider range of microhabitats. Similar findings were previously reported from shallow-water sites off Ithaka, Lefkada and Cyprus (Mediterranean Sea, Mouanga and Langer, 2014).



**Fig. 4** Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in 124 selected samples from the central and eastern Mediterranean Sea (including the new material from the Adriatic Sea). Note the negative correlation and decrease in species richness with increasing abundances of amphisteginid foraminifera. The regression line is shown superimposed on the individual data points.

It should also be noted, however, that the displacement of native species may be of local nature and that natives may persist in nearby uninvaded areas. It is also not known, if amphisteginids are displacing any species other than foraminifera and what role they play in the food web of metacommunities.

Hyperabundances, mass occurrences and the appearance of invasive amphisteginids in monocultures were previously shown to lead to a homogenization of the foraminiferal fauna (Langer et al. 2012). They modify the grain size and have the capability to transform the composition, nature and chemistry of sediments from predominantly siliceous to carbonate deposits. Yokes and Meric (2004) have reported depositional rates of amphisteginid foraminifera to range between 2.5 and 4.0 cm year-1. At some sites along the coast of Turkey, amphisteginid foraminifera were reported to constitute 75 % of the sediment and up to 80 % of the 0.5-1 mm size fraction (Meric et al. 2008a). The large contribution of amphisteginid tests to the sediment resulted in sand accumulations, that "changed the habitat type and coastal structure" (Yokes and Meric, 2004). Test of larger foraminifera were also shown to act as "convenient benthic islands" providing additional attachment surfaces for other smaller foraminifera (Martin, 2008). Hallock and Talge (1994) and Hallock et al. (1998) described predation on Amphistegina by Floresina amphiphaga. As such, mass abundance of amphisteginid foraminifera inflict changes to the conditions and resources for other organisms and were considered true ecosystem engineers (Langer et al. 2012). Further studies and a refinement of methods are required to fully address the impact of amphisteginid invasions over larger spatial scales to assess their role on the diversity of native communities. The present warming trend will continue to reinforce the spread of tropical organisms towards higher latitudes. Given their abundance, rapid range expansion, and prolific production of calcium carbonate, amphisteginid invasions are likely to impact native ecosystems and to trigger changes in ecosystem functioning.

# 2.2.6 Conclusion

The Mediterranean Sea is among those oceanic regions that are most affected by the ongoing warming trend. Rising temperatures caused by climate change have favored poleward migrations and range expansions in many groups of organisms. Among the key species that are currently expanding their biogeographic range are amphisteginid foraminifera, a group of symbiont-bearing and prolific carbonate producing protists. Quantitative analyses of benthic foraminiferal assemblages from new sites in the southern Adriatic Sea show, that amphisteginid foraminifera continue to expand their range and have crossed the Strait of Otranto to invade the Adriatic Sea. Parallel examination and monitoring of sampling sites along the Albanian and the Italian side of the southern Adriatic reveals an asymmetric colonization, where the progressive invasion follows the major surface currents along the eastern coast along Albania. The proliferation and recent range expansion rates of amphisteginid foraminifera provide strong support for previous species distribution models projecting the northward migration and invasion of the Adriatic Sea. Our results also corroborate previous findings that rising water temperatures and warm currents are the most likely agents controlling the latitudinal extension.

The range expansion of amphisteginid foraminifera primarily affects the shallow-water environments (<20 m) where habitat invasibility is documented by high numerical abundances and associated with a reduction in species richness. Amphisteginid invasions also affect the structure of native foraminiferal assemblages and are likely to trigger changes in ecosystem functioning. Climate change and the northward moving of surface isotherms will continue to support the range expansion of tropical species ultimately leading to a homogenization of the Mediterranean biotas.

## Part 3 Foraminiferal assemblages in anthropogenic impacted and non-impacted areas

# **3.1** Shallow-water benthic foraminiferal assemblages from the coast of Albania (Mediterranean Sea)

Gloria H. Mouanga & Martin R. Langer

Manuscript in preparation

# 3.1.2 Abstract

Albania is located in a peculiar position bordering three biogeographical regions (Eastern-, Western Mediterranean Sea, Adriatic) of the Mediterranean Sea. Its shallow waters provide a wide range of habitat for a high number of marine species. We document the composition and distribution of shallow-water benthic foraminiferal assemblages in conjunction to given substrates and ecological conditions. The samples collected show high species richness values (277 species, 112 Genera) with taxa known to be distributed in the Adriatic as well as in the Eastern and Western Mediterranean Sea. The performed hierarchical cluster analysis reveal the presence of two distinct clusters and biofacies characterized for the northern and southern coastline respectively. The disparity between the two biofacies and clusters along the northern and southern coastline is related to geomorphological and hydrological differences and intensified by human mediated action. The two biofacies regimes are characterized by specific foraminiferal assemblages and differ in the composition of functional groups of foraminifera (heterotrophic, opportunistic, mixotrophic). Opportunistic and heterotrophic foraminifera characterize the southern coastline.

Increasing anthropogenic pressure accompanied with pollution from sewage, urban wastes, maritime traffic, and building activities lead to partly degrading conditions within certain areas. The Gulf of Vlore and Sarande Bay were subjected to increasing anthropogenic pressure and have favoured the establishment and accumulation of mainly opportunistic species. We, furthermore, documented the presence of non-indigenous (NI) benthic foraminifera with Indo-Pacific and Atlantic origin in the samples sites off Albania. The presence of NI benthic foraminiferal species is mainly controlled by rising sea surface temperatures and the subsequent dispersal by currents. Ballast ship water is also considered to be a major source of non-native species introductions. The invasive benthic foraminifera along the Albanian coastline with severe consequences on native biotas and ecosystem functioning. Current climate warming will enhance the introduction of NI (non-indigenous) species into the Adriatic Sea, so that they can be expected to invade the shallow waters of Montenegro and Croatia, before the dispersal is getting limited through the eutrophic conditions and cooler sea surface temperatures in the Northern Adriatic Sea.

# **3.1.3 Introduction**

The Mediterranean Sea is a hotspot for marine biodiversity with approximately 17000 marine species. All biogeographic areas are well documented and investigated in terms of biodiversity and macrohabitats, including the northernmost part of the Mediterranean, the Adriatic Sea. An exception is built by the beautiful country Albania. Albania is located in a transition zone bordering three biogeographical areas of the Mediterranean Sea (Eastern- and Western Mediterranean and Adriatic Sea). There are limited existing studies on the marine habitats and marine biodiversity in general. But the development of project related inventories of coastal habitats lead to an increasing rate of publications in the last two decades (among others: Kashta, 1992, Gjiknuri, 1995, Guelorget et al. 2000; Kashta et al. 2007; Xhulaj and Miho, 2008; Bequiraj et al. 2008a; Kashta et al. 2010 (PAGA); REC JL; Telo et al. 2011; Maiorano et al. 2011; RAC/SPA - UNEP/MAP, 2013). The shallow coastal waters off Albania are an environmentally sensitive region, which comprise a high biodiversity, including rare, endemic and endangered species registered on the red list such as loggerhead and leatherback turtles, cetaceans, sharks and monk seals (Gjiknuri, 1995, Simeoni et al. 1997, Kashta et al. 2010/PAGA REC JL; RAC/SPA - UNEP/MAP, 2013). About 109km<sup>2</sup> of coastal wetlands and lagoons provide wintering and breeding grounds for more than 70 water bird species (including the endangered Dalmatian pelican *Pelecanus crispus* and pygmy comorant *Phalacrocorax pygmaeus*) (Gjiknuri, 1995; Simeoni et al. 1997; Cullaj et al. 2005). But many habitats are seriously endangered by human mediated impacts as they are most exposed and unprotected (Cullaj et al. 2005, 2007). Anthropogenic impacts include (e.g) maritime traffic, coastal pollution due to urban and industrial sewage discharges, building activities and forest mismanagement enhancing (coastal) erosion rates, tourism with uncontrolled activities, hydrocarbon exploration, agricultural overproduction and aquaculture accompanied with eutrophication. Natural mediated impacts concern geomorphology controlled erosion rates along the Adriatic coastline, which in combination with human forced erosion leads to massive deposition of solid material in the coastal areas, resulting in unfavorable conditions for life in rivers, lagoons and the marine coast (Cullaj et al. 2005). Current climate warming, the opening of the Suez Canal in 1869, ship fouling and ballast water transportation supplementarily enhances the invasion of thermophilic NI species. The Mediterranean Sea and especially the Eastern biogeographical province is to date invaded by 56% established NI species, of which 25% are invasive (Zenetos et al. 2010; Kastanevakis et al. 2011). The proliferation of invasive marine species has severe consequences and result in alterations of ecosystem functioning, biodiversity loss and negative effects on human activities, such as fishery, tourism and aquaculture.

Albania's shoreline is therefore also influenced by the introduction and proliferation of northward expanding NI species, which are already established in the Eastern Mediterranean Sea and by ballast ship transfer due to high maritime traffic along the coast. The protection of Albania's coastal area and biota is of international importance. Benthic foraminifera form the most diverse and frequent group of shelled microorganism (Sen Gupta, 1999; Debenay, 2012) and are widely used as bioindicators to evaluate biological and ecological conditions in a wide range of environments. This is the first survey of benthic foraminifera along nearly the entire seacoast of Albania. We investigated the structure, composition, distribution and diversity of benthic foraminiferal assemblages in impacted and non-impacted sites along the seacoast. Furthermore, we focused on NI benthic foraminifera that have invaded shallow-water sites off Albania and attempt to assess introductory pathways for instance the introduction through surface currents or ballast ship water. This study serves as baseline for further assessment of environmental changes (human or natural induced) and ongoing range expansions of NI benthic foraminiferal species. Furthermore, the established survey and the atlas fill a knowledge gap on benthic foraminifera in shallow waters off Albania.

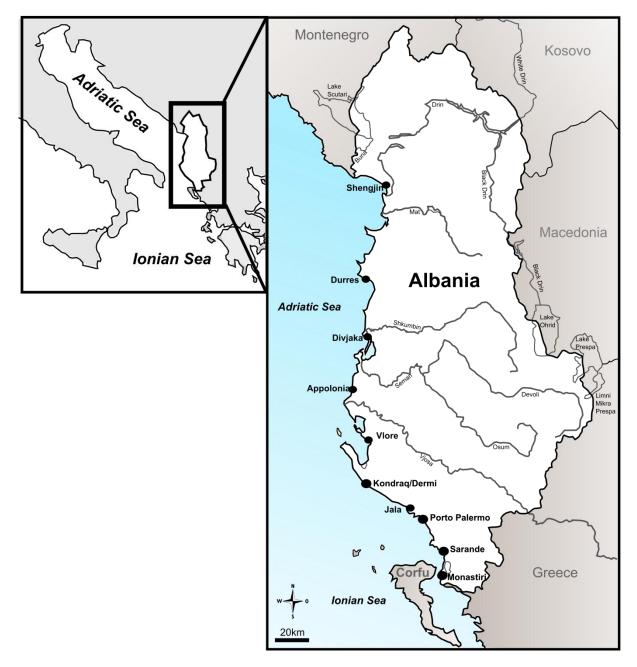


Fig. 1. Location of the collection areas along the coastline of Albania located in the north eastern Ionian and south eastern Adriatic Sea.

#### **Previous Studies**

Mediterranean foraminifera have been studied since the 17<sup>th</sup> century. They are prominent components of the meiofauna and play a major role in oceanic food webs, carbon cycles and as indicators for biomonitoring and hydrocarbon reservoirs (Cimerman and Langer, 1991). Inventories of Mediterranean foraminifera comprising local faunal assemblages and selected groups of foraminifera have been published by Schlumberger (1893, Miliolacea, Marseille), Fornasini (1902, 1904-1906, Rimini), Sidebottom (1904-1909, Delos), Buchner (1940, Lagenidae, Gulf of Neaples), Parker (1958, Eastern Mediterranean Sea), Todd (1958, Western Mediterranean Sea), Le Calvez, J. and Y. (1958b, Miliolacea, Villefranche), Hofker (1960, Gulf of Naples), Cherif (1970, Miliolacea, Naxos), Colom (1974, Balearic Sea), Langer (1988, Tyrrhenian Sea, Vulcano), Cimerman and Langer (1991, Adriatic

and Tyrrhenian Sea), Sgarella and Moncharmont-Zei (1993, Gulf of Naples), Milker and Schmiedl (2012, Western Mediterranean Sea, Alboran Platform, Oran Bight, SW shelf of Mallorca), Meric et al.

(2004; Eastern Aegean Sea, Turkey; Meric et al. 2014, Turkey). There are various additional publications on foraminiferal taxonomy and their distribution in respect to environmental parameters (among others, Blanc-Vernet et al. 1979; Favry et al. 1996; Samir and El-Din, 2001; Hyams et al. 2002; Samir et al. 2003; Mendes et al. 2004; Triantaphyllou et al. 2005; Debenay et al. 2005; Hyams et al. 2008; Frezza and Carboni, 2009; Milker et al. 2009; Elshanawany et al. 2011; Koukouisoura et al. 2010;Triantaphyllou et al. 2012; Buosi et al. 2012).

The first foraminifera described in the 18<sup>th</sup> century (Beccarius 1731; Plancus 1739; Gualtieri 1742) originate from the Adriatic Sea. The type locality for many species described by d'Orbigny in 1826 is the beach of Rimini, which makes the Adriatic Sea a site for many widely used taxa (Jorissen, 1988). Langer (2008a) estimated that a total of approximately 450 species of modern foraminifera currently live in the Adriatic Sea. A more recent study (Cosovic et al. 2011) on foraminiferal species of the eastern shelf of the Adriatic Sea revealed a total of 599 recent (altogether 693 named and undefined species) classified into 232 genera. The northern Adriatic is inhabited by 536 species grouped into 211 genera, the central Adriatic revealed 296 species belonging to 153 genera and the southern Adriatic Sea is inhabitated by 272 species from 133 genera.

Benthic foraminiferal assemblages from various locations in the Adriatic Sea have been intensively studied. In particular, benthic foraminifera along the seacoast of Italy, the former Yugoslavia, Croatia and Montenegro have been investigated in terms of vertical and horizontal distribution patterns in and on the sediment, seasonal and habitat specific abundances (micro- and macrohabitats), and the influence of abiotic factors including temperature, salinity, pH, oxygen, nutrient content and pollution (natural and anthropogenic; Chierci, 1962; Drobne and Cimerman, 1984; Cimerman, 1985; Jorissen, 1987, 1988; Cimerman et al. 1988; Hohenegger, et al. 1993; Donnici et al. 1997; Rossana Serandrei-Barbero et al. 1999; Stigter et al. 1999; Rada and Milat, 2002; Duijinstee et al. 2004; Cosovic et al. 2006; Frontalini and Coccioni, 2007; Borcic et al. 2009; Vidovic et al. 2009, 2010, 2012; Bogner et al. 2010; Katsanevakis et al. 2011; Popadic et al. 2013; Pecarevic et al. 2013; Shaw et al. 2016). Detailed environmental and taxonomic investigations were carried out by Wiesner (1923), von Daniels (1970), Haake (1977), Cimerman (1984), Jorissen (1987, 1988), Cimerman and Langer (1991), Jorissen et al. (1992, 1995), Barmawidjaja et al. (1993, 1995), Albani et al. (2007), Sabbatini et al. (2010) and Cosovic et al. (2011).

Wiesner (1923) published a detailed work of miliolid foraminifera from near Rovigno (Istria/Croatia/Eastern Adriatic Sea) and described more than 200 species in detail. Von Daniels identified 97 living benthic foraminifera from 11 stations in the Limski Canal (Croatia, Northern Adriatic Sea). He investigated the distribution and abundance of benthic foraminifera in terms of temperature, salinity, pH and oxygen content. Haake (1977) described living benthic foraminifera from 16 stations located in the northern, eastern and southeastern Adriatic Sea (Italy). He found 50 living benthic foraminiferal species, described their depth distribution and provided the systematic information for 20 species. Cimerman (1984) investigated the abundance of benthic foraminifera from the Island of Mljet (Croatia, Northern Adriatc Sea) and identified 175 species. Jorissen, (1987, 1988) investigated the distribution and morphology of benthic foraminifera in the Adriatic Sea is strongly dependent on two controlling environmental parameters: oxygen concentration and food availability. These parameters are influenced by the input of large amounts of nutrients from river runoff and by surface currents and substrates. They result in extreme

environmental and faunal differences over short distances. A comprehensive and fully illustrated monograph of modern Adriatic and Tyrrhenian Sea foraminifera, including the systematic description of 334 benthic foraminiferal species has been published by Cimerman and Langer (1991). Jorissen et al. (1992) investigated the vertical distribution of benthic foraminifera in 14 sediment samples in the northern Adriatic Sea. They observed that the downward organic flux appears to be the main factor determining the distribution of benthic foraminifera, with opportunistic taxa in areas with highest downward organic flux. Less stress-tolerant epifaunal species were found to be dominant in areas with lower organic fluxes. Their data showed, that microhabitat differentiation is minimal in month of low oxygen values and that individual taxa are useful for the reconstruction of ancient organic flux rates. Later, Jorissen et al. (1995) presented a conceptual model, which explains benthic foraminiferal microhabitat preferences in terms of differences in the downward organic flux. They argue that the microhabitat depth under oligotrophic conditions is controlled by the availability of metabolized food particles in the sediment, whereas under more eutrophic conditions the ecosystem is controlled by critical oxygen levels. The investigated sample transect through the Adriatic Sea provide both microhabitat controls (food-limited and oxygen limited). The rather shallow depth on the shelf and upper part of the slope are controlled by critical oxygen-levels, whereas food availability in the southern Adriatic Pit and on the lower part of the slope determines to what depth living foraminifera are found. Barmawidjaja et al. (1992) studied microhabitat selection of benthic foraminifera near the Po river outlet and identified more than 30 living species. They distinguished three categories of benthic foraminifera (epifaunal, infaual, potential infaunal) on the basis of their vertical distribution patterns. Barmawidjaja et al. (1995) analysed the vertical distribution of benthic foraminifera in a sediment core in front of the Po Delta and identified 59 taxa. Local benthic foraminiferal associations indicate a steadily increasing nutrient load from 1900 AD onward and a more intense and prolonged anoxia, which started 10 years ago. This provides evidence that the ecological conditions in this part of the northern Adriatic Sea probably continue to deteriorate. Albani et al. (2007) analysed 559 bottom samples in the lagoon of Venice/Italy (Northern Adriatic Sea) and identified up to 42 species on average. Sampling in 1983 has delineated the extent of various biotopes for the entire lagoon which are controlled by the following parameters: exchange with the sea, pollution, fresh water input and the presence of intertidal morphologies. Sabbatini et al. (2010) studied the distribution and abundance of modern benthic foraminifera in the Gulf of Trieste. They identified a total of 76 species (polythalamous and monothalamous), of which all monothalamous species were unreported from the northern Adriatic Sea. An updated and annotated checklist including all literature records of foraminiferal species from the eastern Adriatic coastal region and their geographic occurrences has been compiled by Cosovic et al. (2011).

## **Albanian Foraminifera**

Studies on (benthic) foraminiferal community structures in Albanian seawaters are very limited. Guelorget et al. (2000) investigated foraminiferal populations from three paralic systems of Albania in terms of species richness, density and spatial distribution. A total of 35 species were identified in 0.5-20m water depth in sediment samples from the Karavasta, Narta and Butrinti lagoons. All investigated basins display similar quantitative trends, with declining species richness and abundance values from areas with sea communication towards marginal zones. Multivariate analyses illustrate that each ecosystem is characterized by a distinct foraminiferal community, which is similar to other paralic foraminiferal assemblages.

Langer and Mouanga (2016) studied the impact of the invasive benthic foraminifera *Amphistegina lobifera* in shallow-water coastal areas of Corfu and southern Albania. The sediment samples from

southern Albania (also included in this study) comprise foraminiferal assemblages from Gijri Monastiri Bay, Sarande Bay, Dermi Beach and Porto Palermo and revealed a total of up to 71 species in 5-30m water depth. The samples were collected in coarse to fine grained siliceous bay or port

habitats as well as in seagrass habitats in deeper waters. They showed that the invasion and current range expansion of amphisteginid foraminifera primarily affects the shallow-water environments (<20 m) where habitat invasibility is documented by high numerical abundances and associated with a reduction in species richness. A study on the benthic macrofauna of *Posidonia oceanica* meadows along the Albanian coast published by Beqiraj et al. (2008a) and a bioecological study of benthic communities on the soft bottom of the Vlora Gulf released by Maiorano et al. (2011), mention the benthic foraminifera *Miniacina miniacea*, because of its size (reaching up to 1cm length) and high abundance, especially in the seagrass meadows, along the Albanian coast.

## Oceanographic and regional setting

Albania is situated in a unique position with 154 km of mostly steep and rocky coastlines in the south and 273 km of a mostly low-lying, shallow and flat coastline in the north. The southernmost areas belong to the Ionian Sea while the more northern areas are situated within the Adriatic Sea. The Adriatic and Ionian Seas are connected by the Strait of Otranto, bordering both seas. The northern coastline of Albania is known for its shallow waters, large protected bay and harbor inlets, including ~ 109 km of coastal wetlands and lagoons, and many rivers that flow into the Adriatic Sea. The southern coastline of Albania is characterized by the absence of large rivers and the presence of firm calcareous rocks building cliffs which vertically fall into the Sea.

The Albanian waters have a narrow continental shelf (20-60 km wide to the shelf break at 200m depth), a steep continental slope and a fairly flat abyssal plain. The shoreline is influenced by surface currents and circulation patterns of the Adriatic Sea, which consist of an elongated basin-wide cyclonic gyre with northward flow on the eastern side and a returning southward current near the Italian coast. Gyres and coastal currents in the southern Adriatic sub-basin are modulated seasonally and are more intense in summer, fall, and winter, whereas in spring they are rather weak (Poulain et al. 1999, 2001). Currents straining the Albanian seacoast display a three to four layer vertical structure with a mainly northward flow direction (East Adriatic Current, EAC), excluding bottom currents and currents due to seasonal upwelling phenomena with an opposite flow direction. The EAC is composed of (1) warm and salty Ionian sea surface waters (0-100m deep), which enter the flank of the Strait of Otranto to proceed northward along the Albanian shelf slope to feed the cyclonic gyre circulation around the deepest Adriatic depression (Southern Adriatic pit), and (2) Levantine Intermediate water, which also penetrates the flank of the Strait of Otranto in between 100 and 600m to pass the Albanian shelf and continental slope and mix with denser Adriatic water to form the Modified Levantine Intermediate waters (winter temp. 14°C, salinity 38.7, core at about 200m) (Zore-Armanda, 1969; Orlic et al. 1992; Poulain et al. 1999). In the centre of the Strait as well as near the eastern coast, outflowing bottom currents are characterized by the southern Adriatic Deep water (T=13.16°C +/- $0.30^{\circ}$ C, S= 38.61 +/- 0.09 psu, from the bottom to a depth of 400-600m), which eventually become the bottom layer of the Eastern Mediterranean Deep water (Orlic et al. 1992; Artegiani et al. 1996, 1997; Giorgetti, 1999).

Strong upwelling events occur on the Albanian shelf in summer and along the Albanian/Greek shelf in late spring. These upwelling events are due to offshore bora winds, which are efficient in generating a well-defined upwelling front of about 30km width (and about 10m deepness in the surface layer). The

LIW inflow is weakened or occasionally blocked by bora induced undercurrents in intermediate depths leading to temporary current reversals along the Albanian shelf. A phenomen probably linked with offshore bora winds are wide areas of cold waters appearing along the Albanian coast. But it is not clear whether they are related to upwelling events, so that they result from outcropping or if they are simply due to the vertical mixing induced by the wind (Bergamasco and Gacic, 1995).

The northern Albanian seacoast is characterized by a high river runoff (discharge of 1000m<sup>3</sup>/s, Zore-Armanda and Gacic, 1987; Bergamasco et al. 1996). This discharge enhances the general circulation pattern in the Adriatic Sea but also influences the thermal structure of the water column especially in the winter months (January, February and March), where waters of coastal origin have lower temperatures than the ambient seawater (Gacic et al. 1997). River waters are confined near the coast during winter, whereas during summer and spring, thermal stratification allows a wide horizontal distribution of these river waters inside of the southern Adriatic basin (and vertically they are confined within a 10-30m thick mixed layer) (Gacic et al. 1997). In spring, the noticeable influence of the Albanian rivers' runoff is shown by the wide area with salinity less than 38.0 psu in front of the southeastern coastline (Artegiani, 1997).

Tides along Albanias's seacoast have a small amplitude averaging 30-40cm. Tidal ranges are influenced by the intensity, direction and velocity of the winds and show highest levels during November-December and the lowest during July-August (Gjiknuri, 1995). Large areas of the Albanian shoreline are influenced by strong currents (current speed > 25cm s-1) and high eddy kinetic energy in summer, fall and winter (Poulain et al. 2001). Wind regimes, wave power, sea surface currents and littoral sediment transport on the Adriatic Albanian shoreline indicate intense water movements along the coastline (erosion and siltening up rate of 1:3, Balla, 1995) with shoreline migration rates of up to 5-10m/year (during 1918-1998; Pano, 1995). The surface waters undergo a seasonal temperature cycle with maximum values during summer and maximum mixed layer depths during winter (Artegiani et al. 1996). The average annual temperature of the water varies from 20.8°C in Shengjin to 19.8°C in Sarande Bay (seatemperature.info).

## 3.1.4 Material and methods

Sediment samples for foraminiferal analysis were collected in September 2014 along the southern coastline of Albania (8 samples; see Table 1: sample numbers 1-13, Fig. 2F-J) and October 2015 along the northern coastline of Albania (13 samples; Table 1, sample numbers 14-21, Fig. 2A-E). The samples cover a depth range of 0.5-30m and were collected in habitats of the shallow-water rocky coastline of southern Albania with coarse and fine grained sediments and phytal substrates (algal and seagrass associations) and in shallow-water terrigenous muds and fine to medium grained sandy sediments and phytal substrates (algae) of the northern coastline of Albania. The sample sites are located between 40°27'11.22"N and 19°28'44.66"E and 39°48'51.71"N and 20°0'34.89"E. Samples from the southern coastline derive from Monastiri Bay (MB), Sarande Bay (SB), Porto Palermo (PP), Jala (J) and Dermi (Der). Samples from the northern coastline were collected in Vlora (V), Darezeze e Re (Dar), Divjaka (Di), Durres (Du), and Shengjin (Sh). Samples were taken by SCUBA diving, grab sampling or by hand, filling plastic bags and cans with substrata from the top 2 cm and subsequently transported to the laboratory. To provide time-averaged means to assess the structure of foraminiferal biotas, live foraminifera were grouped with dead tests. A portion of the foraminifera recovered (especially that of amphisteginid foraminifera) were checked for the presence of vital protoplasm to assure that a fraction of the taxa was alive at the time of the collection. All samples were washed over 63  $\mu$ m sieves, dried in the oven at 50°C and at least 300 specimens were then picked from each. Sample number, depth, location, coordinates and sediment character are listed in Table 1. Selected specimens were coated with gold using a Cressington 108 Auto Sputter Coater and photographed with

a CamScan MV 2300 Scanning Electron Microscope (SEM) Unit using the computer program Vega TC in the Steinmann Institute for Geology, Mineralogy and Paleontology of the University Bonn. All 277 species figured here are deposited in the micropaleontological collection in the Steinmann Institute for Geology, Mineralogy and Paleontology of the University Bonn. To determine the structure in the foraminiferal dataset, we analyzed percent abundances of wall structural types (miliolid, perforate and agglutinated foraminifera), functional groups (symbiont-bearing, non symbiont-bearing foraminifera) and diversity indices for each assemblage. Species richness and Fisher alpha indices were calculated for each sample and are listed in Table 2. A subset of 36 species reaching at least 5% of the foraminiferal assemblage has been used for Hierarchical cluster analysis (HCA) to detect similarities and dissimilarities between sample stations and the foraminiferal biota (Table 5). The HCA were computed with the software PAST (Paleontological Statistics, version 3.14), based on Euclidean distance correlation coefficients using the constrained Ward's method criterion. Quantitative analysis of the 12 most abundant species was examined and listed in Table 5 (in bold letters). Based on their ecological roles all genera included in the performed HCA classified into three functional groups of foraminifera (mixotrophic, heterotrophic and opportunistic taxa, Table 3) and percent abundances of each group were determined (included in Table 2 and 4).

Collection Site	Number Depth (m)		Latitude	Longitude	Collection Date	substrate type	Collectors
Shengjin 1 (Sh1)	1	2	41°48'34.30"N	19°35'21.37"Е	10/2015	muddy fine sand	Langer & Mouanga
Shengjin 2 (Sh2)	2	8	41°48'48.40"N	19°35'14.20"E	10/2015	muddy fine sand	Langer & Mouanga
Durres 1 (D1)	3	4	41°19'08.06"N	19°25'52.99"Е	10/2015	calcar. medium grained	Langer & Mouanga
Durres 2 (D2)	4	5	41°19'07.88"N	19°25'51.92"Е	10/2015	calcar. medium grained	Langer & Mouanga
Divjaka (Div)	5	4	40°57'46.96"N	19°27'41.02"E	10/2015	fine and	Langer & Mouanga
Darezeze e Re (Dar)	6	4	40°42`54.99"N	19°21'43.67"E	10/2015	fine and	Langer & Mouanga
Vlore 1 (V1)	7	0.5	40°27'11.06"N	19°28'40.20"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 2 (V2)	8	10-12	40°27'05.01"N	19°28'38.51"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 3 (V3)	9	13-14	40°27'03.20"N	19°28'37.31"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 4 (V4)	10	17	40°27'02.17"N	19°28'36.78"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 5 (V5)	11	18	40°27'00.09"N	19°28'34.87"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 6 (V6)	12	21	40°26'58.87"N	19°28'33.68"E	10/2015	muddy fine sand	Langer & Mouanga
Vlore 7 (V7)	13	20-22	40°26'58.18"N	19°28'36.36"E	10/2015	coarse to med. grained	Langer & Mouanga
Dermi (Der)	14	5	40°08'38.48''N	19°37'41.08"E	10/2014	coarse to med. grained	Grzegorz Deregowski
Jala (Ja)	15	4	40°07'07.90"N	19°42'01.64"E	10/2015	coarse to med. grained	Grzegorz Deregowski
Porto Palermo 1 (PP1)	16	5	40°3'51.14"N	19°47'33.98"E	10/2014	coarse to med. grained	Grzegorz Deregowski
Porto Palermo 2 (PP2)	17	30	40°3'51.30''N	19°47'31.89"E	10/2014	coarse to med. grained	Grzegorz Deregowski
Sarande Bay 1 (SB1)	18	5	39°52'23.04"N	20°0'29.19"E	10/2014	coarse to med. grained	Grzegorz Deregowski
Sarande Bay 2 (SB2)	19	30	39°52'20.82"N	20°0'28.16"E	10/2014	calc. fine grained	Grzegorz Deregowski
Gjiri Monastiri Bay 1 (MB1)	20	5	39°48'49.79"N	20° 0'36.49"E	10/2014	coarse to med. grained	Grzegorz Deregowski
Gjiri Monastiri (MB2)	21	30	39°48'51.71"N	20° 0'34.89"E	10/2014	coarse to med. grained	Grzegorz Deregowski



**Fig. 2** Selected sample site locations (A) Port of Shengjin, (B) Beach of Durres, (C) Divjaka Beach, (D) Darezeze e Re (Dar) Beach, (E) Vlore, (F) Beach of Dermi, (G) Jala Beach, (H) Porto Palermo, (I) Sarande Bay, (J) Monastiri Bay.

# 3.1.5 Results

# **Diversity and Quantitative analysis**

Quantitative faunal analysis and species level identification of the foraminiferal assemblages from shallow-water sites off Albania reveal the following results: A total of 6096 specimens were recovered from all sample sites belonging to 277 species and 112 genera. Perforate foraminifera account for 59 genera and 113 species, miliolids attain 30 genera and 121 species, and agglutinated foraminifera are represented by 23 genera and 43 species. Some species are present as single individuals only. Perforate foraminifera are most abundant (27.7-90.9%) followed by miliolids (9.1-68.1%) and arenacous taxa (0-34.6%). Species richness in all samples ranges between 6 and 99 taxa. The number of species is moderate to high in nearly all samples (50-99 taxa per sample) excluding the sample stations at Vlore (0.5m, 14 taxa), Jala (4m, 19 taxa), Darezeze e Re (4m, 6 taxa) and Gijri Monastiri Bay (5m, 22 taxa). Fisher  $\alpha$ - and Shannon (H) indices vary between 5.403 and 44.18 and 1.085 and 4.037 respectively.

Symbiont-bearing foraminifera (excluding elphidiids) make up 0-78.2% of the foraminiferal assemblages and include the invasive species *Amphistegina lobifera* (0-76.1%), *Peneroplis planatus* (0-10.4%), *Peneroplis pertusus* (0-8.5%), *Laevipeneroplis karreri* (0.5%) and *Sorites orbiculus* (0-1.9%). Among all symbiont-bearing foraminifera amphisteginids comprise up to 97.4% (Table 4). Among perforate species, *A. lobifera* attain 0.7-94.9%, but is just present in the southern sample stations (Ja, Der, SB, MB, PP). Elphidiid foraminifera known to sequester diatom plastids, vary between 0-9.6%. Non symbiont-bearing smaller porcelanous taxa range between 9.1 and 68.1%. Percent abundances of functional groups of foraminifera (heterotrophic, opportunistic, mixotrophic) were assessed for species reaching at least 5% of the foraminifera (2 taxa) show fluctuating percent abundances within the sample sites. Opportunistic and heterotrophic foraminifera characterize the northern sample sites built by finer grained substrates, whereas mixotrophic and hetrotrophic foraminifera characterize the southern sample sites, built by coarser grained sediments and phytal substrates.

Heterotrophic foraminifera show the greatest distribution, as they are present in all sample sites. They reach their highest percent abundances at Shengjin 1 (73.5%), Durres 1 (73.2%), Durres 2 (79.5%), Darezeze e Re (54.5%), Vlore 1 (51.4%) and Vlore 3 (62.4%), whereas they range between 3.0-41.0% at other sample sites. Opportunistic foraminifera reach their highest percent abundances at Shengjin 2 (51.7%), Divjaka (97.4%), Vlore 2 (63.4%), Vlore 5-7 (59.4-77.2%) and Jala (79.4%). They are further distributed at all sample sites except of Gijri Monastiri Bay 30m. Mixotrophic foraminifera are most abundant in 4-5m water depth at Gijri Monastiri Bay (97%), Sarande Bay (42%), Porto Palermo (29.8%), Dermi (21.3%) and Jala (13.9%), whereas they fluctuate between 0.4-5.5% in 30m water depth or are absent (in 10-22m, 0%).

The 12 dominant species reaching 10% (or more) of the foraminiferal assemblage (Table 5 in bold characters) are *Eggereloides scabrus* (0-14.5%), *Quinqueloculina* aff. *Q. viennensis* (0-16.2%), *Pseudotriloculina* sp. 2 (0-14.0%), *Peneroplis planatus* (0-10.4%), *Neoconorbina terquemi* (0-36.4%), *Rosalina floridensis* (0-17%), *Cibicides refulgens* (0-14%), *Amphistegina lobifera* (0-76.1%), *Buccella* sp. 1 (0-27.3%), *Ammonia inflata* (0-23.1%), *Ammonia tepida* (0-18.6%) and *Porosononion granosum* (0-10.3%). *Eggereloides scabrus* has its maximum relative abundance in Sarande Bay (SB2 30m, 15.1%) and Vlore (V4, 17m, 14.5%). Maximum percent abundances of *Quinqueloculina* aff. *Q. viennensis* are found in shallow-water sites of Shengjin (Sh2 2m, 16.2%) and Vlore (V1, 0.5m,

10.3%). *Pseudotriloculina* sp. 2 reaches its maximum percent abundances in muddy sand substrates in Vlore (V4, 17m, 14.0%) and Shengjin (8m, 9.1%). *Peneroplis planatus* occurs most abundant in 5m water depth in Sarande Bay (SB1, 10.4%) and Porto Palermo (PP1, 8.8%). *Neoconorbina terquemi* reaches 36.4% of the foraminiferal assemblage in Darezeze e Re (Dar, 4m) and 4.7% in Jala (Ja), whereas its abundance in all other sample stations ranges between 0 and 1.6%. *Rosalina floridensis* make up to 17.0% in Vlore 3 (13-14m) and 4.5-4.9% in Vlore 2 (10-12), Vlore 5 (18m) and Vlore 6 (21m). *Cibicides refulgens* has its maximum percent abundance in Jala (14.0%).

Heterotrophic genera	Opportunistic genera	Mixotrophic genera
Quinqueloculina	Ammonia	Peneroplis
Adelosina	Nonionella	Amphistegina
Triloculina	Haynesina	
Pseudotriloculina	Porosononion	
Sigmoilinita	Bulimina	
Cibicides	Epistominella	
Planorbulina	Eggereloides	
Rosalina	Aubignya	
Lobatula	Buccella	
Neoconorbina	Labrospira	
Conorbella	_	
Lenticulina		
Textularia		

**Table 3.** Functional groups of foraminifera included in the HCA.

**Table 2.** Quantitative faunal analysis of foraminiferal assemblages from Albania, including percent abundances of miliolid (Mil), perforate (Perf) and agglutinated (Agg) foraminifera, the number of species and genera, percent abundances of selected groups of foraminifera (Larger-benthic foraminifera = LBF, elphidiids, smaller miliolids, heterotrophic (h), opportunistic (o) and mixotrophic (m) foraminifers).

Collection Site	Mil %	Perf %	Agg %	species	genera	Fisher α	LBF %	Elphidiids %	Smaller miliolids	H%	0%	M%
									%			
Sh1	68.1	28.4	3.4	55	28	24.7	0	2.9	68.1	73.5	26.5	0
Sh2	39.9	55.8	4.3	62	31	29.9	0	9.6	39.9	48.3	51.7	0
D1	42.9	55.1	2.1	90	41	45.1	1.7	8.4	41.1	73.2	23.6	3.2
D2	65.2	33.0	1.8	72	32	28.0	3.2	3.2	61.9	79.5	15.0	5.5
Div	23.1	72.5	4.4	50	29	17.3	0	4.4	23.1	20.6	79.4	0
Dar	9.1	90.9	0	6	6	5.4	0	0	9.1	54.5	45.5	0
V1	51.3	48.7	0	14	7	7.83	0	2.6	51.3	51.4	48.6	0
V2	25.9	53.9	20.2	90	47	40.6	0	5.1	25.9	36.6	63.4	0
V3	31.4	55.7	12.9	71	35	31.86	0	7.6	31.4	62.4	37.6	0
V4	46.0	27.7	25.4	61	36	26.7	0	2.1	46.0	50.0	50.0	0
V5	31.1	35.0	34.0	61	41	29.3	0	1.9	31.1	40.6	59.4	0
V6	30.8	47.5	21.7	75	45	32.2	0	4.0	30.8	41.0	59.0	0
V7	15.0	61.3	23.7	72	48	32.45	0	3.4	15.0	22.8	77.2	0
Der	39.9	57.4	2.7	89	43	29.1	13.4	8.8	28.7	76.1	2.6	21.3
Ja	25.6	74.4	0	19	15	13	11.6	4.7	23.3	75.0	11.1	13.9
PP 1	50.5	47.2	2.2	71	32	21.3	18.0	8.8	32.9	67.3	2.9	29.8
PP 2	46.8	49.5	3.7	94	43	38.61	0.5	7.0	46.3	89.5	10.1	0.4
SB 1	48.8	39.5	11.7	60	31	20.2	26.9	4.8	33.9	56.7	1.3	42.0
SB 2	15.1	50.3	34.6	81	48	33.77	1.2	5.3	14.8	30.7	67.2	2.1
MB 1	9.2	80.2	10.8	22	13	5.51	78.2	2	7.2	3.0	0	97.0
MB2 2	37.9	58.6	4.4	99	44	37.29	2.6	5.7	36.5	87.7	7.3	5.0

The invasive larger benthic foraminifera *Amphistegina lobifera* is most abundant in coarse to medium grained substrates in 4-5m water depth, where its reaches up to 76.1% (MB1) of the foraminiferal assemblage. *Buccella* sp. 1 is dominant in 0.5-8m water depth, reaching up to 27.3% in Darezeze e Re

(Dar, 4m), 10.3% in Vlore (V1, 0.5m), 9.3% in Jala (Ja) and 6.7% in Shengjin (Sh2, 8m). *Ammonia inflata* is dominant in 0.5-4m water depth making up to 23.5% of the foraminiferal assemblage in Vlore (V1, 0.5m) and 11.9 % in Divjaka (Div, 4m). *Ammonia tepida* occurs most abundantly in medium to fine grained substrates in 4-8m water depth, reaching 18.6% at Divjaka (Div, 4m) and 8.2% at Shengjin (Sh2, 8m). *Porosononion gransoum* has its maximum relative abundance in Vlore (V1, 0.5m, 10.3%) and Divjaka (Div, 4m, 8.1%).

## **Two-way HCA**

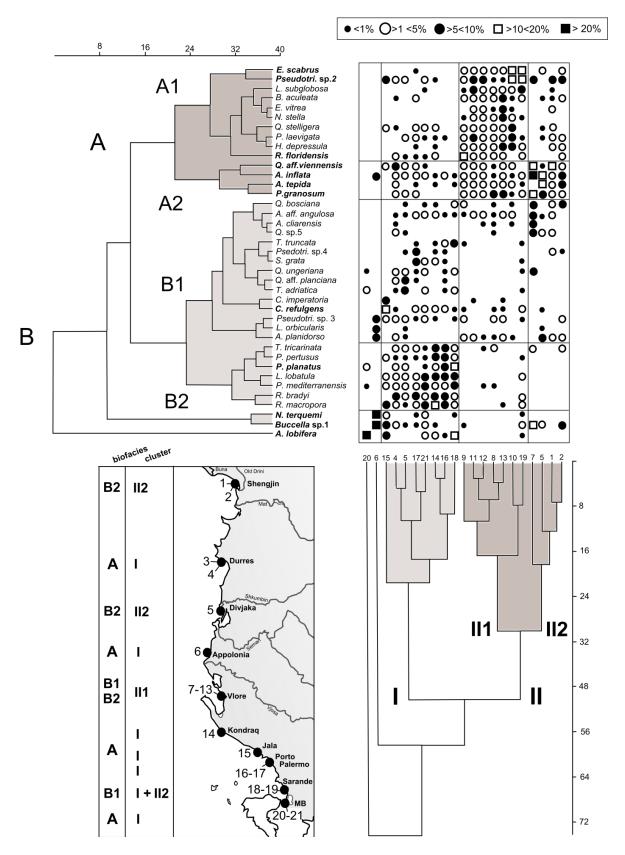
The Q-mode Cluster analysis resulted in two major clusters (I and II), with two additional isolated samples (Gijri Monastiri Bay 5m and Darezeze e Re 4m). Q-mode Cluster I contains 10 sample stations with medium to coarse grained substrates in 4-30m water depth. Cluster II includes 11 sample stations characterized by fine sand to muddy sand substrates at 0.5-30m water depth. Q-mode Cluster II is subdivided into two sub-clusters: II1 and II2. Cluster II1 is represented by 4 sample stations (0.5-8m water depth), whereas Cluster II2 includes 4 sample stations from deeper areas (10-30m water depth). Mapping of the Q-mode clusters shows that Cluster I is mainly located in the southern Albania, except the sample stations from Durres. Cluster III is located along the northern coast in between Vlore and Shengjin, except the sample station from Sarande Bay 30m.

The R-mode cluster distinguishes two major assemblages (A and B) divided into four sub-assemblages (A1, A2, B1 and B2). There is one outstanding taxon (*Amphistegina lobifera*) situated in sub-assemblage B2. Assemblage A includes seven of the thirteen dominant species: *Eggereloides scabrus*, *Pseudotriloculina* sp. 2, *Pseudotriloculina laevigata* and *Rosalina floridensis* comprise assemblage A1. *Ammonia inflata*, *Ammonia tepida* and *Porosononion granosum* comprise assemblage A2. Assemblage B may be divided into two sub-assemblages (B1 and B2). The dominant taxa *Cibicides refulgens* lies in sub-assemblage B1, whereas sub-assemblage B2 is characterized by the dominant species *Peneroplis planatus*, *Neoconorbina terquemi*, *Buccella* sp.1 and *Amphistegina lobifera*.

Each Q-mode cluster is related to at least two R-mode sub-assemblages (Fig. 3). Q-mode Cluster I is characterized by R-mode sub-assemblage B2 associated with the dominant taxa *P. planatus* (0-10.4%) (to a lower extend) sub-assemblage B1 associated with *Cibicides refulgens* (0-4.7%) and sub-assemblage A2 associated with *Q. aff. Q. viennensis* (0-8%), *Ammonia inflata* (0-9.1%), *A. tepida* (0-1.4%) and *P. granosum* (0-3.2%). Additional species characterizing Q-mode Cluster I are *Rosalina macropora* (0-10.7%), *Planorbulina mediterranensis* (0-8.7%), *Lobatula lobatula* (0-9.6%), *P. pertusus* (0-8.5%), *Triloculina tricarinata* (0-5.8%), *C. refulgens* (0-4.7%), *Conorbella imperatoria* (0-4.7%), *Triloculina adriatica* (0-5.6%), *Qinqueloculina.* aff. *Q. planciana* (0-8.3%), *Textularia truncata* (0-6.4%), *Q.* aff. *Q.viennensis* (0-8%), *Sigmoilinita grata* (0-6.2%), *Q. ungeriana* (0-4.7%), *Q.stelligera* (0-4.7%) and *Pseudotriloculina* sp. 2 (0-7%).

The sample station Monastiri Bay (5m) included in Cluster I is closely related to *A.lobifera* (76.1%) of sub-assemblage B2. The sample station Darezeze e Re (4m) included in Q-mode Cluster I is related to *Buccella* sp. 1 (27.3%) and *N. terquemi* (36.4%) included in sub-assemblage B2.

Q-mode Cluster II1 is related to sub-assemblage A associated with the species *E. scabrus* (0-15.1%), *Pseudotriloculina* sp. 2 (0-13.6%), *Pseudotriloculina laevigata* (0-1.5%), *R. floridensis* (0-1.5%), *A. inflata* (4.1-23.1%), *A. tepida* (0.3-18%) and *P. granosum* (1.5-10.3%) and to a lower extend sub-assemblage B1 with the associated taxa *C. refulgens* (0.5-14%).



**Fig. 3** Q-mode cluster dendogram (right) with two major clusters I and II (with two sub-clusters II1 and II2) and R-mode cluster dendogram (above) including species reaching at least 5% of the total foraminiferal assemblage (dominant taxa in bold characters) defines two biofacies (A and B) with four sub-biofacies (A1, A2, B1, B2). Distinct grey tones show q- and r-mode related relationships. Relative percent abundances for each species are indicated with individual symbols (see legend and Table 4).

Q-mode Cluster II2 is closely related to R-mode sub-assemblage A, associated with *E.scabrus* (2.3-14.5%), *Pseudotriloculina* sp. 2 (0.3-14%), *Pseudotriloculina laevigata* (2-5.1%) and *R. floridensis* (0-4.9%) and sub-assemblage A2 characterized by the dominant species A. *inflata* (0.4-2.3%), *A. tepida* (1.8-4.5%) and *P. granosum* (0.4-5.6%). Additional species associated with Q-mode Cluster II are *Labrospira subglobosa* (0.8-7.3%), *Bulimina aculeata* (0.9-5.3%), *Epistominella vitrea* (0.9-7.1%), *Nonionella stella* (0.8-5.6%), *Haynesina depressula* (2.3-6.4%), *Quinqueloculina bosciana* (0-2.7%), *Adelosina* aff. *A. angulosa* (0.8-2.3%) and *Aubignya planidorso* (0.9-2.4%).

## Non-indigenous species

The sample stations in Albania contain a low number of NI benthic foraminiferal species (2.5% of the foraminiferal fauna; Table 4).

The invasive benthic species *Amphistegina lobifera* Larsen (Plate 15, Figs. 3a-d) is distributed in varying percent abundances in Gijri Monastiri Bay (5m, 76.1%; 30m, 1.2%), Sarande Bay (5m,12%; 30m, 0.9%), Porto Palermo (5m, 0.3%), Jala (5m, 9.3%) and Dermi (5m, 2.2%). It is a Lessepsian migrant, listed in the EASIN network (European alien species information network: easin.jr.ec.europa.eu) and was first detected in Israel in 1959 by Emery and Neev (1960). It is further abundantly distributed in the Eastern Mediterranean (Turkey: Meric et al. 2001, 2004, 2008a, b; Greece: Koukouisoura et al. 2010, Triantaphyllou et al. 2012; Egypt: Samir and El-Din, 2001, 2003; Lybia: Bazairi et al. 2013, Pelagian Islands: Caruso and Cosentino, 2014; Malta: Yokes and Meric, 2009) and recently invaded the Marmara Sea (Meric et al. 2005). Its circumtropical distribution includes occurrence records in the Indian Ocean (from Mozambique to the Red Sea east to the shores of Indonesia and south to the western coast of Australia/Shark Bay), Pacific Ocean (from Japan to Midway Island and as far south of Lord Howe Islands and east to the Easter Island, Colombia) (Langer and Hottinger, 2000; pers.observ.).

Sorites orbiculus Forskal (Plate 10, Figs. 21a,b) was rarely found in shallow waters (5m) of Dermi (Der, 0.2%), Porto Palermo (PP1, 0.2%), Sarande Bay (SB1, 1.9%) and Gjiri Monastiri Bay (MB1, 0.3%). It is included in the EASIN network and classified as primary Lessepsian migrant. However, Soritidae are already present in the Mediterranean from Paleocene to Miocene before they went to extinction during the Messinian Salinity Crisis. Sorites orbiculus is therefore a successful returnee, which most probably re-colonized the Mediterranean from the Atlantic during warm periods of the Pleistocene (Reiss and Issar, 1961). Therefore it is classified as native species and excluded from the alien species list of Zenetos et al. (2012). But molecular investigation of Sorites orbiculus individuals from the Gulf of Elat and specimens found off Israel have shown that the species are genetically identical, so that foraminifera found on the Mediterranean coast of Israel are most probably 'lately introduced' Lessepsian migrants (Merkado et al. 2013). It is distributed in nearly the entire Mediterranean Sea (excluding the Alboran Sea). Sorites orbiculus is a cosmopolitan species that has a circumglobal/tropical spatial extension (Langer and Hottinger, 2000) including the Pacific Ocean (Palau: Hallock, 1984; Japan: Nomura, 1997, Hohenegger et al. 1999; China: Papua Neuginea: Langer and Lipps, 2003; French Polynesia: Langer and Lipps, 2006; Zheng and Fu, 2008; Caroline Islands: Makled and Langer, 2011), Indo-Pacific (Red Sea: Hottinger et al. 1993; Chagos Archipelago: Murray, 1994; Maledives: Parker and Gischler, 2011; Mozambique: Langer et al. 2013b), Atlantic Ocean (Gross, 2001).

*Nodophtalmidium antillarum* (Cushman) (Plate 3, Figs. 7a, b) is a NI species of Indo-pacific origin, and occurs in the Bay of Vlore (V7, 20-22m, 0.4%). This species was also rarely found in sample sites from the Port of Oranto (Appendix 7.3). It is included in the EASIN network and was first detected in

Israel by Yanko (1995) and further by Hyams-Kaphzhan et al. (2008), who suggested it to be a Lessepsian migrant. It is also distributed in Turkey (Meric et al. 2010; Cinar et al. 2010). Apart from its natural distribution in the Gulf of Aqaba (Hottinger et al. 1993) it is further common in the North Atlantic Ocean (Georgia Shelf; Culver and Buzas, 1980), North Pacific Ocean (Caroline Islands; Makled and Langer, 2011), Indian Ocean (Mozambique; Langer et al. 2013b) and the United States (Rabbit Key Basin).

*Loxostomina* ? *limbata* (Brady) *costulata* (Plate 12, Figs 10a, b) is distributed very rarely in Porto Palermo (PP1, 30m, 0.2%). It is also listed in the EASIN network as alien species (*Loxostomina costulata*) and was first described in the Mediterranean realm by Hyams-Kaphzan et al. (2008) in Israel. A potential pathway is not given in the list but it may also be a Lessepsian migrant as it is common in the Gulf of Aqaba/Red Sea and has never been recorded in the western Mediterranean Sea. It is further distributed in the Pacific including the Japanese (Nomura, 1982, 1997) and Caroline Islands (Makled and Langer, 2011).

	Amphistegina lobifera	Loxostomina ? limbata costulata	Sigmamiliolinella australis	Sorites orbiculus	Mimosina a <u>f</u> finis
D1	0,0	0,0	0,0	0,0	0,0
D2	0,0	0,0	0,0	0,0	0,0
Sh1	0,0	0,0	0,0	0,0	0,0
Sh2	0,0	0,0	0,0	0,0	0,0
Div	0,0	0,0	0,0	0,0	0,0
Ja	9,3	0,0	0,0	0,0	0,0
Dar	0,0	0,0	0,0	0,0	0,0
V1	0,0	0,0	0,0	0,0	0,0
V2	0,0	0,0	0,0	0,0	0,3
V3	0,0	0,0	0,0	0,0	1,8
V4	0,0	0,0	0,0	0,0	0,2
V5	0,0	0,0	0,0	0,0	3,3
V6	0,0	0,0	0,0	0,0	2,9
V7	0,0	0,0	0,0	0,0	0,0
Der	2,2	0,0	0,0	0,2	0,0
PP1	0,3	0,0	0,0	0,2	0,0
PP2	0,0	0,2	0,0	0,0	0,0
SB1	12,0	0,0	0,0	1,9	0,0
SB2	0,9	0,0	0,0	0,0	0,0
MB1	76,1	0,0	0,0	0,3	0,0
MB2	1,2	0,0	0,2	0,0	0,0

**Table 4** Percent abundances of NI benthic foraminiferal species and the successful returnee Sorites orbiculus in shallow-waters off Albania.

*Sigmamilionella australis* (Parr) (Plate 8, Figs. 15a, b) is considered here to be a NI species as it is not reported within other Mediterranean assemblages. Within the Albanian sample area it is distributed in Shengjin (2m, 2.5%), Vlore (V4, 17m, 0.4%) and Dermi (Der, 5m; 0.3%). It is generally common in the Pacific (Japan: Nomura, 1982, 1997; China: Zheng and Fu, 2008; New Caledonia: Debenay, 2012) and Indian Ocean (Sahul Shelf: Loeblich and Tappan, 1994; Bazaruto: Langer et al. 2013b).

Another NI taxa of Indo-Pacific origin is *Mimosina affinis* (Millet) (Plate 13, Figs. 1a, b), which is distributed in the Bay of Vlore (V2-6; 0.4-3.3%). It is not mentioned in the EASIN network, and it has never been identified in the Mediteranean Sea/Adriatic Sea before. It is distributed in the Gulf of

Aqaba (Hottinger et al. 1993) and also occurs in the Pacific Ocean (around New Caledonia; Debenay, 2012).

# **3.1.5 Discussion**

## **Taxonomy and Foraminiferal Diversity**

Albania situated in a transition zone between three Mediterranean sub-regions (Eastern and Western Mediterranean Sea and Adriatic Sea) has remained an "unknown territory" for foraminiferal studies for several years. The numbers of publications on Albania's marine biotas has increased steadily over the last decade, and indicated a high biological diversity, including rare, endemic and endangered species. The diverse ecosystem is thus of international significance especially during times of current climate warming and increased pollution due to (uncontrolled) anthropogenic activities. This study constitutes the first comprehensive survey of shallow-water benthic foraminiferal assemblages and their spatial distribution along the seacoast of Albania.

The number of species and genera (277 taxa, 112 genera) identified in 21 samples is high but consistent with the amount of foraminiferal taxa identified in other studies from the central (296 taxa, 153 genera) and southern Adriatic Sea (272 species within 133 genera), (Cosovic et al. 2010).

The number of taxa per sample in our study (6-99 taxa) is somewhat higher compared to nearby investigated areas (Croatia: Drobne and Cimerman, 1984; Bogner et al. 2010; Vidovic et al. 2009, 2012; Shaw et al. 2016; Montenegro: Vidovic et al. 2010; Slovenia: Sabbatini et al. 2010; Italy: Jorissen et al. 1992; Hohenegger et al. 1993; Barmawidjaja et al. 1992, 1995; Donnici et al. 1997; Stigter et al. 1999; Serandrei-Barbero et al. 1999; Albani et al. 2007; North central and south Adriatic Sea: Haake, 1977; Jorissen, 1987) ranging between 6-60 taxa per sample in general, but may due to different reasons such as sampling and examination techniques, different collection locations and available (published) literature data.

We investigated the total standing stock of living and dead foraminiferal species along a transect of approximately 472 km covering different habitats (Port, Bay and lagoon areas at 0.5-30m water depth), whereas other studies in the Adriatic Sea partly focused on living foraminifera in selected or more limited geographical regions for specific time periods, sometimes just concerning certain groups of foraminfera (Fornasini, 1900; Schaudinn, 1911; Stiasny, 1911; Wiesner, 1911a, b, 1912, 1913, 1920, 1923; Vatova, 1928; Alfirević, 1964, 1969a, b; Zavodnik, 1967, 1969; Daniels v., 1970 a, b; Meischner, 1970; Haake, 1977; Drobne and Cimerman, 1984; Cimerman, 1985; Jorissen, 1987, 1988; Jorissen et al. 1992; Barmawidjaja et al. 1995; Donnici et al. 1997; Serandrei-Barbero et al. 1999; Guelorget et al. 2000; Rada and Milat, 2002; Vidović et al. 2009, 2010, 2012; Albani et al. 2007; Bogner et al. 2010; Sabbatini et al. 2010; Popadic et al. 2013; Shaw et al. 2016).

A further cause concern the highly eutrophicated northern Adriatic Sea (also influencing the western seacoast), which is characterized by foraminiferal assemblages adapted to extreme habitat conditions and therefore lower species richness values compared to the mainly oligotrophic eastern Adriatic Sea coast. Deep-sea benthic foraminiferal species are in addition also characterized by lower species richness values. Another reason may be related to limited declared data on total standing stock, as various publications just mention the most abundant taxa, or species used for statistical analysis. Nevertheless the ternary plot of wall types as well as computed Fisher *alpha* indices from Albania indicate normal marine conditions found in shelf seas (Murray, 2006).

Benthic foraminiferal taxa identified in this study are apart from some differences on species level consistent with faunal assemblages and assemblage variations investigated along the entire Adriatic Sea coast, but include species which are also known to be distributed in the Eastern and Western Mediterranean Sea.

# Foraminiferal assemblage variations: Spatial distribution and environmental characteristics of foraminiferal biofacies

Foraminiferal assemblage variations from northern to southern sample sites correlate with varying geomorphological and hydrological conditions. Variations in the substrate types can be related to lithological differences in the source areas. Other parameters influencing coastal substrate types are distinct erosion rates, (different amounts of) fresh water input and sediment loads through rivers influencing the seacoast as well as human mediated impacts. Those conditions lead to the formation of two distinct clusters and biofacies, whith a spatial distribution that is mainly controlled by substrate type and water depth. This is also shown in the two-way HCA (Fig. 3).

The northern coast of Albania (including Cluster A and biofacies II) is characterized by low lands with high river runoff. Shallow-water bottom communities in the marine realm are therefore subjected to a high input of terrigenous material leading to turbidity and high loads of nutrients in the water column. Those regions, and especially that between Vlore and Shengjin (235km in total length), are also characterized by ascending erosion and silting up events, whereas the ratio between silting up and erosion is 3:1 (Balla, 2013). Such a domination of silting up has led to the deposition of additional sediment loads thus leading to a significant increase of land surface (Balla, 2013) affecting established shallow-water benthic communities. The anthropogenic impact include building activities along the seacoast (e.g extension of Ports, Beaches, construction of tourist residences) resulting in massive coastal erosion processes. Further problems are triggered by untreated sewage from disposal sites and industrial factories discharged directly into the sea or coastal zone (Cullaj et al. 2005; Anonymous, 2008; Maiorano et al. 2011).

Samples collected in those areas (Shengjin Port, Divjaka, Vlore Bay,) are characterized by muddy to silt and fine sand substrates at 0.5-22m water depth. Foraminiferal assemblages are composed of small heterotrophic and opportunistic species including characteristic taxa like Eggereloides scabrus, Bulimina aculeata, Epistominella vitrea, Ammonia tepida, Porosononion granosum, Bulimina marginata, Haynesina depressula, Nonionella stella, Labrospira subglobosa and Aubignya planidorso, Brizalina dilatata, Laevidentalina spp.. These species are known to live as (semi-) infaunal or mud dwelling taxa. Their occurrence strongly correlates with the presence of organic matter and negatively correlates with the coarsness of the substratum and the percentage of calcium carbonate (Jorissen, 1987; Hohenegger et al. 1993; Murray, 2006). The species mentioned above are mainly found in oxygenated layers, near the sediment surface, although some taxa (Nonionella turgida, Epistominella vitrea, Eggerelloides spp.) seem to co-vary temporarily with low oxygen index values (Jorissen, 1987; Duijunste et al. 2004). Other species present in this area like Porosononion granosum, Elphidium advenum, Stainfortia concava and Bulimina marginata are known to live exclusively infaunally. They show a preference to live deeper in the sediment, thus tolerating lower oxgen conditions and avoiding the competitive pressure present in shallower sediment depths (Hohenegger et al. 1993; Alve, 1994, 1995a; Barmawidjaja et al. 1995; Duijunste et al. 2004). However, the low amount of foraminiferal taxa known to have an epifaunal life strategy (Rosalina floridensis, Aubignya planisorso, Spirillina vivpara, Discorbinella bertheloti, Tretomphalus bulloides, *Rosalina vilardeboana*) indicate the presence of phytal substrates, such as algae and seagrasses.

Our observations made in the sediment samples in 10-22m water depth in the Vlore Bay (Cluster III and Biofacies A) are in line with observations made by Maiorano et al. (2011), who investigated the soft-bottom communities in the Gulf of Vlore. They describe the formation of terrigenous mud, characterizing larger part of the Bay. Species assemblages identified are progressively mud-covered by excess sedimentation rates and generally characterized by a few broadly tolerant species (mainly opportunistic) adapted to environmental instability. Most of the samples that we collected in Vlore Bay are also characterized by opportunistic and heterotrophic foraminiferal species showing an infaunal to mud dwelling life strategy (Eggerela scabrus, Bulimina aculeata, Epistominella vitrea, A. tepida, A.inflata, Havnesina depressula, Porosononion granosum, Bulimina marginata, Havnesina depressula, Nonionella stella, L. subglobosa, Aubignya planidorso, Brizalina dilatata, Brizalina striatula). As mentioned above, they cope well with environmental instabilities such as fluctuating oxygen conditions, higher amounts of organic matter and high sedimentation rates. Microhabitat preferences of epifaunal foraminiferal species present in lower percent abundance in our samples sites (Cibicides refulgens, Aubignya planidorso, Conorbella imperatorial, Triloculina tricarinata, Rosalina floridensis, R. bradvi, Planorbulina mediterranensus, Neoconorbina terguemi) point to a minimal vegetation cover as described by Maiorano et al. (2011) (Posidonia oceanica meadows, Posidonia matte, Cymodocea nodosa, Caulerpa racemosa) for the shallower coastal belt of the Eastern Gulf, located some km's away from our sampling sites (Fig. 1, Fig. 2E). The Bay of Vlore is a primary pollution hotspot in the country, where sewage and industrial waters from the former polyvinyl chloride, chlorine alkali complex and stony salt factory are discharged directly into the sea or coastal zone. Very high levels of mercury (mean value of 0.92mg kg 1 dry weight; Baraj et al. 1994) were found in the bay sediments. Sediments near the PVC plant are highly Hg contaminated, but show a roughly downward depletion trend due to the increase of silt content and fluctuations of the water table (Bequiraj et al. 2008b). Species considered as tolerant at least in low polluted environments (Frontalini and Coccioni, 2007) such as Nonionella turgida (0-0.4%) and Eggereloides scabrus (0-14.5%) show their highest percent abundances in the Vlore Bay samples (N. turgida only occurs in Vlore Bay and is absent from all other sample sites). Ammonia tepida and A. parkinsoniana (both present in the sampled area) can be considered good bioindicators for heavy metal pollution (Frontalini and Coccioni, 2007). Especially A. tepida has been reported to dominate close to outfalls discharging heavy metals (Yanko et al. 1992), sewage (Seiglie, 1971), chemical and thermal effluents (Seiglie, 1975), caustic soda and chlorine complexes and fertilizer byproducts (Setty, 1976) (Alve, 1995a). The presence of Ammonia parkinsoniana, which is very sensitive to heavy metal content even at low concentrations (Frontalini and Coccioni, 2008), indicate no serious impact at least in the samples V 0.5, V10-12, V13-14, V21. It is absent at V17, V18 and V20-22m, where A. tepida reciprocally occurs with 1.9-3.4%. Samples where A. parkinsoniana occurs with percent abundances lower than 1% (0.3-0.7%) A. tepida reaches 1.8-4.5%. This alternating occurrence and the presence of E.scabrus and N. turgida may indicate a minor impact of heavy metals on the foraminiferal fauna. Another indication for no serious Hg contamination is the absence of *Elphidium aculeatum*, which has been observed to be positively correlated with Hg contents (Bergin et al. 2006). Further indices of heavy metal pollution such as test abnormalities, small test sizes and low species richness (Alve, 1995a; Bergin et al. 2006; Murray, 2006; Fronatlini and Coccioni, 2007) also observed for A. tepida around Hg contaminated environments (Yanko et al. 1994) are not observed in Vlore Bay, thus implementing no strong impact due to heavy metals in the investigated area.

The sample stations characterizing Cluster II2 and Biofacies A (Shengjin, Vlore 0.5m, Divjaka) show similar granulometric features (mud to fine sand) and foraminiferal assemblages built by infaunal and mud-dwelling species as included in biofacies II1. The difference is marked by a higher amount of opportunistic taxa and decreasing percent abundances of heterotrophic species. This is accompanied with lower species richness values and individuals per sample (density). The difference may be also

related to lower water depths (0.5m-8m) compared to sample sites in Vlore (10-22m) as well as distinct macrohabitats.

The samples collected in Shengjin were taken inside the port area, whereas the assemblages in biofacies II1 (Vlore Bay) are more exposed to the Bay as they are located outside of the port (ca. 50km away). The exchange with the open sea is more limited at Shengjin compared to Vlore Bay. The coastal area around Shengjin is also impacted by three of the large rivers in Albania (Buna, Old Drini and Mati, Ishmi) and is therefore influenced by polluted waters due to sewage discharge from large towns (Cullaj et al. 2005). Although the water quality of the Mati river ameliorated according to the EC environmental standards (BMZ, 1995), relatively high concentrations of copper in the sediments and algae reflect the natural pollution from copper containing-minerals and pollution from dumping of solid wastes from mines and former metallurgical plants (Cullaj et al. 2007). Nutrification of coastal waters due to untreated sewage runoff in rivers may also play an important role in the port of Shengjin. This may explain the low numbers of species and individuals in general, with a dominance of opportunistic taxa coping well with fluctuating environmental conditions such as temporal anoxia (Ammonia tepida, Ammonia inflata, Porosononion granosum, Haynesina depressula and Eggereloides scabrus). Smaller sized individuals present in Shengjin additionally underline more unfavorable conditions compared to Cluster II1, as they occur in high productive and oxygen-poor settings (Rathburn et al. 2001) or even in trace metal polluted regions (Yanko et al. 1994). The presence of the sensitive species Ammonia parkinsoniana, however, points to a minor impact of heavy metals in the port area. Rare occurrences of epifaunal species (Aubignya planisordso, Triloculina tricarinata, Buccella sp. 1, Adesosina aff. A. angulosa, Pseudotriloculina sp. 4, Spirillina vivipara, Cibicides advenum, Tretomphalus bulloides) suggest the presence of phytal substrates, which are most likely built by algae and algae coating the bottom substrates.

The sample station in Divjaka (also included in Cluster II2 and biofacies A) is located northwards of the great Karavasta lagoon and is affected by brackish or freshwater due the influence of the Semani and Shkumbin rivers. The sample station is situated westward of the Divjaka dune forest. Species composition is similar to the species assemblage in the Karavasta Lagoon identified by Guelorget et al. (2000). The samples include a high amount of opportunistic taxa (Ammonia inflata, A. tepida and Aubignya planidorso, Bulimina aculeata, P. granosum, Eggereloides scabrus) and to a lesser degree heterotrophic species (Pseudotriloculina laevigata, Quinqueloculina stelligera, Adelosina aff. A. angulosa, Quinqueloculina sp. 5, Buccella sp. 1, Lenticulina orbicularis, Conorbella imperatoria) with a mainly infaunal or mud dwelling life strategy. This in combination with characteristic taxa like Jadammina macresens, (widespread on high to mid marshes; Murray, 2006; Shaw et al. 2016) indicate fluctuating salinity values, changing oxygen conditions as well as the influence of tides present in this region. The influence due to river discharge is not to neglect as especially the outlets of the Shkumbini and Semani Rivers are characteristic for high rates of suspended matter in their watersheds due to erosion (Shkumbini: average sediment load of 7.2 x 10<sup>6</sup> tons/year; Simeoni et al. 1997; Semani: 16.5 x 10<sup>6</sup> tons/year; Pano, 1992). The coastal sediments show a high Cr content resulting from the meatallurgical plants. This is also underlinded by the absence of Ammonia parkinsoniana and high percent abundances of A. tepida (18.6%) at this sample site. Million m<sup>3</sup> of liquid waste with a high content of toxic compounds discharged directly in the Shkumbini River in combination with 300 000 tons of waste disposed on the riverbanks per year led to elevated amounts of nitrite, nitrate and ammonium in the river waters (reducing conditions) and leave a mesosaprobic to polysaprobic state in the sediments (Cullaj et al. 2005), furthermore, affecting shallow-water benthic communities along the seacoast.

The rocky coast of southern Albania (Cluster I and biofacies B) is less affected by erosional processes due to the presence of consolidated calcareous rocks and the absence of large rivers, leading to an erosion rate, which is less than a few mm/year (Gjiknuri, 1995). The southern coast is also influenced

by warm Ionian sea surface waters that pass the coastal flanks, before they get mixed with freshwater along the northern coasts. Sediment samples collected in this area (4-30m water depth) are characterized by coarse to medium grained sand substrates with a high calcium carbonate content. Typical foraminiferal assemblages are composed of symbiont-bearing and heterotrophic species, with a mainly epifaunal life strategy (*Amphistegina lobifera*, *Peneroplis* spp., *Rosalina* spp., *Cibicides* spp., *Planorbulina mediterranensis*, *Lobatula lobatula*, *Conorbella* spp., *Quinqueloculina* spp., *Adelosina* spp., *Siphonaperta* spp., *Vertebralina striata*, *Cibicidella variabilis*, *Daitrona* sp., *Iridia diaphana* etc.). The species composition in biofacies B points to a relatively high amount of vegetation cover such as seagrasses (*Posidonia oceanica*) and algae. This is also underlined by the foraminiferal assemblage, containing taxa known to prefer photophile and sciaphile microhabitats of seagrasses and algae (Langer, 1993; Langer et al. 1998). The high percent abundance of symbiont-bearing species and the smaller quantity of stress tolerant opportunistic species (e.g. *Ammonia, Haynesina, Bulimina*) included in assemblage B indicate a better water quality and more oligotrophic conditions compared to the more eutrophic samples sites included in Cluster II.

The presence of well-developed *Posidonia oceanica* meadows associated with different algae in oligotrophic water conditions along the southern shoreline were previously described by Kashta et al. (2007) and Bequiraj et al. (2008a) and thus agree with our environmental assessment based on the composition of the foraminiferal assemblages in this area. Especially shallow water samples (4-5m) contain a large quantity of larger-symbiont bearing species (1.7-78.2%), whereas the amount decreases in greater water depth (30m, 0.5-2.6%). Oppositional trends were found in opportunistic and heterotrophic species, which increase in deeper water. This may be related to decreasing grain size in deeper waters accompanied with a larger amount of suspension loads of sediments. The increasing number of species in deeper sample sites may be due to the presence of more microhabitats in greater water depth.

Sample stations Gijri Monastiri Bay, Jala, and Darezeze e Re show a significant distance to other sample sites included in Cluster I, because they contain lower species richness values (6-22 taxa) and display a dominance of certain epiphytic species. Gijri Monastiri Bay is characterized by a high percent abundance of the invasive species *Amphistegina lobifera*, which leads to a loss of foraminiferal diversity and certain groups of foraminifera (trochospiral, planispiral and LBF, epiphytes in general; Langer and Mouanga, 2016).

The distance of the Jala sample site to other sites included in Cluster I and biofacies B, may be due to lower species richness value (19 taxa). Foraminiferal assemblages at that site are also characterized by epifaunal species, known to live on phytal substrates (*A. lobifera, Buccella* sp. 1, *Neoconorbina terquemi, Rosalina bradyi, Rosalina macropora, Planorbulina mediterranensis, Lobatula lobatula, Peneroplis pertusus, Pseudotriloculina* sp. 3, *Cibicides refulgens, Conorbella imperatoria),* some heterotrophic and to a lesser extend opportunistic species which are often correlated with fine grained substrates (*Q.* aff. *Q. viennensis, Q. stelligera, Pseudotriloculina* sp. 2, *Q. parvula, Elphidium transculens, Globocassidulina subglobosa*). This sample contains a relatively large amount of planktonic foraminifera (7%) and radiolarians. Jala is one of the principle strongholds for tourism along the southern coastline. The bay with its broad sandy beach, is strongly influenced by tourist activities, leading to degrading *Posidonia oceanica* occurrences and increased amounts of *Posidonia* matte affecting the foraminiferal assemblages.

The sample site in Darezeze e Re is characterized by few epifaunal species (*Buccella* sp. 1, *Neoconorbina terquemi, Aubignya planisorso, Lenticulina orbicularis*), few semi-infaunal taxa (*A. inflata, Pseudotriloculina* sp. 3) and a relatively large amount of planktonic foraminifera and radiolarians (10%). The lowest species richness value (6 taxa) found in Darezeze e Re may be a combination of different factors. Such as the influence of the Vjosa River located approximately 8km southwards, which inserts 8.3 x  $10^6$  million tons sediment/year (Simeoni et al. 1997). The watershed is characterized by high loads of suspended material continuously modifying the coastal shape, which impact benthic communities. A further strong impact is given by the petroleum industry and the resulting leaching from the pumping networks, which pollutes surface waters so that about 1-2% of the amount processed escapes into the environment (UNEP 2000; Cullaj et al. 2005). The beach fringing the coastal area, were we collected the samples showed a relatively high rate of oil patches. The coastal sediments in this area are further characterized by a high content of Cr resulting from the metallurgic industry (Celo et al. 1999; Cullaj et al. 2000, 2005).

An additional influence on benthic communities in Darezeze e Re and Jala is given by upwelling events due to Bora offshore winds occurring in summer within this area (Bergamasco and Gacic, 1995). Upwelling events introduces cold-nutrient rich water delivering most of the organic matter to the sea bottom as phytodetritus. This is accompanied with oxygen minimum zones, where the bottom waters may become dysoxic and anoxic pore waters occur (Murray, 2006). Although opportunistic taxa known to survive short time perturbations after upwelling events (*Bolivina, Brizalina, Stainforthia, Nonionella*) (Diz et al. 2006; Murray, 2006) lack in Darezeze e Re and Jala, the amount of epifaunal or semi-infaunal taxa points to a time period after upwelling. Most of the individuals (mainly opportunistics) live on the sediment and increasing wave regimes in combination with mobile sediments let foraminifera seek the sanctuary of plants (once again) (Murray, 2006).

Sen Gupta (1999) mentions that many subtropical as well as those taxa that are enriched in the sediments due to (spring) upwelling are relatively susceptible to dissolution and that differential removal of these species increases the cold water aspect of sediment-surface assemblages (Ruddiman, 1977). This may be a further explanation for the low species richness, the dominance of opportunistic epifaunal or mud dwelling taxa and a high percent abundance of planktonic species at these sites.

The sample sites in Durres (4m) are more closely related to the deeper water sites in 30m depth as they generally contain more opportunistic and heterotrophic species, than found in the shallow-water sites (5m water depth). Samples were collected in small seagrass patches of *Zostera noltii* since there have been no *Posidonia oceanica* meadows present. This is in line with observations made by Bequiraj et al. (2008a), who described almost only a *Posidonia* matte present with rare shoots of *Posidonia oceanica* meadows at 15m water depth. Durres is also one of the principle port areas in Albania, affected by increasing anthropogenic activities (maritime traffic, tourism, building activities etc.) accompanied with high levels of Cd, Pb, Ni and Cr (Cullaj et al. 2005). Although samples collected in this study were taken outside of the port area, foraminiferal assemblages here show degrading environmental conditions compared to the other samples along the southern shoreline included in biofacies I. However, the presence of larger symbiont-bearing foraminifera indicates oligotrophic conditions for these sites.

Another exception is found in the Bay of Sarande, which is also influenced by an increasing anthropogenic impact, due to the discharge of waste water, building/construction activities (leading to higher erosion rates) and increasing tourist and port activities. The bay is fed by the moderately polluted Bistrica River, which is characterized by high flow rates during October to May, which amounts to 73% of the total annual water (Kabo 1990; Cullaj et al. 2005). The water quality in the Bay

of Sarande is of oligotrophic nature, despite the current pressure from contaminants, such as heavy metals and increasing nutrients (Malltezi et al. 2010). This is also confirmed through the presence of symbiont-bearing foraminifera, which act as bioindicators for oligotrophic conditions. The samples collected in 5 and 30m water depth show a disparity in substrate type and foraminiferal assemblage. The species composition in 5m water depth (included in Cluster I and Biofacies B) is that of a typical Posidonia oceanica meadow in good state, with a abundant symbiont-bearing and heterotrophic species and a low amount of opportunistic species, mainly inhabiting the muddy sediments trapped in the rhizomes of the seagrass meadows or dwelling on algae substrates in more shaded/scaiphile habitats. The sample collected in Sarande Bay 30m is the only sample station located along the southern coastline of Albania included in biofacies II and Cluster A. The sediment type is composed of relatively fine grained sand with a high amount of calcium carbonate. The species assemblage at this site is characterized by a abundant infaunal taxa with a heterotrophic and opportunistic life strategy (e.g. Eggereloides scabrus, Labrospira subglobosa, Brizalina dilatata, B. aff. B. striatula, Bulimina marginata, B. aculeata, B. elongata, Brizalina striatula, Brizalina aff. B. dilatata, Porosononion granosum, Haynesina depressula, Nonionella stella, Valvulineria bradyana, Astrononion stelligerum, Pseudotriloculina sp. 2, Reophax spp.) known to prefer fine grained sediments rich in organic matter. The amount of larger-symbiont bearing species is remarkedly low and only represented by *Peneroplis pertusus* and *Amphistegina lobifera* with low percent abundances (0.3-0.9). Epifaunal species present are most abundant on algae substrates (Buccella sp.1, Asterigerinata mamilla, Peneroplis pertusus, Textularia truncata, Textularia bocki, Elphidium crispum, Elphidium jenseni, Eggereloides advenus, Cibicides refulgens, Rosalina floridensis, Rosalina bradyi, Lobatula lobatula, Sigmoilinita grata and Gavelinopsis praegeri are known to settle in microhabitats of algae and seagrasses (Langer, 1993). The species composition in addition to the absence of typical foraminiferal taxa living permanently attached on seagrass leaves (Planorbulina mediterranensis, Cyclocibicides vermiculatus) or species living in rhizomal habitats, (e.g. Miniacina miniacea, Cibicidella variablis, Q. pseudobuchiana) point to a degraded Posidonia oceanica meadow or Posidonia matte, which is probably overgrown with algae species and contain a significant amount of muddy sediment inhabited by biofacies A.

Our observations made in Sarande Bay 30m are consistent with observations made by Bequiraj et al. (2008a) who state the presence of patchy *Posidonia oceanica* meadows in good state located in the north and northwestern part of the Bay at 5-18m water depth, whereas very shallow areas and the centre of Bay (including our sample station in 30m water depth) exhibit degrading meadows partly replaced by *Caulerpa racemosa*, *Zostera noltii* and *Flabellia petiolata* covering the *Posidonia* matte.

The disparity between the two sample stations in Sarande Bay may be related to an increasing anthropogenic impact in the bay leading to degrading *Posidonia oceanica* occurrences thus influencing accompanied biotic assemblages.

## Non-indigenous benthic foraminifera

Dispersal modes of benthic foraminifera have been discussed by many authors. It is generally accepted that the dispersal of benthic foraminifera is possible through self-locomotion over short distances (some tens of cm's/7days; Schafer and Young, 1977; <1mm to a few cm/h, Weinberg, 1991; Hemleben and Kitazato, 1995; Bornhalm et al. 1997; Kitazato, 1988; Wetmore, 1988;) or by passive transport through currents, sediment transport and storm events. This has been documented through the observation of living individuals at various growth stages that have been reported from the water column (Arnold, 1964; Lidz, 1966; Loose, 1970; Hueni et al. 1978; Alve, 1999; Kitazato, 1995; Alve and Goldstein, 2002). Further dispersal modes may include the attachment to floating objects or larger

animals (Myers, 1936; Lessard, 1980) or gastrointestinal transport in fishes (Ichthyoendochory) or other marine organisms (Guy-Haim et al. 2016, 2017).

The dispersal through currents enlarges the geographical extension, so that non-native species are able to settle in new geographical environments. The range extension may result in severe consequences for the native biota and for ecosystem functioning. Alve and Goldstein (2002) documented that many benthic foraminiferal species produce propagules that may enter resting stages (cysts) and are further released in large numbers to the water masses, where they may be widely dispersed by physical processes (currents, sediment transport) and ultimately settle over a range of habitats and conditions that are suitable. This has been documented in growth experiments for certain species (Alve and Goldstein, 2002, 2003; Weinmann and Goldstein, 2016; Kitazato, 1995) and therefore could be a significant common mechanism for the dispersal over long distances. This supports the assumption for the transport of foraminifera through currents but also cope well with human mediated transport of benthic foraminifera via ballast ship water. It is suggested that benthic foraminifera due to their minute size and presence in virtually all environments as well as occurrences in geographically separated areas makes them particularly susceptible to ship ballast transfer (Witte, 1994; McGann and Sloan, 2000; Calvo-Marcilese and Langer, 2010; Schweizer et al. 2011; Asteman and Schönfeld, 2015). Some studies already demonstrate the presence of benthic foraminifera in ballast ship water (Galil and Hülsmann, 1997; Chu et al. 1997; Lavoie et al. 1999; Radziejewska et al. 2006; Bouchet et al. 2007). However, little is known about the introduction and extent of foraminiferal species dispersed across oceans by humans (McGann et al. 1996, 2000; Calvo-Marcilese and Langer, 2010).

The sample stations along the southern shoreline of Albania contain low numbers of NI foraminiferal species which have an Indo-Pacific or Atlantic origin as mentioned at the beginning of the discussion. The most prominent is Amphistegina lobifera, which is among the 100 worst invasive marine species in the Mediterranean Sea (Zenetos et al. 2005, 2008). Although classified as a cryptogenic species newly arriving amphisteginids most probably enter the Mediterranean through the Suez Canal or are transported via ballast ship water. They are among the key invasive species currently extending their ranges and have locally become extremely abundant thus representing the most abundant taxon at almost every site colonized (Langer and Mouanga, 2016). The range expansion of amphisteginid foraminifera severely impacts native foraminiferal assemblages and is reflected in a loss of benthic foraminiferal biodiversity, alterations of foraminiferal community structures and shifts in abundances of functional groups of foraminifera (Mouanga and Langer 2014; Langer and Mouanga, 2016). They are currently distributed along the southern coastline of Albania (MB, SB, PP, Ja, Der), where they make up to 76% of the foraminiferal assemblage, thus ranging among the most abundant species. It remains to be seen how far they will invade the Adriatic Sea. Species Distribution Models (SDM's) for amphisteginid foraminifera in the Mediterranean Sea projected by Langer et al. (2012) and Weinmann et al. (2013a), prognosticated suitable habitats along the southern area of Albania (already colonized by now), and predict the migration of amphisteginids along the NE Adriatic Sea coast to Krk Island (Croatia) by the year 2050. The Species Distribution Model also indicate potentially suitable regions in the central part of the Adriatic Sea pointing to potential migration pathways (Langer et al. 2012). Sea surface temperature and calcite concentration are the main factors regulating the dispersal of amphisteginids in the generated SDM's, which coincides with current dispersal patterns in the Mediterranean Sea (Langer et al. 2012). These factors will most likely also determine the distribution of amphisteginids in the Adriatic Sea. Current climate warming facilitates the distribution of thermophilic species. The distribution of amphisteginid foraminifera is limited by the 14°C winter isotherm (Zmiri, 1974; Langer and Hottinger, 2000; Langer et al. 2012), although the invasion in northern parts of the Mediterranean (Aegea Sea) as well as in the southeastern Sea of Marmara (Meric et al. 2005) suggests an adaptation to lower water temperatures (Langer et al. 2012;

Triantaphyllou et al. 2012). Despite this, the range expansion of amphisteginids along the seacoast of Albania is in line with recent SST increases and isotherm shifts recorded in the Mediterranean Sea

(Coll et al. 2010; Lejeusne et al. 2010; Francour et al. 1994, 2010; Bianchi et al. 2013; Langer and Mouanga, 2016). The absence of amphisteginid foraminifera along the southern boot of Italy, also demonstrate that the non-uniform colonization of the Adriatic Sea provides further evidence that SST is a key environmental predictor driving the range extension of amphisteginids (Langer and Mouanga, 2016). The observation of benthic foraminiferal assemblages in the Port of Otranto (SE boot of Italy), however, reveals a low abundance of 3 NI foraminiferal species (*Euthymonacha polita, Spiroloculina antillarum* and *Loxostomina limbata costulata*) of Indo-Pacific, Pacific or respectively Atlantic origin, which most probably were introduced via ballast ship water (Appendix 7.3).

The elevated freshwater and terrigenous input due to rivers and erosion along the eastern coast will limit the distribution of invasive amphisteginds locally. Weinmann et al. (2013) mentioned that increasing eutrophication and nutrient influx will locally impact the range expansion of Amphistegina spp., especially in the northern Adriatic, so that the total extend of the predicted future range expansion of this taxon may not fully be realized in future, even though the temperatures will become more suitable. However, the presence of larger symbiont-bearing species along the coastline of Croatia including Peneroplidae and Soritidae (Wiesner, 1913; Vatova, 1928; Alfirevic, 1964, 1998; Drobne and Cimerman, 1984; Cimerman and Langer, 1991; Vanicek et al. 2000; Vidovic et al. 2009; Cosovic et al. 2002, 2011) show that those species are able to overcome natural barriers such as rivers accompanied by massive terrigenous input. This is also shown in the distribution of foraminiferal species from the eastern and central Mediterranean Sea, where larger symbiont-bearing species were able to overcome the Nile barrier now settling along the northern coastline of Egypt, Lebanon, Tunisia, the Pelagian Islands and Sicily (Blanc-Vernet et al. 1979; Samir et al. 2001, 2003; Elshanawany et al. 2011; Caruso and Cosentino, 2014). Sea surface currents will help to extend the distribution range of Amphistegina spp. by several hundred kilometers (Saidova, 1961; Todd, 1976; Lessard, 1980; Langer and Hottinger, 2000; Langer et al. 2012). Gastrointestinal transport (Ichthyoendochory) of amphisteginids in fishes has recently been suggested by Guy-Haim et al. (2016, 2017, in press) which eases and accelerates the dispersal and may be an explanation for increased dispersal rates of amphisteginids determined by Langer and Mouanga (2016).

The successful returnee *Sorites orbiculus* Forskal has rarely been reported from the southern coast of Albania. This larger-symbiont bearing foraminifera is able to tolerate temperatures as low as 14°C (Langer, 2008a), which enables this taxon to inhabit also shallow-waters of the western Mediterranean Sea (Tyrrhenian Sea), where it is a common species in phytal substrate dominated habitats (Langer, 1988; Cimerman and Langer, 1991; Langer, 1993; Langer et al. 1998; Langer and Schmidt-Sinns, 2006b). The introduction pathway within shallow waters off Albania may be also sea surface currents like in amphisteginids as it inhabits shallow-water sites in the Ionian Sea (Ionian Islands: Triantaphyllou and Dimiza, 2013; Mouanga and Langer, 2014; Corfu: Langer and Mouanga, 2016). This species is the only species among the NI taxa, which originally had an Atlantic origin, although individuals distributed in the Eastern Mediterranean Sea also have an Indo-pacific gene pool (Merkado et al. 2013).

Other NI species comprise *Nodophthalmidium antillarum*, sparsely recorded from the Bay of Vlore (20-22m, 0.4%), *Loxostomina? limbata costulata* occurring rarely in Porto Palermo (30m, 02%), *Mimosina affinis* distributed in Vlore Bay (10-22m, 0.4-3%) and *Sigmamiliolinella australis* occurring in Shengjin (2m, 2.5%), Vlore (17m, 0.4%) and Dermi (5m, 0.3%) .The percent abundances of the above mentioned species are low and in most cases locally restricted.

Only *Amphistegina lobifera, Sorites orbiculus* and *Sigmamilionella australis* are geographically more extended. They occur in different bays and ports (Shengjin, Vlore, Sarande) along the seacoast of Albania. *Amphistegina lobifera* and *Sorites orbiculus* are the only taxa where the introduction via currents appears to be the most plausible means of introduction. The distance between the established populations around northern Corfu and southern Albania (Langer and Mouanga, 2016) is around 40km, so that the crossover through Ionian surface currents is likely.

The local restriction of the other NI foraminifera present in the investigated samples (Mimosina affinis, Loxostomina? limbata costulata, Nodophtalmidium antillarum) and their appearance in or near the principal ports in Albania suggest the transportation via ballast ship water in combination with current dispersal. Mimosina affinis and Nodophthalmidium antillarum only occur in Vlore Bay, whereas Sigmamilionella australis occur in two of the principle ports (Shengjin and Vlore) and is further distributed in Dermi. The transportation via ballast ship water is possible through shipping routes connecting the Eastern Mediterranenan Sea, respectively Indo-Pacific and Pacific Ocean with the Adriatic Ses. It is not necessary that ships containing living foraminiferal tests or foraminiferal propagules have to land in the ports, as the distribution is also given by dumping of ballast water outside of the ports. This underlines the hypothesis of Alve and Goldstein (2003) that foraminiferal propagules are present in the water column, where they are further dispered by currents to arrive in different localities, where they start to flourish when suitable habitats are available. The dispersal of propagules through currents may also explain the distribution of NI taxa around Dermi (S. australis) and Porto Palermo (Loxostomina? limbata (Brady) costulata), which are some km away from the principle ports, but all connected through northwards flowing Ionian surface currents und opposite underwater currents.

The amount (3%) and numbers (4 species) of NI benthic foraminifera is currently low, excluding the amount of invasive amphisteginids along the southern shoreline. But the numbers will increase in the future as current climate warming facilitates the distribution of established populations in the central and eastern Mediterranean Sea via natural expansion or human mediated (shipping, aquaculture).

The number of other NI species along the seacoast of Albania is small (20 taxa; Katsanevakis et al. 2011) compared to nearby located areas (such as Greece: 113 species; Kashta et al. 2010; Pecarevic et al. 2013; northern Adriatic: 171 species; Zenetos et al. 2010). This may be related to limited existing studies on marine benthic species along Albania in general. Currently severe consequences on native biotic communities are documented for the invasive algae *Caulerpa racemosa* and the invasive Nimble spray crab *Percnon gibbesi*, which are distributed along the southern Albanian seacoast (Kashta et al. 2010/PAGA). The number of NI species in the Adriatic Sea and especially at the southern entrance is expected to increase due to the establishment and expansion of NI species in the central Mediterranean, especially in the Ionian Sea (Katsanevakis et al. 2011). This has been shown by the presence of *Amphistegina lobifera* along the southern coastline of Albania.

Climate models predicted that by 2041-2060, the major part of the Mediterranean Sea will become warmer except of the northern Adriatic, which is expected to become cooler (Coll et al. 2010). Continuing isotherm shifts thus will enhance the introduction of thermophilic species, especially in the southern and central Adriatic Sea. It remains to be seen how invasion processes continue in the eutrophic northern Adriatic as cooling events may limit the establishment of thermophilic NI species. The northern Adriatic is to date inhabited by the largest amount of NI species of the whole Adriatic Sea (Zenetos et al. 2010). The introduction is mainly due to aquaculture, ship fouling and ship ballast water. NI species introduced via aquaculture, may well adapt to lower water temperatures, so that further invasions and establishment processes are quite possible.

NI benthic foraminiferal species are expected to migrate further into the Adriatic Sea via currents or by ballast ship water. The detection of NI benthic foraminiferal species along the seacoast of Albania in this study serves as baseline for future assessments of introduced benthic foraminiferal species (including invasive species).

## 3.1.6 Conclusion

This is the first survey of benthic foraminiferal assemblages distributed along nearly the entire coastline of Albania.

The foraminiferal assemblages along the coastline of Albania are characterized by high species richness values (277 species, 112 Genera). The peculiar position of Albania, situated in a transition zone between three (bio-) geographical areas, lead to the distribution of foraminiferal taxa typical for the Adriatic as well as species known to be distributed in the Eastern and Western Mediterranean Sea.

Two major types of biofacies were recorded along the coast of Albania. The biofacies types divide the shallow-water sediments into a northern and a southern region. Each biofacies region is characterized by specific assemblages of benthic foraminifera.

This is underlined through the composition of mixotrophic, heterotrophic and opportunistic species in both biofacies. The northern sample sites are characterized by the dominance of opportunistic and heterotrophic foraminifera, as they tolerate waters with high turbidity and nutrients as well as more stressful conditions such as high heavy metal concentrations and low oxygen conditions. The southern sample stations contain a larger portion of mixotrophic and heterotrophic species, due to the absence of large rivers and oligotrophic water conditions.

Increasing anthropogenic pressure accompanied with pollution from sewage, urban wastes, maritime traffic, and building activities lead to partly degraded conditions within certain areas. Especially the Gulf of Vlore and Sarande Bay are known for increasing anthropogenic pressure leading to the establishment and accumulation of mainly opportunistic species. Foraminiferal assemblages especially around Darezeze e Re (lowest species richness), as well as around Shengjin, Durres, and Divjaka show likewise increasing degradation rates traced back to human mediated impacts (urban and industrial sewages, hydrocarbon exploration, building activities) and natural forcing (river discharge, erosion rates).

The presence of NI species of Indo-Pacific and Atlantic origin is considered to be the result of rising water temperatures, and ballast ship water. The benthic foraminifera *Amphistegina lobifera* has settled along the southern coastline, with locally severe consequences on native diversity and ecosystem functioning. With current climate warming they are expected to invade shallow waters off Montenegro and Croatia, before the dispersal is getting limited through the eutrophic conditions and cooler sea surface temperatures in the Northern Adriatic Sea.

	D1	D2	Sh1	Sh2	Div	Ja	Dar	<b>V1</b>	V2	<b>V3</b>	V4
Labrospira subglobosa	0,0	0,0	0,5	0,0	0,0	0,0	0,0	0,0	3,3	0,8	2,1
Eggereloides scabrus	0,0	0,0	0,0	1,4	1,4	0,0	0,0	0,0	4,2	3,4	14,5
Textularia truncata	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0
Adelosina aff. A. angulosa	0,3	0,9	2,9	0,0	0,7	0,0	0,0	7,7	0,3	0,8	1,3
Adelosina cliarensis	0,3	0,0	0,0	0,0	0,0	0,0	0,0	5,1	0,3	0,0	0,4
Quinqueloculina bosciana	0,0	0,6	2,0	8,7	0,0	0,0	0,0	7,7	0,3	2,7	0,4
Quinqueloculina aff. Q. planciana	3,5	8,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Quinqueloculina stelligera	0,3	0,0	2,5	0,0	0,7	4,7	0,0	0,0	3,6	4,9	8,1
Quinqueloculina ungeriana	2,1	4,7	0,0	0,0	0,0	0,0	0,0	7,7	0,0	0,0	0,0
Quinqueloculina aff. Q. viennensis	8,0	4,7	16,2	3,8	0,7	4,7	0,0	10,3	0,6	1,5	1,7
Quinqueloculina sp. 5	2,4	0,6	1,5	0,0	3,1	0,0	0,0	5,1	0,6	0,0	0,0
Pseudotriloculina laevigata	0,0	1,8	1,5	1,4	0,3	0,0	0,0	0,0	1,8	4,2	5,1
Pseudotriloculina sp. 2	1,0	1,2	8,8	9,1	6,8	7,0	0,0	0,0	0,3	3,0	14,0
Pseudotriloculina sp. 3	1,7	3,5	0,0	1,0	0,0	4,7	9,1	0,0	1,2	2,3	0,0
Pseudotriloculina sp. 4	0,0	0,9	1,5	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Triloculina adriatica	0,7	5,6	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Triloculinatricarinata	1,0	2,4	0,0	1,0	0,0	0,0	0,0	2,6	1,8	0,0	0,0
Sigmoilinita grata	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Peneroplis pertusus	0,3	0,6	0,0	0,0	0,0	2,3	0,0	0,0	0,0	0,0	0,0
Peneroplis planatus	1,4	2,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Lenticulina orbicularis	0,0	0,9	0,0	0,0	0,3	0,0	9,1	0,0	0,0	0,0	0,0
Lenticulina orbicularis	0,0	0,9	0,0	0,0	0,3	0,0	9,1	0,0	0,0	0,0	0,0
Bulimina aculeata	0,3	0,0	0,5	1,0	0,7	0,0	0,0	0,0	4,2	2,3	0,9
Neoconorbina terquemi	0,0	0,0	0,0	0,0	0,0	4,7	36,4	0,0	0,0	0,0	0,0
Rosalina bradyi	9,8	4,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Rosalina floridensis	1,4	0,3	0,0	1,4	0,0	0,0	0,0	0,0	4,5	17,0	0,0
Rosalina macropora	3,1	0,9	0,0	0,0	0,0	9,3	0,0	0,0	0,0	0,0	0,0
Conorbella imperatoria	0,0	0,0	0,0	0,0	0,0	7,0	0,0	0,0	0,0	0,0	0,0
Epistominella vitrea	0,0	0,0	1,0	0,0	0,0	0,0	0,0	0,0	0,9	0,0	0,9
Cibicides refulgens	0,3	0,0	0,0	0,0	0,7	14,0	0,0	0,0	0,3	0,4	0,0
Lobatula lobatula	1,7	2,7	0,0	0,0	0,0	4,7	0,0	0,0	0,0	0,0	0,0
Planorbulina mediterranensis	2,1	2,7	0,0	0,0	0,0	2,3	0,0	0,0	0,3	0,0	0,0
Amphistegina lobifera	0,0	0,0	0,0	0,0	0,0	9,3	0,0	0,0	0,0	0,0	0,0
Haynesina depressula	0,0	0,0	1,0	2,4	0,0	0,0	0,0	0,0	3,6	4,2	6,4
Nonionella stella	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	3,0	0,8	1,3
Aubignya planidorso	2,4	0,9	1,0	1,4	8,1	0,0	9,1	0,0	0,3	2,3	0,9
Buccella sp. 1	2,1	0,3	0,0	6,7	2,0	9,3	27,3	10,3	0,0	0,4	0,0
Ammonia inflata	4,2	4,4	4,9	5,3	11,9	0,0	9,1	23,1	0,9	1,9	0,4
Ammonia tepida	1,4	0,0	2,9	8,2	18,6	0,0	0,0	0,0	1,8	4,5	3,4
Porosononion granosum	2,4	3,2	1,5	2,4	8,1	0,0	0,0	10,3	5,4	1,9	0,4

**Table 5** Abundance records of foraminiferal species reaching at least 5% of the foraminiferal assemblages. Dominant species (reaching at least 10%) were designated in bold characters.

	<b>V</b> 5	<b>V6</b>	<b>V7</b>	Derm	PP1	PP2	SB1	SB2	MB1	MB2
Labrospira subglobosa	7,3	3,0	3,4	0,0	0,0	0,0	0,0	8,6	0,0	0,2
Eggereloides scabrus	3,9	4,7	2,3	0,0	0,0	0,7	0,0	15,1	0,0	0,0
Textularia truncata	0,0	0,0	0,0	0,5	1,0	0,5	6,4	0,3	0,0	0,0
Adelosina aff. A. angulosa	1,9	2,3	1,1	1,2	0,5	2,0	0,3	0,0	0,0	1,0
Adelosina cliarensis	0,0	0,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Quinqueloculina bosciana	0,0	0,0	0,0	0,3	0,0	0,0	1,1	0,0	0,0	0,6
Quinqueloculina aff. Q. planciana	0,0	0,0	0,0	0,0	0,5	0,5	0,0	0,0	0,0	0,0
Quinqueloculina stelligera	1,0	1,3	1,1	2,2	0,0	4,2	0,0	0,0	0,0	2,0
Quinqueloculina sp. 5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Pseudotriloculina laevigata	5,3	2,0	2,6	0,3	0,3	1,7	0,0	0,9	0,0	0,6
Pseudotriloculina sp. 2	5,3	6,0	0,8	0,2	0,0	0,0	0,0	3,6	0,0	1,2
Pseudotriloculina sp. 3	0,0	0,0	1,5	0,3	0,0	0,2	0,8	0,3	0,0	1,6
Pseudotriloculina sp. 4	0,0	0,0	0,0	0,2	0,3	5,5	0,0	0,0	0,0	0,0
Triloculina adriatica	0,0	0,0	0,0	0,0	0,2	0,0	1,6	0,6	1,4	3,7
Triloculinatricarinata	0,0	0,7	0,0	5,8	5,0	3,2	1,6	0,0	0,0	0,6
Sigmoilinita grata	0,0	0,0	0,0	1,0	0,7	6,2	0,0	0,3	0,0	2,6
Peneroplis pertusus	0,0	0,0	0,0	5,6	8,5	0,2	2,7	0,3	0,0	0,6
Peneroplis planatus	0,0	0,0	0,0	4,9	8,8	0,0	10,4	0,0	1,7	0,8
Lenticulina orbicularis	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Quinqueloculina stelligera	1,0	1,3	1,1	2,2	0,0	4,2	0,0	0,0	0,0	2,0
Quinqueloculina ungeriana	0,0	0,0	0,0	0,0	0,7	0,7	2,7	0,3	0,7	2,2
Bulimina aculeata	1,9	3,3	5,3	0,0	0,0	1,0	0,0	4,7	0,0	0,0
Neoconorbina terquemi	0,0	0,0	0,0	1,0	0,0	0,7	0,3	0,9	0,0	1,6
Rosalina bradyi	0,0	0,0	0,0	9,2	7,6	8,7	2,7	4,4	0,0	4,7
Rosalina floridensis	4,9	4,7	1,5	1,5	0,0	0,5	0,0	1,5	0,0	0,2
Rosalina macropora	0,0	0,0	0,4	10,7	8,7	4,5	1,1	2,1	0,0	5,5
Conorbella imperatoria	0,5	0,0	0,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Epistominella vitrea	2,9	1,7	7,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Cibicides refulgens	0,0	0,0	0,4	2,9	2,9	4,7	0,5	1,2	0,0	1,0
Lobatula lobatula	0,0	0,0	0,0	6,5	8,3	4,5	9,6	1,2	0,0	7,9
Planorbulina mediterranensis	0,0	0,3	0,0	1,7	2,9	3,2	5,3	0,0	0,3	8,7
Amphistegina lobifera	0,0	0,0	0,0	2,2	0,3	0,0	12,0	0,9	76,1	1,2
Haynesina depressula	3,9	2,3	5,6	0,2	0,0	0,7	0,0	1,2	0,0	0,0
Nonionella stella	2,9	4,0	5,6	0,0	0,0	0,0	0,0	0,3	0,0	0,0
Aubignya planidorso	2,4	0,3	1,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Buccella sp. 1	0,0	0,0	0,0	0,3	0,0	0,2	0,0	1,5	0,0	1,0
Ammonia inflata	1,0	2,3	1,5	0,7	1,7	1,5	0,5	4,1	0,0	2,6
Ammonia tepida	2,9	4,0	1,9	0,3	0,0	0,5	0,3	0,3	0,0	0,0
Porosononion granosum	1,5	1,7	5,6	0,0	0,0	1,2	0,0	2,4	0,0	0,0

## **Plate Descriptions**

#### PLATE 1

- 1. Lagenammina atlantica (Cushman) a) side view 100mµ, b) apertural view 100µm
- 2. *Lagenammina* sp. 1, a) side view 100mµ, b) apertural view 100µm
- 3. Saccammina difflugiformis Brady side view 100µm
- 4. Iridia diaphana Heron-Allen & Earland, attached specimen, dorsal view 100µm
- 5. Daitrona sp.1 a) dorsal view 100µm, b) ventral view 100µm, c) edge view 100my
- 6. Hyperammina sp.1 a) side view 100 μm, b) aperture 50μm
- 7. Ammodiscus planus Höglund a) side view 100 µm, b) edge view 100µm
- 8. Ammodiscus sp.1 a) side view 50µm, b) edge view 50µm
- 9. Ammodiscus sp. 2 a) side view 100mµ, b) aperture 50µm
- 10. Ammodiscus sp. 3 a) side view 50µm, b) edge view 50µm
- 11. Miliammina fusca (Brady) a) side view 100µm, b) edge view 50µm
- 12. Trilocularena ? sp.1 a) side view 100µm, b) apertural view 25µm
- 13. Reophax fusiformis Williamson a) side view 50µm, b) apertural view 50µm
- 14. Leptohalysis scotti Chaster side view 50µm
- 15. Reophax nana (Rhumbler) a) side view 50µm
- 16. *Reophax* sp. 1 a) apertural view 50µm b) side view 100µm
- 17. *Reophax* sp. 2 a) apertural view 50μm b) side view 100μm
- 18. *Reophax* sp. 3 a) apertural view 50µm b) side view 50µm
- 19. Warrenita sp.1 a) apertural view 50µm b) side view 50µm
- 20. Labrospira sp.1 a) apertural view 50µm b) side view 50µm, c) face view 50µm, d-e) side view 100µm
- 21. Ammoscalaria pseudospiralis (Williamson) a) side view 100µm, b) apertural view 100µm
- 22. Ammoscalaria tenuimargo (Brady) a) side view 100µm, b) apertural view 100µm
- 23. Ammoscalaria sp. 1 a) side view 100µm, b) apertural view 100µm
- 24. Spirolectinella earlandi Parker a) side view 50µm, b) apertural view 50µm
- 25. Trochammina inflata (Montagu) a) side view 50µm, b) apertural view 50µm

- 1. Jadammina macrescens (Brady) a) side view 100 µm, b) apertural view 100µm
- 2. Trochamminula sp. 1 a) side view 100mµ, b) apertural view 100µm
- 3. Deuterammina dubliensis Brönnimann & Whittaker a) side view 100mµ
- 4. Eggerelloides advenus (Cushman), a) side view 100 µm
- 5. Eggerelloides scabrus (Williamson) a) side view 100 µm
- 6. Textularia agglutinans d'Orbigny a) side view 100 µm, b) apertural view 100µm
- 7. Textularia bocki Höglund a) side view 100 µm, b) apertural view 100µm
- 8. Textularia conica d'Orbigny a) side view 100 µm, b) apertural view 100µm
- 9. Texularia lateralis Lalicker a) side view 100 µm, b) apertural view 100µm
- 10. Textularia porrecta Brady a) side view 100µm, b) edge view 25µm
- 11. *Textularia* sp. 1 a) side view 50µm, b) apertural view 50µm
- 12. *Textularia* sp. 2 a) side view 100μm, b) apertural view 100μm
- 13. *Textularia* sp. 3 a) side view 100μm, b) apertural view 100μm
- 14. Siphotextularia flintii (Cushman) a) side view 100µm, b) apertural view 100µm
- 15. Siphotextularia sp. 1 a) side view 50µm, b) apertural view 50µm
- 16. Spirillina limbata Brady a) side view  $50\mu m$ , b) apertural view  $50\mu m$
- 17. Spirillina vivipara Ehrenberg a) apertural view 50µm, b) side view 50µm
- 18. Patellina corrugata Williamson a) dorsal view 50µm, b) umbilical view 50µm, c) edge view 50 µm

- 1. Cornuspira foliacea (Philippi) a) side view 100µm, b) apertural view 50µm
- 2. Cornuspira sp. 1 a) side view 50µm, b) aperture view 50µm
- 3. Cornuspira sp. 2 a) side view 50µm, b) aperture view 50µm
- 4. Vertebralina striata d'Orbigny a) side view 50µm, b) side view 50µm
- 5. Vertebralina striata d'Orbigny a) side view 100µm
- 6. Wiesnerella auriculata (Egger) a) side view 50µm, b) side view 50µm
- 7. Nodophthalmidium antillarum (Cushman) a) side view 50µm, b) apertural view 25µm
- 8. Nubecularia lucifuga Defrance a) dorsal view 100µm, b) umbilical view 100µm
- 9. Spirophthalmidium sp. 1 a) side view 50µm, b) apertural view 50µm
- 10. Adelosina aff. A. angulosa Wiesner a) side view 100µm, b) apertural view 50µm
- 11. Adelosina carinata-striata Wiesner a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- Adelosina cliarensis (Heron-Allen and Earland) a) side view 100μm, b) side view 100μm, c) apertural view 50μm
- 13. *Adelosina* cf. *A. cliarensis* (Heron-Allen and Earland) a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 14. Adelosina dubia (d'Orbigny) a) side view 25µm, b) apertural view 25µm
- 15. Adelosina dubia (d'Orbigny) a) side view 50µm, b) side view 50my
- 16. Adelosina mediterranensis (Le Calvez, J. and Y. a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 17. Adelosina pulchella d'Orbigny a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 18. Adelosina pulchella d'Orbigny a) side view 100µm, b) apertural view 100µm
- 19. Adelosina striata (Wiesner) a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 20. Adelosina striata (Wiesner) a) side view 50µm

- 1. Adelosina sp. 1 a) side view 50µm, b) apertural view 50µm
- 2. Adelosina sp. 1 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 3. Adelosina sp. 2 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 4. *Adelosina* sp. 3 a) side view 50µm, b) side view 50µm, c) apertural view 25µm
- 5. Adelosina ? sp. 4 a) side view 50µm, b) side view 50µm, c) apertural view 25µm
- 6. Spiroloculina angulosa Terquem a) side view 100µm, b) apertural view 100µm
- 7. *Spiroloculina* cf. *S. antillarum* a) side view 100µm, b) apertural view 100µm
- 8. Spiroloculina cf. S. carinata, Wiesner a) side view 100µm, b) apertural view 100µm
- 9. Spiroloculina dilatata d'Orbigny a) side view 100um. b) apertural view 100um
- 10. Spiroloculina krumbachi Wiesner a) side view 100µm, b) apertural view 100µm
- 11. Spiroloculina ornata d'Orbigny Le Calvez, J. and Y. a) side view 100µm
- 12. *Spiroloculina ornata* d'Orbigny var. *tricarinata* Le Calvez, J. and Y. a) side view 100μm, b) apertural view 100μm
- 13. Siphonaperta agglutinans (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 14. Siphonaperta aff. S. aspera (d'Orbigny) a) side view 50µm
- 15. *Siphonaperta dilatata* (Le Calvez, J. and Y) a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 16. *Siphonaperta dilatata* (Le Calvez, J. and Y) a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 17. Siphonaperta cf. S. dilatata (Le Calvez, J. and Y) a) side view 100µm, b) apertural view 100µm
- 18. Siphonaperta cf. S. hauerina (Wiesner) a) side view 100µm, b) apertural view 100µm
- 19. Siphonaperta sp. 1 a) side view 100µm, b) apertural view 100µm
- 20. *Siphonaperta* sp. 2 a) side view 50µm, b) apertural view 25µm
- 21. Siphonaperta sp. 3 a) side view 50µm, b) apertural view 50µm

- 1. Cycloforina juleana (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 2. Cycloforina rugosa (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 3. Cycloforina tenuicollis (Wiesner) a) side view 50µm, b) side view 50µm, c) apertural view 25µm
- 4. Cycloforina aff. C. tenuicollis (Wiesner) a) side view 50µm, b) apertural view 50µm
- 5. Lachlanella planciana (d'Orbigny) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 6. Lachlanella undulata (d'Orbigny) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 7. *Lachlanella variolata* (d'Orbigny) a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- 8. *Massilina gualteriana* (d'Orbigny) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 9. *Massilina* aff. *M. secans* (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 10. Massilina aff. M. secans (d'Orbigny) a) side view 100µm, b ) side view 100µm, c) apertural view 100µm
- Massilina obliquistriata Cushman & Valentine a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 12. *Quinqueloculina adelaidensis* (Howchin & Parr) a) side view 50μm, b) side view 50μm, c) apertural view 25μm
- 13. Quinqueloculina berthelotiana d'Orbigny a) side view 100µm, b) apertural view 100µm
- 14. Quinqueloculina aff. Q. berthelotiana d'Orbigny a) side view 100µm, b) apertural view 100µm
- 15.  $\tilde{Q}$ uinqueloculina aff.  $\tilde{Q}$ . berthelotiana d'Orbigny a) side view 100µm, b) apertural view 100µm
- 16. *Quinqueloculina* aff *Q. bicornis* Williamson var. *angulata* Wiesner a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 17. *Quinqueloculina bidentata* ? d'Orbigny a) side view 100μm, b) side view 100μm, c) apertural view 100μm

- 1. *Quinqueloculina bosciana* d'Orbigny a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 2. *Quinqueloculina canaliculata* **Terquem** a) side view 50μm, b) side view 50μm, c) apertural view 50μm
- 3. *Quniqueloculina carinata* Wiesner a) side view 50µm, b) apertural view 50µm
- 4. *Quinqueloculina contorta* (d'Orbigny) a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 5. Quinqueloculina contorta (d'Orbigny) a) side view 50µm, b) apertural view 50µm
- 6. *Quinqueloculina* cf. *Q. contorta* a) side view 50μm, b) apertural view 50μm
- 7. Quinqueloculina disparilis d'Orbigny a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 8. *Quinqueloculina irregularis* d'Orbigny a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 9. Quinqueloculina italica, Terquem a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- 10. Quinqueloculina laevigata d'Orbigny a) side view 50µm, b) side view 50µm, c) apertural view 25µm
- 11. *Quinqueloculina longidentata* **Terquem** a) side view 50µm, b) apertural view 50µm
- 12. Quinqueloculina cf. Q. partschii d'Orbigny a) side view 50µm, b) apertural view 50µm
- 13. Quinqueloculina parvula Schlumberger a) side view 50µm, b) side view 50µm, c) apertural view 25µm
- 14. *Quinqueloculina parvula* ? Schlumberger a) side view 50μm, b) side view 50μm, c) apertural view 25μm
- 15. *Quinqueloculina* aff. *Q. parvula* Schlumberger a) side view 50μm, b) side view 50μm, c) apertural view 50μm
- 16. *Quinqueloculina* aff. *Q. planciana* (d'Orbigny) a) side view 100μm, b) side view 100μm, c) apertural view 100μm

- 1. *Quinqueloculina* aff. *Q. pseudobuchiana* Luczkowska a) side view 50µm, b) apertural view 50µm
- 2. Quinqueloculina pygmaea Reuss a) side view 50µm, b) apertural view 50µm
- 3. Quinqueloculina rugosa d'Orbigny a) side view 100µm, b) apertural view 100µm
- 4. *Quinqueloculina stelligera* Schlumberger a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 5. *Quinqueloculina* aff. *Q. tricarinella* (Wiesner) a) side view 50μm, b) side view 50μm, c) apertural view 50μm
- 6. *Quinqueloculina ungeriana* d'Orbigny a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 7. *Quinqueloculina viennensis* Le Calvez, J. & Y. a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 8. Quinqueloculina aff. Q viennensis Le Calvez, J. & Y. a) side view 100µm, b) apertural view 100µm
- 9. *Quinqueloculina* cf. *Q. villafranca* (Le Calvez, J. & Y.) a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 10. *Quinqueloculina* aff. *Q. villafranca* (Le Calvez, J. & Y.) a) side view 100μm, b) side view 100μm, c) apertural view 100μm
- 11. Quinqueloculina aff. Q. wiesneri (Parr) a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 12. Quinqueloculina sp. 1 a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 13. Quinqueloculina sp. 2 a) side view 50μm, b) side view 50μm, c) apertural view 50μm
- 14. Quinqueloculina sp. 3 a) side view 50µm, b) apertural view 50µm
- 15. Quinqueloculina sp. 4 a) side view 50µm
- 16. *Quinqueloculina* sp. 5 a) side view 50μm, b) apertural view 50μm
- 17. Quinqueloculina sp. 6 a) side view 100μm, b) apertural view 50μm

- 1. Quinqueloculina sp. 7 a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- 2. Quinqueloculina sp. 8 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 3. Quinqueloculina sp. 9 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 4. Affinetrina planciana (d'Orbigny) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 5. *Biloculinella labiata* (Schlumberger) side view 50µm
- 6. *Mesopateoris* sp. 1 a) apertural view 100µm ,b) side view 100µm
- 7. Milionella dilatata (d'Orbigny) a) side view 50µm ,b) side view 50µm ,c) apertural view 50µm
- 8. Milionella dilatata (d'Orbigny) a) side view 50µm, b) apertural view 50µm
- 9. Miliolinella grata (Terquem) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 10. Miliolinella labiosa (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 11. Miliolinella labiosa (d'Orbigny) a) side view 100µm, b) apertural view 100µm
- 12. Miliolinella semicostata (Wiesner) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 13. Miliolinella trigonina (Wiesner) a) side view 100µm, b) apertural view 100µm
- 14. *Miliolinella* sp.1 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 15. Sigmamiliolinella australis (Parr) a) side view 50µm, b) apertural view 50µm
- 16. *Pseudomassilina* sp. 1 a) side view 100μm

- 1. *Pseudomassilina* sp. 1 a) side view 50µm, b) apertural view 50µm
- 2. *Pseudomassilina* sp. 1 a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 3. Pseudotriloculina laevigata (d'Orbigny) a) side view 100µm, b) apertural view 50µm
- 4. *Pseudotriloculina* sp. 1 a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 5. *Pseudotriloculina* sp. 2 a) side view 25µm, b) side view 25µm, c) apertural view 25µm
- 6. *Pseudotriloculina* sp. 3 a) side view 50µm
- 7. *Pseudotriloculina* **sp. 4** a) side view 50µm, b) side view 50µm
- 8. *Pseudotriloculina* sp. 5 a) side view  $100\mu m$ , b) apertural view  $100\mu m$
- 9. Pseudotriloculina sp. 6 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 10. Pseudotriloculina sp. 7 a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 11. Pseudotriloculina sp. 8 a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 12. Triloculina adriatica Le Calvez, J. and Y. a) front view 100µm, b) apertural view 100µm
- 13. Triloculina adriatica Le Calvez, J. and Y. a) front view 100µm
- 14. Triloculina asymmetrica Said a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 15. Triloculina asymmetrica Said a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 16. Triloculina plicata Terquem a) side view 100µm, b) side view 100µm, c) apertural view 100µm

- 1. Triloculina terquemiana (Brady) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 2. Triloculina tricarinata d'Orbigny a) side view 100µm, b) apertural view 100µm
- 3. Triloculinella sp. 1 a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 4. Varidentella sp. 1 a) side view 50µm, b) side view 25µm
- 5. Sigmoilinita costata (Schlumberger) a) side view 100µm, b) apertural view 100µm
- 6. *Sigmoilinita var. S. costata* (Schlumberger) a) side view 50μm, b) side view 50μm, c) apertural view 50μm
- 7. Sigmoilinita grata (Terquem) a) side view 100µm, b) apertural view 100µm
- 8. Sigmoilinita sp. 1 a) side view 100µm, b) side view 100µm c) apertural view 50µm
- 9. Sigmoinella sp. 1 a) side view 100µm, b) side view 50µm
- 10. Sigmoinella sp. 1 a) side view 100µm, b) side view 50µm
- 11. Sigmoinella sp. 2 a) side view 100µm, b) side view 100µm
- 12. Sigmoinella sp. 2 a) side view 100µm, b) side view 100µm
- 13. Sigmoinella sp. 2 a) side view 100µm, b) apertural view 100µm
- 14. Articulina carinata Wiesner a) side view 100µm, b) apertural view 100µm
- 15. *Parrina bradyi* (Milieu) a) side view 100μm, b) apertural view 100μm
- 16. Parrina bradyi (Milieu) a) side view 100µm
- 17. Laevipeneroplis karreri (Wiesner) a) side view 100µm, b) apertural view 50µm
- 18. *Peneroplis pertusus* (Forskal) a) side view 100µm, b) apertural view 100µm
- 19. Peneroplis pertusus (Forskal) a) side view 100µm, b) apertural view 100µm
- 20. Peneroplis planatus (Fichtel and Moll) a) side view 100µm, b) apertural view 100µm
- 21. Sorites orbiculus Ehrenberg a) side view 100µm, b) apertural view 100µm

- 1. *Botuloides*? **sp. 1** a) side view 100µm, b) apertural view 50µm
- 2. Dentalina subarcuata (Montagu) a) apertural view 50µm, b) side view 50µm
- 3. Laevidentalina filiformis (d'Orbigny) a) side view 50µm, b) apertural view 50µm
- 4. Laevidentalina filiformis (d'Orbigny) a) apertural view 50µm, b) side view 100µm
- 5. Laevidentalina sp. 1 a) apertural view 50µm, b) side view 100µm
- 6. *Laevidentalina* sp. 2 a) side view 100µm, b) apertural view 100µm
- 7. Dentalinoides ? sp. 1 a) side view 50µm, b) apertural view 50µm, c) basis 50µm
- 8. Lenticulina gibba (d'Orbigny) a) side view 100µm, b) apertural view 50µm
- 9. Lenticulina gibba (d'Orbigny) a) side view 50µm, b) apertural view 50µm
- 10. Lenticulina orbicularis (d'Orbigny) a) side view 100µm, b) apertural view 50µm
- 11. Lenticulina sp. 1 a) side view 100 $\mu$ m, b) apertural view 50 $\mu$ m
- 12. Lenticulina sp. 2 a) side view  $50\mu m$ , b) apertural view  $50\mu m$
- 13. Lagena striata (d'Orbigny) a) side view 100µm, b) apertural view 50µm
- 14. Lagena striata (d'Orbigny) a) side view 50µm
- 15. Lagena strumosa Reuss a) side view 50µm, b) apertural view 50µm
- 16. Lagena sp. 1 a) side view 50µm, b) apertural view 25µm
- 17. Pygmaeoseistron ? sp. 1 a) side view 100µm, b) apertural view 50µm
- 18. Polymorphina sp. 1 a) side view 50µm, b) apertural view 50µm
- 19. Sigmoidella sp. 1 a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- 20. Fissurina lucida (Williamson) a) side view 50µm, b) apertural view 50µm
- 21. *Fissurina* sp. 1 a) side view 50µm, b) apertural view 50µm
- 22. *Parafissurina* sp. 1 a) side view 50µm, b) apertural view 50µm
- 23. Bolivina pseudoplicata Heron-Allen and Earland a) side view 50µm, b) apertural view 50µm
- 24. Brizalina aff. B. pygmae (Brady) a) side view 50µm, b) apertural view 50µm
- 25. Brizalina spathulata (Williamson) a) side view 50µm, b) apertural view 50µm

- 1. Brizalina dilatata (Reuss) a) side view 50µm, b) apertural view 50µm
- 2. Brizalina dilatata (Reuss) a) side view 50µm, b) apertural view 25µm
- 3. Brizalina striatula (Cushman) a) side view 25µm, b) apertural view 25µm
- 4. *Brizalina striatula* (Cushman) a) side view 25µm, b) apertural view 25µm
- 5. Brizalina aff. B. striatula (Cushman) a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 6. Brizalina sp. 1 a) side view 50µm
- 7. Cassidulina laevigata d'Orbigny a) side view 50µm
- 8. Globocassidulina subglobosa (Brady) a) side view 50µm, b) side view 50µm
- 9. Stainforthia concava (Höglund) a) side view 50µm, b) side view 50µm
- 10. Loxostomina ? limbata (Brady) costulata (Cushman) a) side view 100µm, b) apertural view 50µm
- 11. *Loxostomina* sp. 1 a) side view 100µm, b) apertural view 50µm
- 12. Loxostomina sp. 2 a) side view 50µm, b) apertural view 25µm
- 13. Rectuvigerina phlegeri Le Calvez a) side view 50µm, b) apertural view 25µm
- 14. *Bulimina aculeata* d'Orbigny side view 50µm
- 15. Bulimina elongata d'Orbigny side view 100µm
- 16. Bulimina marginata d'Orbigny side view 50µm
- 17. *Bulimina* sp. 1 a) side view 50µm, b) apertural view 50µm
- 18. *Praeglobobulimina* sp.1 a) side view 100µm
- 19. Protoglobobulimina pupoides (d'Orbigny) a) side view 50µm
- 20. Buliminella elegantissima, d'Orbigny a) side view 50µm, b) side view 50µm, c) side view 50µm
- 21. Uvigerina mediterranea Hofker a) side view 50µm, b) apertural view 50µm
- 22. Angulogerina angulosa (Williamson) a) side view 50µm, b) side view 50µm, c) apertural view 50µm
- 23. Reussella spinulosa (Reuss) a) side view 100µm, b) side view 100µm, c) apertural view 50µm
- 24. Reussella spinulosa (Reuss) a) side view 50µm, c) apertural view 50µm

- 1. *Mimosina affinis* Millett a) side view 50µm, b) side view 50µm
- 2. Fursenkoina aff. F. pauciloculata (Brady) a) side view 50µm, b) side view 50µm, c) side view 50µm
- 3. *Fursenkoina* sp.1 a) side view 50µm, b) side view 50µm, c) apertural view 100µm
- 4. Valvulineria bradyana (Fornasini) a) side view 100µm, b) side view 100µm, c) apertural view 100µm
- 5. *Pleurostomella* ? sp. 1 a) side view 25µm, b) apertural view 25µm
- 6. *Eponides concameratus* (Williamson) a) side view 100µm, b) side view 100µm
- 7. Gavelinopsis praegeri (Heron-Allen and Earland) a)dorsal view 100 µm, b) umbilical view 50 µm
- 8. Neoconorbina terquemi (Rzehak) a) dorsal view 100 µm, b) umbilical view 50 µm, c) edge view 100 µm
- 9. *Neoconorbina terquemi* (*Rzehak*) a) dorsal view 100 μm, b) edge view 100 μm
- 10. *Rosalina* cf *R. anomala* Terquem a) dorsal view 100 μm, b) umbilical view 100 μm, c) edge view 100 μm
- 11. *Rosalina bradyi* (Cushman) a) dorsal view 100 μm, b) umbilical view 100 μm
- 12. Rosalina floridensis (Cushman) a) dorsal view 100 µm, b) edge view 100 µm, c) umbilical view 100 µm
- 13. *Rosalina macropora* (Hofker) a) dorsal view 100 μm, b) umbilical view 100 μm
- 14. Rosalina obtuse ? d'Orbigny a) dorsal view 100 µm, b) umbilical view 100 µm
- 15. Rosalina orientalis (Cushman) a) spiral side 100μm, b) umbilical view 100 μm
- 16. *Rosalina vilardeboana* d'Orbigny) a) spiral side 100μm, b) umbilical view 100 μm, c) peripheral view 100 μm
- 17. *Tretomphalus bulloides* (d'Orbigny) a) spiral side 100μm, b) specimen with balloon chamber 100μm, c) balloon chamber with rimed apertures 100μm
- Conorbella imperatoria (d'Orbigny) a) spiral side 100μm, b) umbilical view 50 μm, c) peripheral view 50 μm

- 1. Conorbella patelliformis (Brady) a) side view 50µm, b) dorsal view 50µm, c) apertural view 50µm
- 2. *Glabratella erecta* (Sidebottom) a) oblique side view 50µm, b) apertural view 50µm
- 3. *Glabratella hexacamerata* Seiglie and Bermudez a) peripheral view 50μm, b) spiral side 50μm, c) apertural view 50μm
- 4. Siphonina reticulata (Czjzek) a) side view 50µm, b) apertural view 50µm
- 5. *Eilohedra* aff. *E. vitrea* (Parker) a) side view 25µm, b) side view 25µm
- 6. *Discorbinella bertheloti* (d'Orbigny) a) umbilical side 100μm, b) spiral side 100μm, c) peripheral view 100μm
- 7. Cibicides advenum (d'Orbigny) a) umbilical side 100µm, b) peripheral view 100µm
- 8. Cibicides advenum (d'Orbigny) a) umbilical side 100µm, b) spiral side view 100µm
- 9. *Cibicides refulgens* Montfort a) umbilical side 100μm, b) spiral side view 100μm, c) peripheral view 100μm
- 10. *Cibicides* ? *mayori* (Cushman) a) umbilical side 100μm, b) spiral side view 100μm, c) peripheral view 100μm
- Lobatula lobatula (Walker and Jacob) a) umbilical side 100μm, b) spiral side view 100μm, c) peripheral view 100μm
- 12. *Paracibicides* sp. 1 a) spiral side 100µm, b) umbilical side 100µm, c) peripheral view 100µm
- 13. Cyclocibicides vermiculatus (d'Orbigny) a) unattached side 100µm, b) peripheral view 100µm
- 14. *Planorbulina mediterranensis* d'Orbigny a) unattached side 100μm, b) attached side 100μm, c) peripheral view 100μm
- 15. Cibicidella variabilis (d'Orbigny) a) side view 100µm, b) peripheral view 100µm
- 16. Cibicidella variabilis (d'Orbigny) a) side view 100µm, b) side view 100µm
- 17. Cymbaloporetta sp. 1 a) dorsal view  $100\mu m$ , b) apertural view  $100\mu m$
- 18. Miniacina miniacea (Pallas) a) side view 100µm, b) side view 100µm

- 1. Asterigerinata adriatica Haake a) spiral side 50µm, b) umbilical view 50µm
- 2. Asterigerinata mamilla (Williamson) a) spiral side 50μm, b) umbilical view 50μm, c) peripheral view 50 μm
- 3. Amphistegina lobifera Larsen a) side view 100µm, b) side view 100µm, c) side view 100µm, d) peripheral view
- 4. Haynesina depressula (Walker and Jacob) a) side view 50µm, b) apertural face view 50µm
- 5. Haynesina sp. 1 a) side view 50µm, b) apertural face view 50µm
- 6. Haynesina sp.2 a) side view 100µm, b) side view 100µm, c) peripheral view 100µm
- 7. Nonionella stella (Cushman & Moyer) a) side view 50µm, b) side view 50µm
- 8. Nonionella turgida (Williamson) a) side view 50µm, b) side view 50µm
- 9. Nonionoides grateloupi (d'Orbigny) a) side view 50µm, b) side view 50µm, c) face view 50µm
- 10. Astrononion stelligerum (d'Orbigny) a) side view 50µm b) face view 50µm
- 11. Melonis pompilioides (Fichtel and Moll) a) side view 100µm, b) face view 100µm, c) face view 100 µm
- 12. Aubignyna planidorso (Atkinson) a) side view 50µm, b) umbilical side 50µm, c) peripheral view 50µm
- 13. Aubignyna planidorso (Atkinson) a) side view 50µm, b) umbilical side 50µm, c) peripheral view 50µm
- 14. *Buccella* sp. 1 a) umbilical side 100µm, b) spiral side 100µm, b) peripheral view 100µm

#### PLATE 16

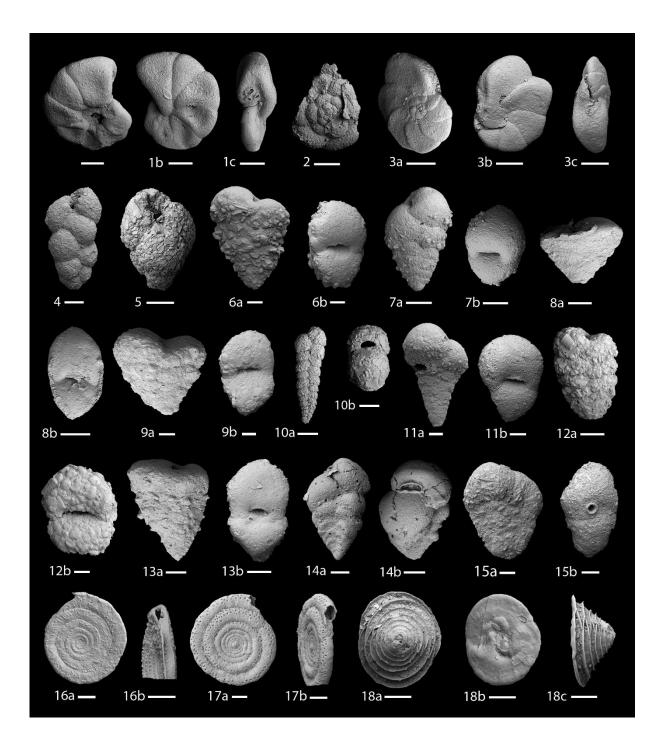
- 1. Ammonia beccarii (Linnaeus) a) spiral side 100µm, b) umblical side 100µm, c) peripheral view 100µm
- 2. Ammonia inflata (Seguenza) a) spiral side 100µm, b) umblical side 100µm, c) peripheral view 100µm
- 3. *Ammonia parkinsoniana* (d'Orbigny) a) spiral side 50µm, b) umblical side 50µm, c) peripheral view 50µm
- 4. Ammonia tepida (Cushman) a) spiral side 50µm, b) umblical side 50µm, c) peripheral view 50µm
- 5. Ammonia sp. 1 a) spiral side 50µm, b) umblical side 50µm, c) peripheral view 50µm
- 6. *Elphidium aculeatum* (d'Orbigny) a) side view 100µm, b) face view 100µm
- 7. *Elphidium* cf. *E advenum* (Cushman) a) side view 100µm, b) face view 100µm
- 8. Elphidium crispum (Linnaeus) a) side view 100µm, b) face view 100µm
- 9. Elphidium cf. E. gerthi van Voorthuysen a) side view 50µm, b) face view 50µm
- 10. Elphidium jenseni (Cushman) a) side view 50µm, b) peripheral view 50µm, c) face view 50µm
- 11. *Elphidium jenseni* (Cushman) a) side view 100µm, b) peripheral view 100µm
- 12. Elphidium macellum (Fichtel and Moll) ) a) side view 50µm, b) face view 50µm
- 13. *Elphidium macellum* (Fichtel and Moll) ) a) side view 50µm, b) face view 50µm
- 14. *Elphidium macellum* (Fichtel and Moll) ) a) side view 50µm, b) face view 50µm
- 15. *Elphidium macellum* (Fichtel and Moll) ) a) side view 100µm, b) face view 100µm
- 16. Elphidium macellum (Fichtel and Moll) ) a) side view 100µm, b) face view 100µm
- 17. Elphidium namibium /advenum a) side view 100µm, b) peripheral view 100µm

- 1. *Elphidium translucens* Natland a) side view 50µm, b) peripheral view 50µm
- 2. *Elphidium williamsoni* Haynes a) side view 50µm, b) peripheral view 50µm
- 3. *Elphidium* sp. 1 a) side view 50µm, b) peripheral view 50µm
- 4. *Elphidium* sp. 2 a) side view 50µm, b) peripheral view 50µm
- 5. *Elphidium* sp. 3 a) side view 50µm, b) peripheral view 50µm
- 6. *Porosononion granosum* (d'Orbigny) a) side view 50µm, b) peripheral view 50µm
- 7. Porosononion aff. P. granosum (d'Orbigny) a) side view 50µm, b) peripheral view 50µm
- 8. Porosononion aff. P. granosum (d'Orbigny) a) side view 100µm, b) peripheral view 100µm
- 9. Porosononion aff. P. simplex (Cushman) a) side view 100µm, b) peripheral view 50µm
- 10. *Porosononion* sp. 1 a) side view 50µm, b) peripheral view 50µm
- 11. *Porosononion* sp. 1 a) side view 50µm, b) peripheral view 50µm
- 12. *Porosononion* sp. 2 a) side view 50µm, b) peripheral view 50µm

## 5ŀ 2b -5a -1a -1b **-**2a -5c 4 3 7b -8b -9a -9b -6b **-**7a -6a -8a -10a **-**10b -11a **–** 11b 🗕 12a **-**12b **–** 13a 🗕 13b -18a -19a 16a • 17a -15• 16b -17b -19b -18b• 20b -20d 20e -20c -14 20a 21b 24b 21a 🗕 22a 22b 🗕 23a 🗕 24a -25a -25b **-**

# Plates 1-17

PLATE 1



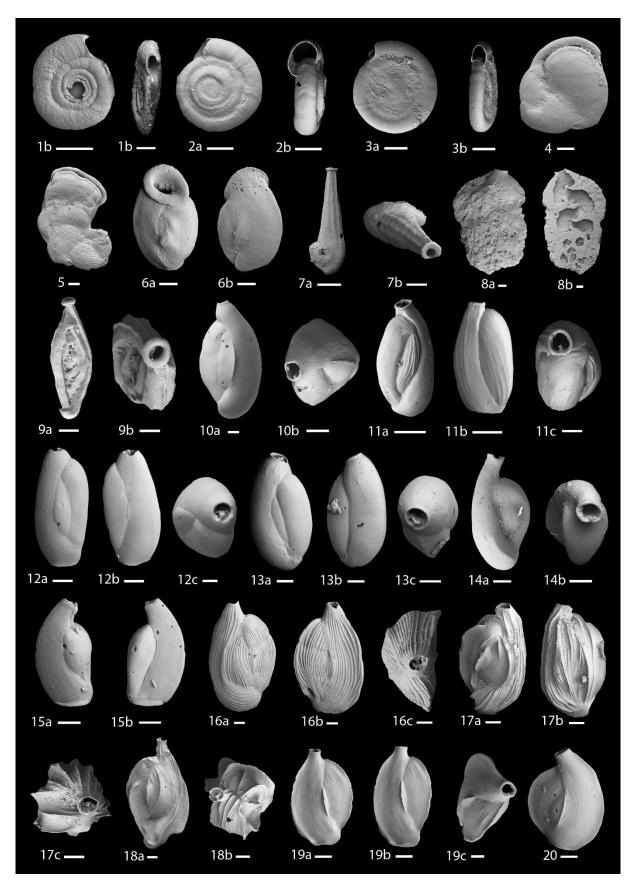


PLATE 3

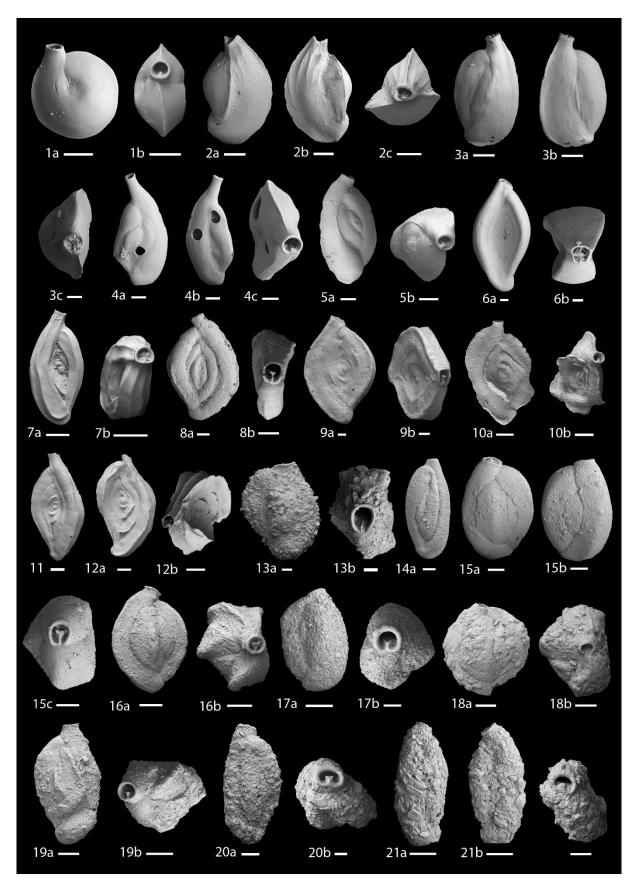
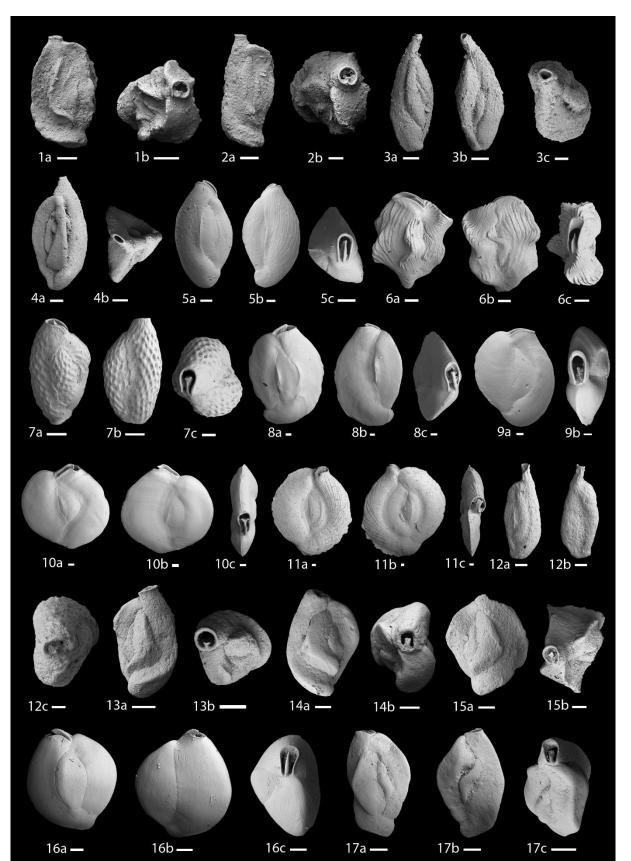
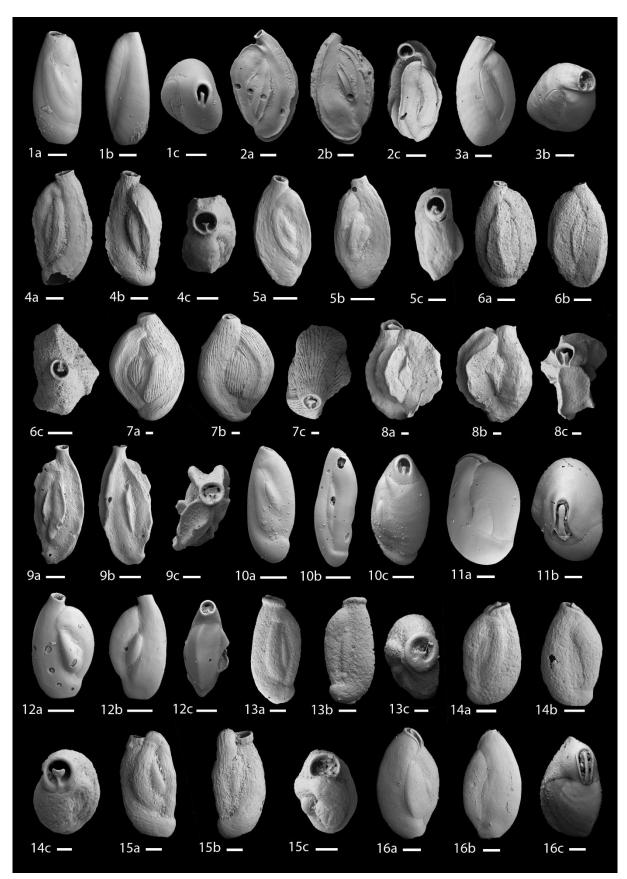


PLATE 4





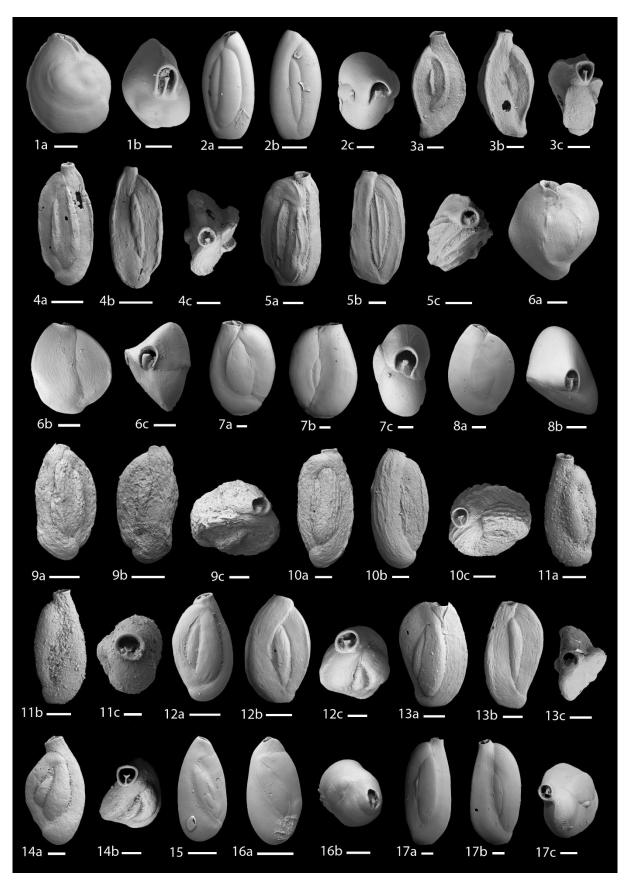
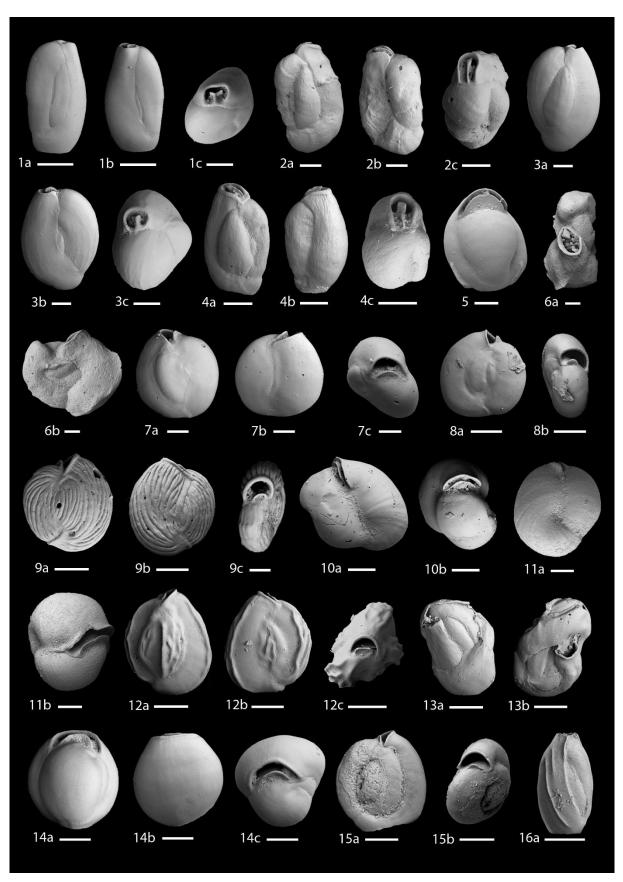
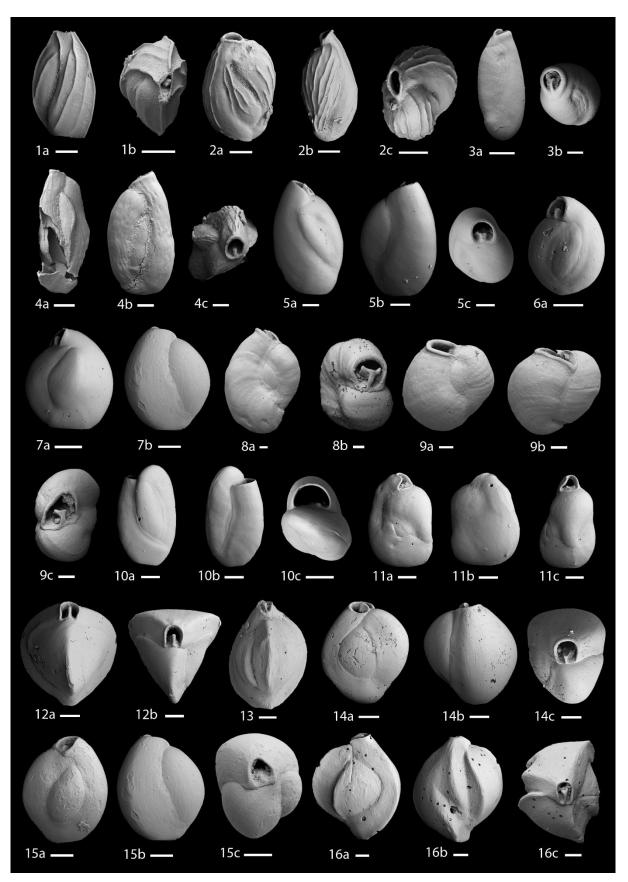


PLATE 7





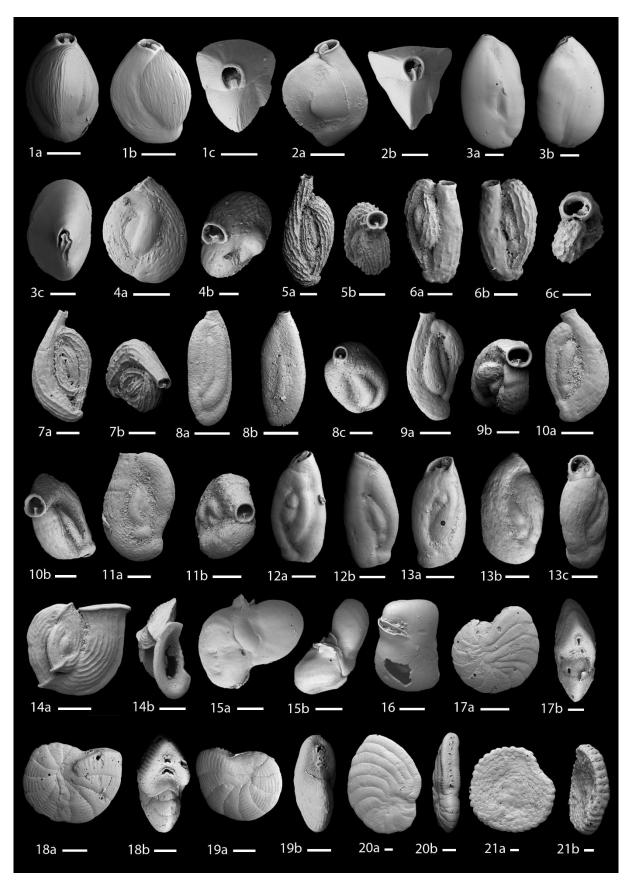


PLATE 10

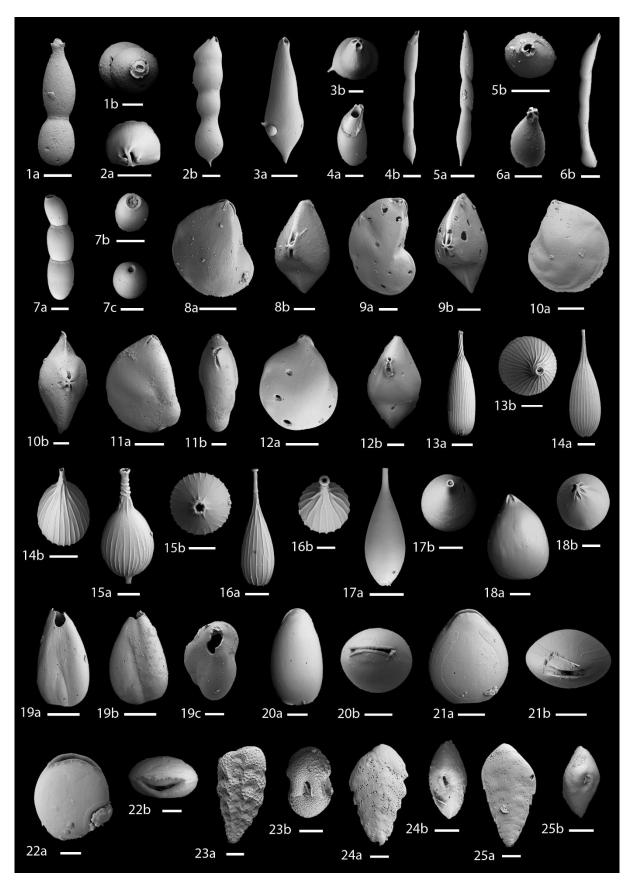


PLATE 11

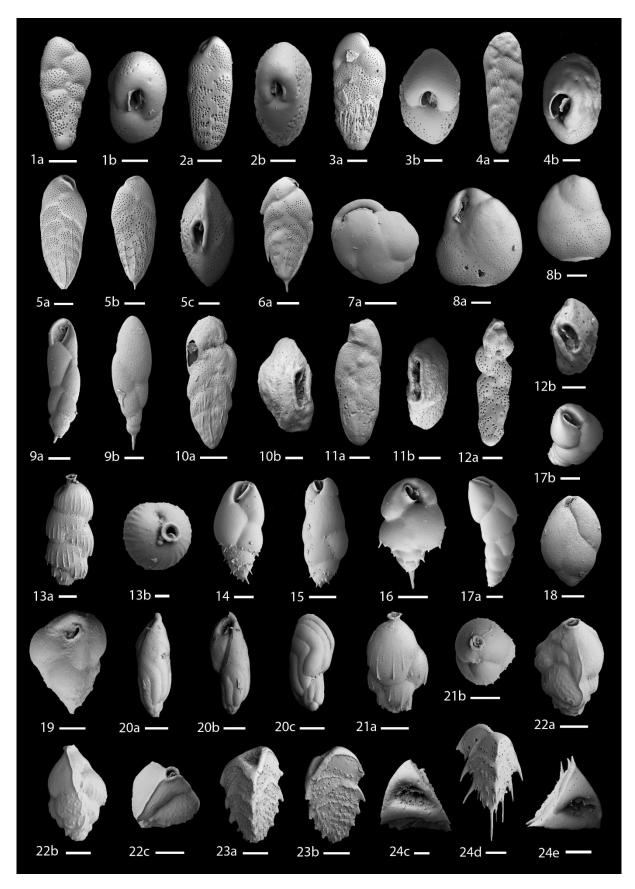


PLATE 12

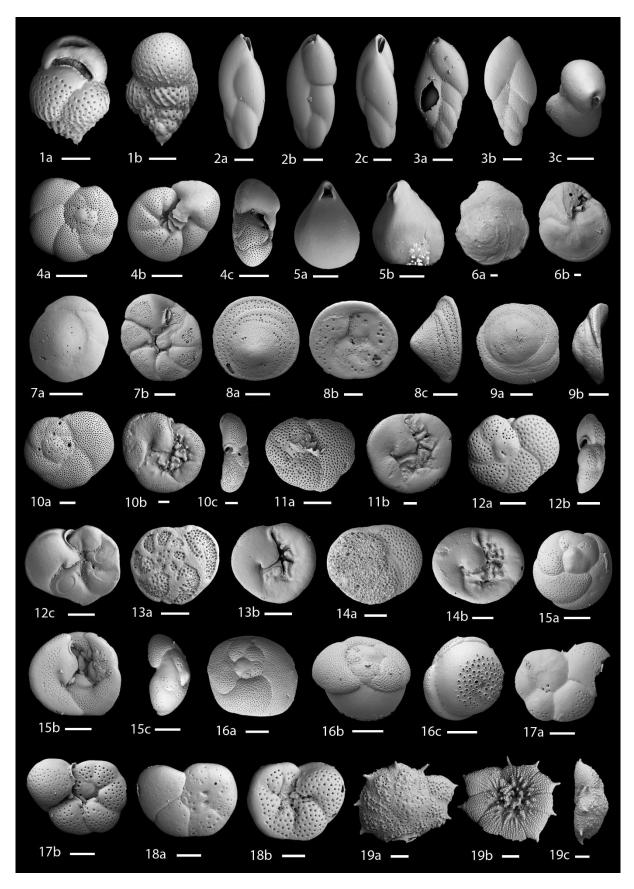


PLATE 13

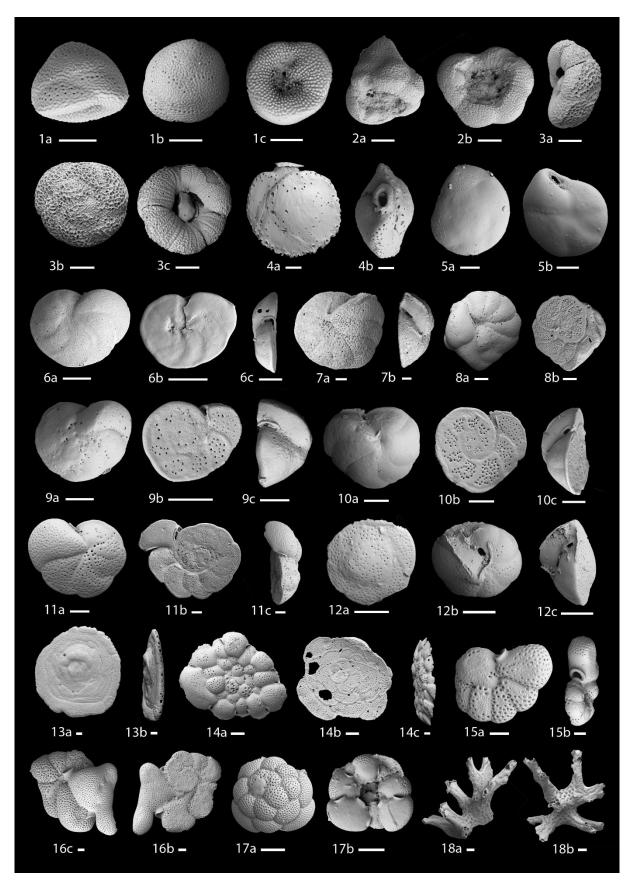
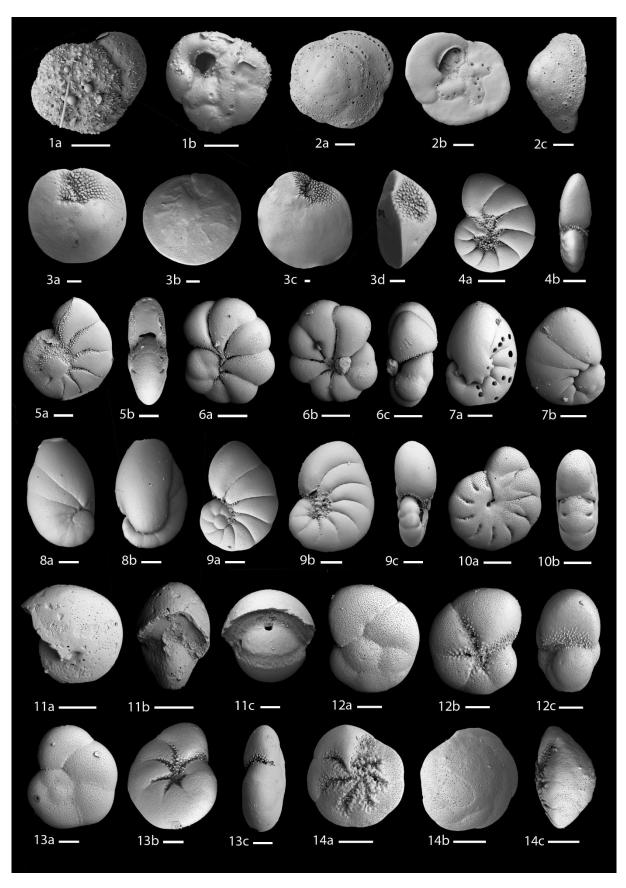
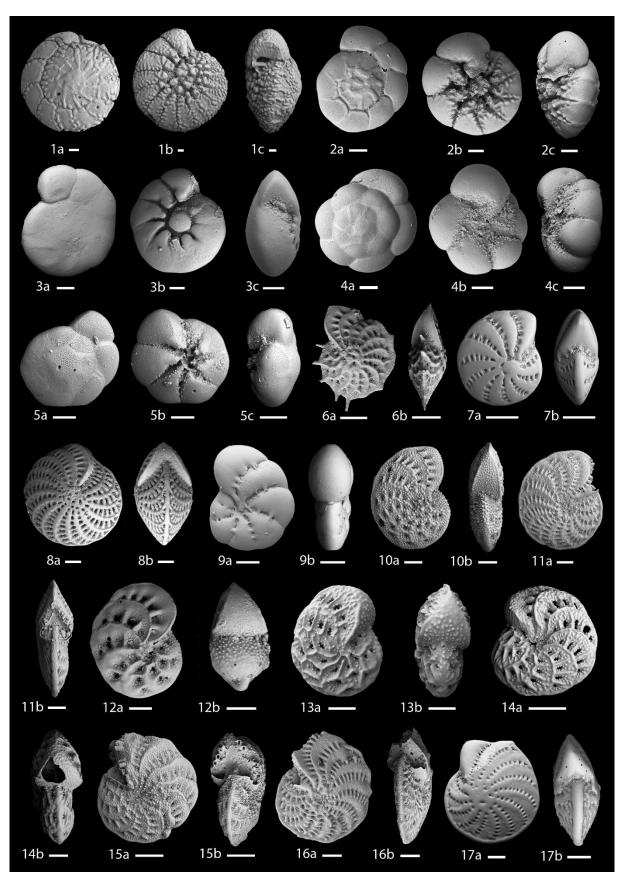
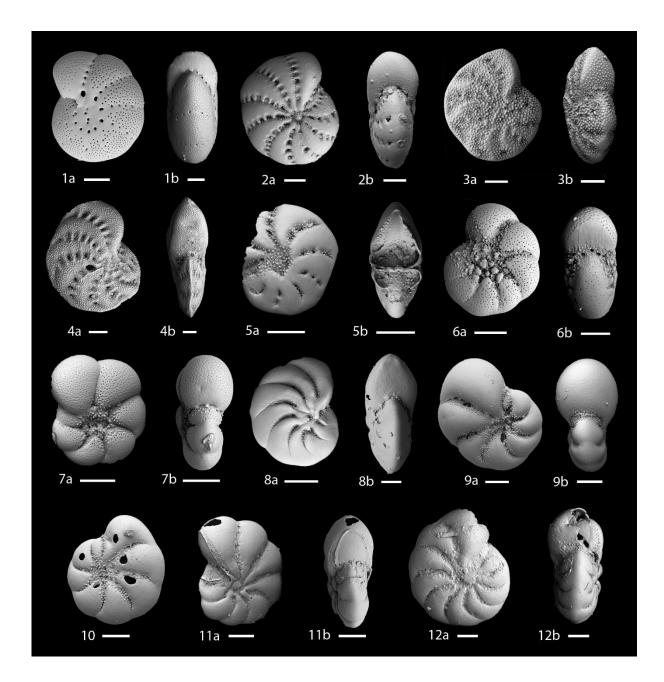


PLATE 14







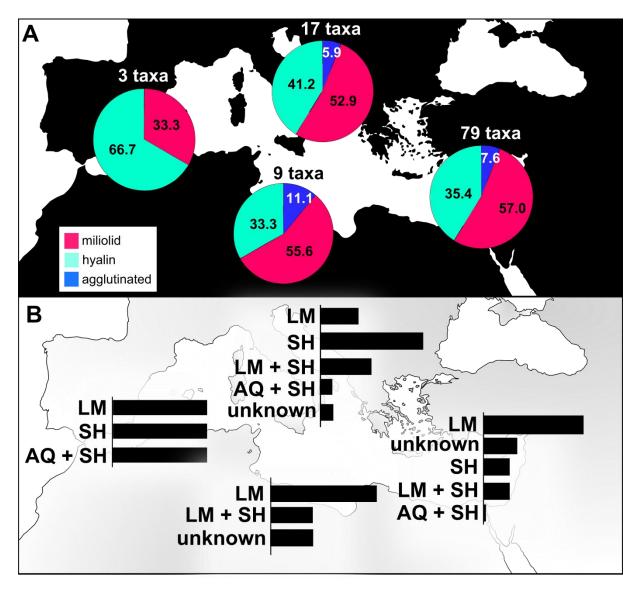
### **Part 4 Conclusions**

#### 4.1 Non-indigenous and cryptogenic benthic foraminifera in the Mediterraean Sea

In recent years, the numbers of NI foraminiferal species, especially in the eastern Mediterranean basin, has been increasing. The most comprehensive foraminiferal alien species lists were provided by Zenetos et al. (2008, 2010, 2012) and the European Alien Species Information Network (EASIN; https://easin.jrc.ec.europa.eu/). As indicated in the introduction, both lists are not consistent, so that the Zenetos et al. (2008, 2010, 2012) lists contain foraminiferal species lacking on the EASIN list and vice versa. Another difference is due to synonymy, so that species under different synonyms are sometimes listed twice on one list. Combining all reported introduced foraminifera for the Mediterranean Sea (Zenetos et al. 2008, 2011, 2012; EASIN data from 2016), as well as species recorded in this thesis reveal a total of 83 species within 59 genera (Appendix 7.4-7.6). Miliolid foraminfera are found to be the most abundant introduced foraminifera (47 species, 56.6%), followed by perforate (31 species; 37.3%) and agglutinated species (6 species; 7.2%). Larger symbiont-bearing foraminifera (17 species) represent up to 20.4% among all introduced foraminifera, whereas elphidiids (2 species), which are known to sequester chloroplasts represent 2.4%. Summarizing all alien and cryptogenic foraminifera, reveal a total of 79 species (95.2%) in the Eastern Mediterranean Sea, 9 species (10.8%) in the central Mediterranean Sea, 3 species (3.6%) in the Western Mediterranean Sea and 17 species (20.5%) for the Adriatic Sea (Fig. 1A). Cryptogenic foraminifera represent 6.0% among all NI foraminifera (0.6% of the entire foraminiferal biota) whereas 94% are characterized as NI species (10% among the whole Mediterranean foraminiferal fauna). Taking into account the numbers of all foraminifera present in the Mediterranean Sea (around 700 species; Langer, 2008a including all alien and cryptogenic species= 783), including new detetected species in this thesis, alien and cryptogenic foraminifera represent up to 10.6% of the whole foraminiferal fauna (Fig. 1A; Appendix 7.5.1, Table 1). Invasive benthic foraminifera built 2.4 % among all NI foraminifera and 0.3% among the whole Mediterranean foraminifera. The majority of new arriving exotic foraminifera occur in low to moderate percent abundances so that they already constitute a significant part within native foraminiferal assemblages. Most of the NI foraminifera present in the Mediterranean Sea are assumed to be Lessepsian migrants (primary), whereas shipping is the second most important introduction pathway, followed by aquaculture (Fig. 1B; Appendix 7.5.2, Table 2). But it is difficult to distinguish Lessepsian migrants from ship transported foraminifera, or ship transported foraminifera from species introduced by aquaculture. Nearly all classifications are assumptions due to spatial distribution patterns and nearby located canals or pathways (apparently providing introduction pathways). Molecular investigations, such as those conducted by Merkado et al. (2013) and Schmidt et al. (2015, 2016b) confirming the molecular homogeneity of invasive Mediterranean symbiont-bearing species (specimens from the eastern Mediterranean and Crete) with individuals from the Red Sea, may solve uncertainties, such as the question of one or several source origins displaying reliable introduction pathways.

It has to be taken into consideration that these data apply solely to littoral (intertidal and subtidal) areas as deep sea sites (bathyal to hadal) were not examined in terms of NI foraminiferal species to date. It also remains to be seen if and to what extend thermophilic species will invade into deep sea environments, as water temperatures there are generally lower than in shallow-water sites and foraminiferal species with endosymbionts are dependent on the photic zone. But studies show that continuously increasing temperatures of deep water in the Western and Eastern Mediterranean Sea are referred to increasing greenhouse gas emissions (Bethoux et al. 1990; Rixen et al. 2005). Climate driven ecosystem disturbances (such as anomalous increases in summer temperatures by 2-3°C) already deepens the thermocline in the western Mediterranean, leading to mass mortality events of the benthic fauna (e.g. sponges and gorgonians) that inhabit hard substrates (Danovaro et al. 2001).

Disturbances such as changes to temperatures regimes and pollution in the recipient environment can increase the susceptibility of a community to arriving invaders (Stachowicz et al. 2002; Clark and Johnston, 2005). It has also been shown in many cases that biotic resistance is conferred by total species richness, suggesting that species rich communities use available space and resources more completely and efficiently (Stachowicz et al. 1999; Olyarnik et al. 2009; Elton, 1958). New arriving thermophilic species may therefore be able to colonize the shallow and deep waters and the invasibility may be increased in this area due to the climatie driven disturbances.



**Fig. 1** Contribution of alien and cryptogenic benthic foraminifera in the Mediterranean Sea (after Zenetos et al. 2008, 2010, 2012, EASIN 2016 and thesis data). (A) Numbers of alien and cryptogenic benthic foraminiferal taxa and percent abundances of miliolid, hyaline and agglutinated taxa in the 4 sub-regions (Western MS, Eastern MS, Central MS, Adria) of the Mediterranean Sea, (B) percentages of alien and cryptogenic benthic foraminifera known or likely to be introduced by each of the main pathways by sub-region (LM = Lessepsian migrant, SH = shipping, AQ = Aquaculture, unknown).

Another aspect attributed to elevated SST is the increase in phytoplankton biomass. Apart from the fact that direct effect of warming on plankton manifests in increasing metabolic rates (of both phytoplankton and zooplankton), and a growing imbalance between photosynthesis and respiration rates as temperatures increases (Lewandoweska et al. 2014; Chapter 1.4), in the first instance an increase in phytoplankton biomass may increase the abundance of foraminiferal species, independent

if native or non-native. Because phytoplankton (such as diatoms) belongs to foraminiferal diet, an increase may favor newly introduced foraminiferal species to establish at a faster rate. An example where high phytoplankton biomass increases the numbers of foraminifera can be found around submarine springs and fountains along the seacoast of Turkey (Pamucak Cove/Gulf of Kusadasi and around Ilica Bay/Cape of Yildiz). Sea surface temperatures are very high in those areas, providing a high abundance of benthic foraminifera (Meric et al. 2010, 2011). Apart from native Mediterranean species and successful returnees (among others Laevipeneroplis karreri, Peneroplis pertusus, Peneroplis planatus and Sorites orbiculus) cryptogenic and NI foraminifera such as Amphistegina lobifera, Nodophthalmidium antillarum, Spiroloculina antillarum, Triloculina fichteliana, Euthymonacha polita, Coscinospira acicularis, Coscinospira hemprichii, Peneroplis arietinus, Amphisorus hemprichii and Cymbalporetta plana are observed around the springs with some reaching high percent abundances (Meric et al. 2010; 2011). A previous study (2008a) reported that the submarine springs found in the Aegean Sea create special ecological conditions, such as high water temperatures, distinct geochemical characteristics and high abundances of diatoms supplying a rich food source, which is affecting the native foraminferal fauna (Yokes and Meric, 2009). This may help alien species to establish stable local colonies before they get dispersed by currents (northwestwards). Increasing phytoplankton biomass due to warming of the upper ocean surface layers may therefore also have facilitated the relatively fast latitudinal and longitudinal migration of NI foraminiferal species since the opening of the Suez Canal in 1869. If the phytoplankton biomass declines, foraminifera are able to revert to different nutrition such as bacteria, fungi and detritus and in terms of larger-symbiont bearing species, they may temporary receive their nutrients from the endosymbiont.

Several kinds of pollution and ecosystem alteration are well-known anthropogenic influences on marine biodiversity (Cognetti and Cognetti, 1992). Bianchi and Morri (2000) advert, that this is even more obvious for the Mediterranean, a semi-closed basin experiencing heavy demographic, urban and industrial pressures (Introduction Chapter 1.3). Increasing pollution due to demographic increases along the eastern and central Mediterranean as well as Adriatic seacoasts may therefore increase the invasibility in these regions, which favors NI foraminifera as well as other NI taxa to establish and expand their distribution ranges.

So what makes an invader more successful than a resident species? The question is quite complex and will not be fully answered in this context here. However, the invasion process is likely to select for species that have a wide environmental tolerance because they must survive the process of entrainment and transport (Johnston et al. 2009). Studies have shown, that the conditions of invaders transported internally (ballast water, e.g foraminifera) or externally (hull fouling, e.g molluscs) by maritime vessels can be highly stressful (Wonham et al. 2001; Minchin and Gollasch, 2003). In addition to surviving high concentrations of heavy metals on the hulls and in the ballast tanks of vessels (Murphy

et al. 2002; Finnie, 2006; Hua and Liub, 2007), marine invaders may be exposed to physical hardships during an oceanic voyage caused by the ship's movement through the water and dramatic changes in the physico-chemical properties of the water body between geographical regions (Dafforn et al. 2009). Surviving such trips may enhance the invaders resilience. In general, within anthropogenic modified systems, many exotics may have an advantage over natives (Dafforn et al. 2009; Johnston et al. 2009), as natives are now existing in conditions different than those in which they have evolved (Dafforn et al. 2009). This has been called the "selection regime alteration" hypothesis, where exotics are in essence "preadapted" to conditions in recipient environments (Byers, 2002). The so called 'habitat-suitability' hypothesis suggests that successful introduction is more likely if species are matched with suitable environments (Willimason et al. 1986; Blackburn and Duncan, 2001). Furthermore, disturbances such as changes to temperature regimes, pollution and physical degradation in the

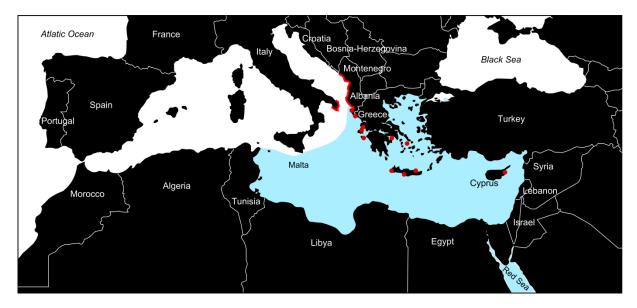
recipient environment can also increase the susceptibility of a community to arriving invaders (Lozon and MacIsaac, 1997; Stachowicz et al. 2002; Clark and Johnston, 2005; Crooks et al. 2011). Invasions may occur when the 'proper' combination of physical, chemical and biological or ecological variables occur, creating an 'opening' within an n-dimensional matrix for a species to enter a new region successfully (Carlton, 1996). Thus Johnston (1986) framed the concept of ,invasion windows', wherein one or more invasion , barriers' are removed. Although observational studies have shown the opposite (Marchetti et al. 2004; Fridley et al. 2004), Stachowicz et al. (1999, 2002a) and several other studies (among others Tilman, 1997; Giller et al. 2004; Hooper et al. 2005; Marraffini et al. 2015) found that biotic resistance is conferred by total species richness. Invasion success therefore decreased with increasing resident species richness because individual species were complementary in their temporal patterns of space occupation (Olyarnik et al. 2009). Temporal niches arise from seasonal differences in recruitment patterns of resident species at large scales (Stachowicz and Byrnes, 2006), so that even a brief window of open space (2 weeks) can increase invasion success by an order of magnitude (Stachowicz et al. 2002). It has often been observed that non-native species are relatively successful during early stages of community development (Lozon and MacIsaac, 1997). The degree of early invader success is (among other factors) therefore related to the degree of environmental degradation. If the new species has optimum performance at resource levels that overlap minimally with the residents, then it will have higher probability of successful invasion compared to other species with resource requirements more similar to the residents (Crooks et al. 2011). Marraffini et al. (2015) found that at most time points, communities with higher total resident species richness (native and NI species) received less recruitment, suggesting that both native and NI species richness contribute to a community's stability. Unfortunately no studies exist to date that examine these processes in terms of foraminifera. Anthropogenic induced disturbance through pollution may, however, not favor (NI) larger symbiont-bearing foraminiferal species as those species are indicative for high water quality and react sensitively to eutrophication or pollution.

Climate warming favors the range extension of NI foraminifera, as already observed for miscellaneous other NI taxa in the Mediterranean Sea (Introduction Chapters 1.4 and 1.5). Disregarding the impact of invasive foraminifera, recently increasing numbers of NI foraminiferal species in the Eastern Mediterranean Sea, which is considered as species poor, increases the foraminiferal diversity in this area. Available data for foraminiferal diversity in the Mediterranean Sea have shown that the centre of foraminiferal diversity is located in the Tyrrhenian Sea (580 species), whereas the eastern Mediterranean Sea is inhabited by a lower diversity (480 species; Langer, 2008a). With the numbers of NI foraminiferal species to date (83 species) the eastern Mediterranean basin is therefore slowly achieving the number of species of the centre of foraminiferal diversity. This may also increase the number of species in other Mediterranean Sea sub-basins. This could be especially important in future for the central Mediterranean foraminiferal diversity, as it displays the lowest species richness (280 species; Langer, 2008a) among all Mediterranean sub-regions.

### 4.2 The NW range extension and impact of *Amphistegina lobifera* on native foraminiferal assemblages in the Mediterranean Sea

The Mediterranean Sea is among those oceanic regions that are most affected by the ongoing warming trend. Among the key species that are currently expanding their biogeographic range are amphisteginid foraminifera, a group of symbiont-bearing and prolific carbonate producing protists. The numerical abundance and biogeographic range of invasive amphisteginids continues to increase in the eastern Mediterranean Sea and they were recently shown to rapidly expand their range to higher latitudes. The distribution and range expansion of amphisteginids is historically well documented and as such they are a particularly well suited genus to explore the scale, magnitude and impact of an

invasion on the composition and mixing of biotas. The new material collected from the NW range front show that amphisteginids have invaded shallow-waters of NW Greece (the Ionian Islands /Ithaka and Lefkada, Corfu) as well as the southern coast of Albania. Based on comprehensive data sets (global biogeographic data base of amphisteginid foraminifera; for details see Chapter 2 and 3) and new occurrence records in shallow-waters off Albania, the current range expansion front of amphisteginid foraminifera have been shown to run from the North African coast off Tunisia to the Pelagian Islands, Malta, and the southeastern coast of Sicily to Corfu (NW Greece) and the southern coast of Albania (Fig. 2 and 3).

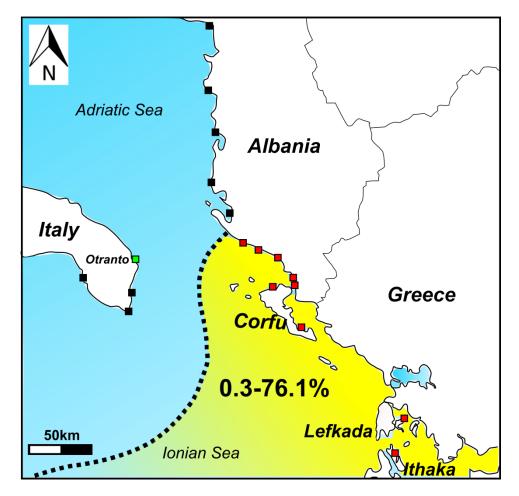


**Fig. 2** Map showing the current range extension of *A. lobifera* in the Mediterranean Sea (shaded in blue), red dots and lines mark the investigated areas in this thesis: coast of Albania, southern boot of Italy, sites in the Ionian (Corfu, Ithaka, Lefkada, Zakynthos), Aegean (Syros, Crete, Aegina) and Eastern Mediterranean Sea (Cyprus).

### 4.2.1 The current NW range expansion front of A. lobifera

The presence of *Amphistegina lobifera* in shallow-waters off Albania now provides the first evidence that amphisteginids have extended their range into the Adriatic Sea by crossing the Strait of Otranto, displaying the northernmost occurrence of this species (40.08°N). The absence along the southern boot of Italy, however, demonstrates that the invasion of amphisteginids progresses along the eastern side of the Adriatic Sea from the northern region around the island of Corfu (Greece) into Albania. The biogeographic range extension thus follows the major current system that transports warm water northwards into the Adriatic along the eastern coastlines and colder water southward along the eastern side of the Italian boot (see Fig. 1; sub-chapter 3 and reference Artegiani et al. 1996, 1997; Poulain, 1999, 2001). In addition, SST distribution shows that warmer waters are present on the eastern side of the Adriatic Sea driven by the inflow of a warm eastern current that originates in the Ionian Sea (Orlic et al. 1992; Artegiani, 1997; Poulain, 1999, 2001). The non-uniform colonization of the Adriatic thus provides further evidence that SST is a key environmental predictor driving the range extensions of symbiont-bearing amphisteginid foraminifera. The absence along the Adriatic coast of southern Italy also demonstrates that amphisteginid foraminifera did not yet underwent transportation via ship ballast water in this region. The observation of benthic foraminiferal assemblages from the Port of Otranto

already confirm the presence of NI foraminiferal species (such as *Euthymonacha polita, Spiroloculina antillarum* and *Loxostomina limbata costulata*) most probably introduced via ballast ship water (for details see Appendix 7.3).



**Fig. 3** Map showing the NW range expansion front of *A.lobifera* highlighted in yellow. Red squares show sample stations from the N Ionian and SE Adriatic Sea containing amphisteginid foraminifera (reaching 0.3-75% of the entire foraminiferal assemblage), black squares show sample stations along the Albania and Italian coast were amphisteginids are absent. Green square displays the Port of Otranto from the south-eastern boot of Italy inhabited by 3 NI foraminiferal species.

### 4.2.2 Key variables and current dispersal rates determining the extension of A. lobifera

The proliferation and recent range expansion rates of amphisteginid foraminifera provide strong support for previous species distribution models projecting the northward migration and invasion into the Adriatic Sea. The new records from Albania indicate a northwestward range shift rate of 10 km per year, slightly lower than the average range shift rate computed for the entire Mediterranean (12.5 km/year-1; Langer et al. 2012), but faster than previously prognosticated for the Adriatic Sea (~ 8.2 km/year-1; Weinmann et al. 2013b). This suggests that either the recent range expansion rate of 10 km per year has slightly increased over the last years or that computations of the previous range expansion calculations were too conservative. However, if the historical sample material from the Greek Island of Aegina (Chapter 3; Fig. 1) is taken as a reference point, than the average range shift is computed to be at around ~4 km per year (Aegina  $\leftarrow \rightarrow$  Albania; chapter 2.2).

The applied Species Distribution Model, based on currently recognized ecological niche constraints to identify potentially suitable and future habitats within the Mediterranean Sea (for details see Langer et

al. 2012; Weinmann et al. 2013b), predicted SST to be a key variable controlling the spatial distribution of symbiont-bearing amphisteginids (Zimiri et al. 1974; Langer and Hottinger, 2000; Langer et al. 2012). This corroborates with observations made along the NW range front that rising sea surface temperatures, isotherm shifts and warm currents are the most likely agents controlling the latitudinal extension. The winter minimum sea surface temperature was identified to be the key variable determining the latitudinal distribution of this taxon. Laboratory experiments of amphisteginid foraminifera have shown that they cease all movements below 13.8 °C (Zmiri, 1974). Its presence in the northern Aegean Sea and in the eastern Sea of Marmara, however, indicates an adaptation to water temperatures as low as 13.8 °C (Triantaphyllou et al. 2012) or even lower (Meric et al. 2001, 2005; Yokes and Meric, 2009). For the latter winter minimum temperatures were not documented. It has to be taken into consideration that Zmiri et al. (1974) tested the temperature tolerance in Amphistegina madagascariensis and Amphistegina radiata, so that A. lobifera may tolerate somewhat lower temperatures ( $<13.8^{\circ}$ C). A. lessonii has been shown to have a depth range limited by the thermocline, indicating a link between the area of distribution of this species with a minimum temperature of 16°C (Hollaus and Hottinger, 1997). The upper temperature limit for Mediterranean and Red Sea amphisteginids were demonstrated by Schmidt et al. (2016) revealing that eastern Mediterranean specimens show a significant reduction in growth at 36°C, while their counterparts in the Gulf of Aqaba already show increases at 34°C.

Although *Amphistegina* spp. are known to tolerate somewhat colder and more nutrient-rich waters (Langer and Hottinger, 2000; Langer, 2008a; Langer et al. 2013), the occurrences of *A. lobifera* in the southeastern Sea of Marmara are surprising and suggest not only an adaptation to lower SST than  $13.8^{\circ}$ C (SST may drop down to 7°C in January and February; seatemperature.info) but also an adaptation of amphisteginids to low salinity conditions and turbidity. Numerical abundances of amphisteginids plotted against salinity values at respective locations (globally) show that *Amphistegina* spp. (including *A. lobifera*) are generally are found in salinities ranging between 32 and 38 psu (Weinmann et al. 2013a). The distribution of shallow-water foraminiferal assemblages in the Sea of Marmara, however, is associated with surface inflow of the Black Sea, river discharges (additional freshwater and organic matter inputs) and salinity fluctuations due to seasonal vertical mixing (Kirci-Elmas and Meric, 2016), so that the upper layer salinity values range between 23 + 2ppt (reaching a maximum in winter) (Besiktepe et al. 1994). Foraminiferal assemblages in the Sea of Marmara generally are constituted of infaunal and epifaunal opportunistic and heterotrophic foraminifera (Kirci-Elmas and Meric, 2016) and the presence of living LBF (*A. lobifera*) have only been documented by Meric et al. (2005).

Climate warming and increasing SST, which facilitate the latitudinal and longitudinal migration of thermophilic NI foraminiferal species in the Mediterranean Sea, furthermore, are also accompanied by ocean acidification. As mentioned in the introduction (Introduction chapter 1.3) the Mediterranean Sea has been identified as important anthropogenic carbon storage, where the column inventory is much higher compared to the Atlantic or Pacific Oceans (Schneider et al. 2010; Lee et al. 2011). Ocean acidification may have severe consequences on calcifying organisms as declines in the concentration of carbonate ions in the water column reduce the fitness of calcifiers and consequently result in decreased abundances and lower species richness (Bambach, 1983; Fabry et al. 2008; Kuffner et al. 2008; Kroeker et al. 2010, 2013; Busch et al. 2013; Fabricius et al. 2014). However, it is not clear how increasing  $CO_2$  concentrations may affect ecosystem functioning in the future, because some calcifying and non-calcifying organisms (echinoids, Wood et al. 2008; coccolithophorids, Iglesias-Rodriguez et al. 2008; seagrasses, Hall-Spencer et al. 2008; some larger benthic foraminifera, Fujita et al. 2011) reacted to increased  $CO_2$  partial pressures by increased rates of calcification, photosynthesis and regeneration.

Benthic foraminifera show different responses to low pH conditions (Le Cadre et al. 2003; Kuroyanagi et al. 2009; Allison et al. 2010; Dissard et al. 2010; Fujita et al. 2011; McIntyre-Wressing et al. 2011; Haynert et al. 2012; Vogel and Uthicke, 2012; Uthicke and Fabricius, 2012; Glas et al. 2012). Most of the laboratory studies showed decreases in calcification in symbiont-free foraminifera (Le Cadre et al. 2003; Allison et al. 2010; Dissard et al. 2010; Haynert et al. 2012), while larger symbiont-bearing species show more variable responses (Fujita et al. 2011; Vogel and Uthicke, 2012; Uthicke and Fabricius, 2012; McIntyre-Wressing et al. 2011, Robbins et al. 2016).

Phototrophic marine calcifiers (such as foraminifera, phytoplankton, calcareous algae and corals) elevate their external oxygen and pH microenvironment in daylight (the Diffusive Boundary Layer DBL), through the uptake of dissolved inorganic carbon (DIC) by photosynthesis, so that surface pH levels of phototrophic or photosymbiotic organisms can differ strongly (>0.1 pH units) from the surrounding seawater (Jörgensen and Revsbech, 1985; Shashar et al. 1993; Kühl et al. 1995; Rink et al. 1998; Wolf-Gladrow et al. 1999; De Beer and Lakum, 2001; Köhler-Rink and Kühl, 2000; Köhler-Rink and Kühl, 2005; Flynn et al. 2012; Glas et al. 2012). A laboratory study conducted by Glas et al. (2012) shows that O<sub>2</sub> and pH levels were significantly higher in symbiont-bearing species in light than in dark conditions and, than observed in symbiont-free foraminifera. It seem to be the surface pH and the resulting gradients within the organisms DBL, rather than the bulk seawater pH, which determine ion availability (Wolf-Gladrow et al. 1999) and consequently transport kinetics between the tissues and surrounding seawater (essential for all transport involving mechanisms such as calcification, photosynthesis or respiration; Glas et al. 2012). Microenvironmental pH dynamics are therefore likely to play an important role in physiological responses to ocean acidification (Glas et al. 2012). However, the findings of the study by Glas et al. (2012) indicate that photosynthesis can only to a minor extend compensate for ambient seawater pH decreases within the microenvironment of photosymbiotic foraminifera as pH at the cell surface decreased during elvevated pCO<sub>2</sub>, also during light incubations. Symbiont-free and photosymbiotic foraminifera are thus likely to experience strongly decreased microenvironmental pH conditions at future pCO<sub>2</sub>, making their cell bodies susceptible to the physiological effects of ocean acidification (Glas et al. 2012).

Volcanic vent systems that emit carbon dioxide from the sea floor at ambient seawater temperatures are not perfect predictors of future ocean ecology owing to temporal variability in pH, spatial proximity of populations unaffected by acidification and the unknown effects of other global changes in parameters such as temperature, currents and sea level (Riebesell 2008). However, such vents acidify sea water on sufficiently large spatial and temporal scales and thus serves as natural laboratories in which to study the long-term biological response to rising  $CO_2$  levels and lower pH values (Dias et al. 2010; Cigliano et al. 2010). Studies in open marine conditions in the Mediterranean reported significantly reduced numbers of calcareous benthic foraminiferal species (hyalines) and the complete absence of important wall structural types (miliolids) at elevated pCO<sub>2</sub> around volcanic vents in shallow-waters off the Island Ischia (Tyrrhenian Sea, Italy) (Dias et al. 2010; Cigliano et al. 2012). The examinations of Mediterranean benthic organisms such as foraminiferal assemblages along pH gradients at CO<sub>2</sub> vents off the coast of Ischia show that the foraminiferal distribution, diversity and nature of the fauna change markedly in the living assemblages as pH decreases (Dias et al. 2010; Cigliano et al. 2012). Similar findings were made around volcanic vents in shallow-waters off Panarea (Tyrrhenian Sea, Italy), were epiphytic foraminiferal assemblages at sites exposed to low pH values are characterized by the absence of miliolid foraminifera and just a low amount of hyaline species of small test sizes (manuscript in prep.). The increased resistance of hyaline species within their natural habitat to high pCO<sub>2</sub> conditions, compared to miliolid species, is likely due to differences in calcification mechanisms (ter Kuile et al. 1989a, b; Bentov et al. 2009; Glas et al. 2012), as well as solubility differences of the calcite tests (Plummer and Mackenzi, 1974; Berner, 1985), so that unaffected or increased calcification rates in hyaline (low Mg-calcite: less soluble) and decreased rates

in miliolid (high Mg-calcite: more soluble) species have been observed in response to elevated  $pCO_2$  in several studies (Uthicke and Fabricius, 2012; Kuroyanagi et al. 2009; Fujita et al. 2011; McIntyre-Wressing et al. 2011). This indicates large scale impacts on future ecosystem functioning of foraminiferal assemblages in the Mediterranean Sea with steadily rising  $CO_2$  values.

Erez (2003) reported that calcification rates in Amphistegina lobifera increased essentially linearly between pH 7.0 and ~8.3, levelling off then declining at pH 9. Further laboratory experiments have shown that low pH values (7.6) did not significantly impact the survival of amphisteginid foraminifera (McIntyre-Wressing et al., 2013). Although long term experiments should be conducted, the results of Erez (2003) and McIntyre-Wressing et al. (2013) suggest that ocean acidification might not influence the ongoing range expansion and future habitat suitability within the Mediterranean for this genus (Winmann et al. 2013b). Amphisorus hemprichii exhibited an exponential increase in calcification rates at pH between 7.0 and 9.5 (Erez, 2003). As Amphistegina and Amphisorus are the most invasive benthic foraminifera in the Mediterraean, and lower pH values do not significantly reduce their fitness (although A. hemprichii owns a miliolid wall structure), these species may take precedence over other foraminiferal species (smaller miliolids and hyaline species) with increasing CO<sub>2</sub> values in the Mediterranean Sea. Future range extensions and proliferations of especially amphisteginid foraminifera may therefore be also facilitated through disturbed ecosystem functioning in foraminiferal assemblages and higher invasibility of (new) invaded territories due to ocean acidification, which may increase the amount of monoculture formations as observed in Miocene amphisteginids in this area (see Chapter 4.2.4).

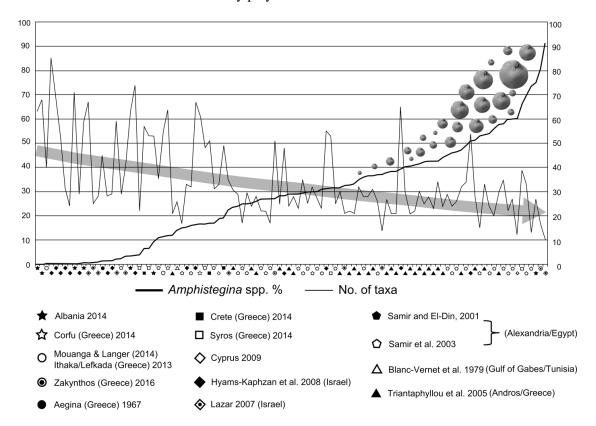
#### 4.2.3 The impact of A. lobifera on native foraminiferal biota and assemblage diversity

To what extent climate-induced range shifts will affect biotic ecosystems are not yet fully understood. Among the unresolved key issues of the rapidly progressing amphisteginid invasions is their impact on native foraminiferal biotas and assemblage diversity.

A comparison of species richness values and amphisteginid percent abundances at the collection sites along the NW range front (Ithaka, Lefkada, Corfu, southern Albania), as well as in collection sites within the Ionian (Zakynthos) and Aegean Sea (Syros, Crete) and Eastern Mediterranean Sea (Cyprus) show that native species richness is reduced at all sites invaded by amphisteginids and correlates with the degree of infestation. High abundance values of *Amphistegina* correlate with low species richness, while higher species richness correlates with low percent abundances of amphisteginid foraminifera. This is also quite visible in a negative correlation between amphisteginid increase and reduced Fisher  $\alpha$  and Shannon (H) indices (Chapter 2.1.5, Table 2; Chapter 2.2.4, Table 2). To place the new amphisteginid range expansion data in perspective a compilation of our data and further 110 sites from the eastern and central Mediterranean Sea (Fig 4, or Chapter 2.2.5, Fig. 4 with 124 sites) have been assessed. The compilation of all data suggests that species richness of foraminiferal biotas and the numerical abundances of invasive amphisteginids are intimately linked, and ultimately lead to the displacement of associated taxa. On average, overall foraminiferal diversity was reduced by more than 30%, when amphisteginid percentages attain values of more than 12-25%.

The examinations of Greek, Albanian and Cyprus amphisteginid invasions have shown that they selectively affect associated taxa of infested foraminiferal assemblages. Comparisons of amphisteginid foraminifera among all perforate species have shown that increasing numerical abundances of amphisteginids correlate with lower percent abundances of other hyaline taxa. Among the taxa that are primarily impacted are other epiphytic perforate trochospiral (e.g. *Rosalina*, *Discorbina*, *Asterigerinata*, *Lobatula*, *Cibicides*, *Eponides*, *Ammonia*, *Pattelina*) and planispiral species of

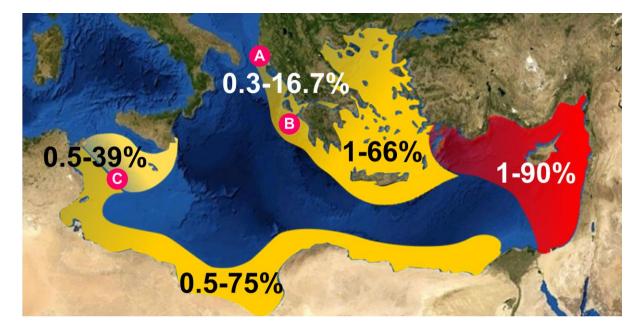
foraminifera (elphidiids). Amphisteginid foraminifera locally also seem to have a selective impact on other larger-symbiont bearing taxa (LBF), such as the native species Peneroplis pertusus, P. planatus and the successful returnee Sorites orbiculus. All these groups appear to share the same microhabitat as A. lessonii and A. lobifera, which were reported as epifaunal and epiphytic constituents from shallow water ecosystems (Langer, 1993; Hallock 1981; Hallock et al. 1988, 1999; Hohenegger, 1994; Hohenegger et al. 1999). The displacement of taxa from similar microhabitats suggests that competitive exclusion (through being a better exploiter of resources such as place and food) is a major driving force regulating species richness in invaded communities. Smaller non-symbiont bearing miliolid foraminifera appear to be less affected by amphisteginid invasions apparently due to their wider range of microhabitats. The effect on diversity is even more pronounced in those foraminiferal communities where amphisteginids make up more than 60% of the assemblage, leading to competitive exclusion. But amphisteginids have also shown to be dominant in new invaded habitats with locally severe consequences on native diversity and ecosystem functioning, as seen along the southern coast of Albania (for details see Chapter 2.2.5 and 3.1.5). Among all detected NI foraminiferal species along the coast of Albania, A. lobifera reaches the highest numerical abundance. Other NI foraminifera, however, settle in different macro- and microhabitats than Amphistegina, which may be due to different 'habitat suitabilitiys', so that competitive exclusion among those NI foraminiferal species can be excluded. The successful returnee Sorites orbiculus shows a decreasing numerical abundance with increasing rates of amphisteginids, which may indicate some competitive exclusion. It should be noted, however, that the displacement of native species may be of local nature and that natives may persist in nearby uninvaded areas. It is also not known, if amphisteginids are displacing any species other than foraminifera and what role they play in the food web of metacommunities.



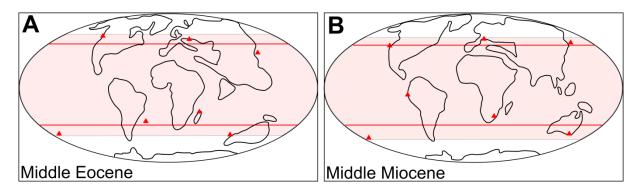
**Fig. 4** Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in 110 selected samples from the central and eastern Mediterranean Sea (including the new material from the Adriatic Sea, Appendix 7.7). Note the negative correlation and decrease in species richness with increasing abundances of amphisteginid foraminifera. The regression line is shown superimposed on the individual data points.

## 4.2.4 Abundance trends of *A. lobifera* in the Mediterranean Sea in relation to Miocene fossil occurrences

Analysis of foraminiferal assemblages along the NW range margin (NW Greece and Albania) and from sites where Amphistegina has long been established (eastern and central Mediterranean Sea) have shown that amphisteginids are continuously expanding their biogeographic range in the Mediterranean and have become the most abundant taxon at almost every site colonized. In sample sites situated at the NW range front (Ithaka, Lefkada, Corfu, southern Albania) amphisteginids generally attain percent abundances of 0.3-16.7% of the entire foraminiferal assemblage (apart from some exceptions mentioned below, Fig. 5), whereas the collection sites off Cyprus which is situated in the centre of invasion reveal percent abundances between 19-60% of the foraminiferal assemblage. Further unpublished data (from the Aegean and Ionian Sea: Syros, Crete, Zakynthos) have shown that amphisteginids reach likewise high percent abundances (4-81%) among the entire foraminiferal fauna. These data are consistent with literature data gathering the numerical abundances of amphisteginids in the eastern and (southern) central Mediterranean Sea. At many eastern Mediterranean sites amphisteginid foraminifera were reported to represent between 30 and 70% or even up to 97% of the total faunal assemblage (Hyams et al. 2002; Gruber et al. 2007; Lazar, 2007; Abu Tair and Langer, 2010; Abu Tair, 2011; Triantaphyllou et al. 2012; Langer et al. 2012; Caruso and Cosentino, 2014). Disregarding some exceptions (Fig. 5A-C; Monastiri Bay, 5m: 76%; Zakynthos, 10m: 81% Linosa Island, 6-11m: 79-97%) the impact of Amphistegina on native biotas gradually increases from the range expansion front towards those sites where infestations took place some decades ago. The state of impact is thus closely linked to the amount of time over which Amphistegina has been active but is also seem to be dependent on macro- and microhabitats present.



**Fig. 5** Map showing the percent abundance of amphisteginid foraminifera in the eastern and central Mediterranean Sea. Percent abundances in the eastern Mediterranean Sea as well as some locations in the central Mediterranean Sea (A-C) show, that amphisteginid foraminifera become extreme abundant locally. The sample sites A-C represent exceptional localities with high percentages of amphisteginids contrary to the in general lower percent ages along the range front (A) Gjiri Monastiri Bay (76.1%), (B) Zakynthos 81%, (C) Linosa Island 79-97%.



**Fig. 6** Fossil distribution ranges of larger foraminifera (based on Adams et al. 1990, modified after Weinmann, 2014). Triangles indicate occurrence records from the middle Eocene (a), middle Miocene (b). For details, see Adams et al. (1990). Red areas display fossil distribution ranges in relation to recent latitudinal ranges of *Amphistegina* spp. (solid red lines).

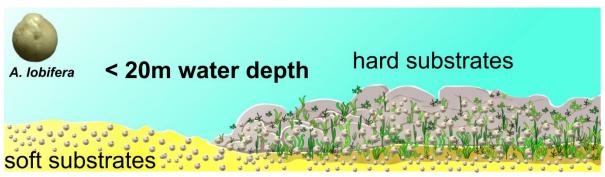
Fossil occurrences of amphisteginid foraminifera indicate a considerably wider latitudinal distribution during Eocene (from 48°N to 36°S) and Miocene times (48-50°N) (Todd, 1976; Fig. 6, recent distribution Chapter 1.8.2, Fig. 8F). At some of the Miocene localities amphisteginids formed thick amphisteginid marls (Fig 8D) similar to the amphisteginid sediments reported by Meric et al. (2008a) from Antalya and by Abu Tair and Langer from Cyprus (2010). Middle Miocene localities from the Weissenegg Quarry (Styrian Basin, Austria) show amphisteginid percent abundances to be between 8 and 24% of all benthic foraminifera (Hansen et al. 1987). These values are comparable to the percent abundance records of modern amphisteginids at the NW Mediterranean range front. In addition, associated foraminiferal faunal elements (elphidiids and various trochospiral taxa) indicate a faunal structure that is similar to modern range front assemblages. Percent abundances and faunal similarities of the Miocene records from Austria and Poland thus suggest a position that represents the northernmost range expansion front of amphisteginid foraminifera (see also Langer and Hottinger, 2000). The assemblages thus retain information that is useful in paleobiogeographic interpretations to assess the extent and magnitude of range shifts along the expansion front.

### 4.2.5 Amphisteginid habitat suitability and invader success in shallow-waters of the Mediterranean Sea

The new findings from the NW expansion front show that amphisteginids (especially A. lobifera) are particularly successful invaders in shallow-water habitats <20 m (Fig. 7). These sites are characterized by medium to coarse grained calcareous/siliceous sediments or by hard substrates/rocky shores that are densely covered by macroalgae or algal mats. Percent abundances of Amphistegina spp. at those sites generally range between 4.0 and 81%. The amount of amphisteginid foraminifera in water depth > 20m gradually decreases, reaching solely 0.3-1.2% of the foraminiferal fauna or they have shown to be absent. The proliferation of amphisteginid foraminifers in shallow-water sites agrees well with previous records from the eastern and central Mediterranean Sea (Samir and El-Din 2001; Hyams et al. 2002; Samir et al. 2003; Triantaphyllou et al. 2005, 2009, 2012; Gruber et al. 2007; Yokes et al. 2007; Lazar, 2007; Hyams-Kaphzan et al. 2008; Meric et al. 2008a, b; 2010; Yokes and Meric, 2009; Koukousioura et al. 2010, 2011; Caruso and Cosentino, 2014). Furthermore, this is also consistent with amphisteginid counterparts in the tropics, which preferentially live on hard and phytal substrates (seagrasses and algae), but are also distributed on carbonate rich coarse to medium grained soft substrates in 5-20m water depth (Hallock, 1981, 1988, 1999; Hohenegger, 1994; Hohenegger et al. 1999; Renema and Trolestra, 2001). The percent abundances of amphisteginids in these habitats often exceed the abundance values of all other foraminiferal species (irrespective if in their tropical places of origin or in the Mediterranean Sea). Extreme forms of ecosystem invasibility have been reported

from several shallow-water Mediterranean sites, where foraminiferal assemblages resemble monocultures of *Amphistegina* (Hyams et al. 2002; Samir et al. 2003; Gruber et al. 2007; Langer et al. 2012; Caruso and Cosentino, 2014; Mouanga and Langer, 2014; Yokes and Meric, 2004; Abu Tair and Langer, 2010; Langer and Mouanga, 2016; Fig. 5 or Chapter 1 Fig. 7B-E).

The impact of amphisteginid foraminifera in shallow-water environments where habitat invasibility is documented by high numerical abundances and associated with a reduction in species richness indicates that Mediterranean ecosystems and native biotas are exceptionally vulnerable to the invasion of Amphistegina. Koukouisoura et al. (2010) suggested that Amphistegina's particularly successful adaptation in the Aegean Sea may be a consequence of a previously 'vacant niche' for symbiontbearing foraminifera in low nutrient areas, perhaps enhanced by increasing sea surface temperatures during the last 30 years as a possible result of human-induced global warming (Theocharis, 2008; Vargas-Yáñez et al. 2008; Lejeusne et al. 2010). This is in line with observations from the NW range front (Adriatic and Ionian Sea) as well as from other sites in the Aegean and Ionian (Zakynthos, Crete, Syros) and Eastern Mediterranean Sea (Cyprus), where the invasion and prolific occurrences of amphisteginids suggest that new invaded habitats obviously provide ideal conditions. Especially shallow-water foraminiferal communities show little resistance to this invasion. However, Shea and Chesson (2002) indicate that invasion success depends not only on 'filling a vacant niche' but on being a better exploiter of resources or a better avoider of natural enemies than resident species. Amphisteginids thus find an 'invasion window' (Carlton, 1996) as well as excellent 'habitat suitability' in shallow-waters, where either their resource level minimally overlaps with that of resident species (maybe due to their endosymbiosis) or they may be better exploiters of available resources (such as place and food), therefore superior to resident species, explaining their dominance in these macro- and microhabitats. The successful invasion of shallow-water habitats in <20m, and a decrease in numerical abundances in water depth >20m also supports the hypothesis by Olyarnik et al. (2009) and Maraffini et al. (2015) that macrohabitats such as the examined phytal substrates (seagrasses and algae) at greater water depth (>20m) show a stronger biotic resistance to invasions due to higher species richness in general. The lower percent abundances of amphisteginid foraminifera in greater water depth may also be accompanied by decreasing microhabitats, as the abundance of hard substrates decreases, soft substrates become finer and seagrass meadows such as Posidonia oceanica, provide a decreasing number of algal habitats in the photic zone. The generally species poorer shallow-water habitats seem to provide greater 'habitat suitability' due to a greater availability of preferential substrates thus increasing invasibility in this area. But also species-rich habitats in >20m are infested by amphisteginid invasions, although amphisteginids there occur in lower numerical abundances (up to 1.2%) and smaller test sizes (<1mm; pers. observ.). Invasions along the range margin have shown to commonly begin with low numerical abundances of amphisteginid individuals as indicated by the findings at Corfu, Ithaka, Lefkada, Aegina, Sicily or Tunisia (Blanc-Vernet et al. 1979; Caruso and Cosentino, 2014; Langer, unpubl. data). Community invasibility then increases over time and Amphistegina rapidly becomes the most abundant taxon. At those sites where Amphistegina has been established for one or two decades, invasibility of foraminiferal communities intensifies. Amphisteginid foraminifera are among the most successful invaders in the Mediterranean Sea with higher dispersal rates as prognosticated by performed Species Distribution Models (SDM's; Chapter 2.2.5).



phytal substrates

**Fig. 7** Preferred macrohabitats of *A. lobifera* in the Mediterranean Sea. High percent abundances of amphisteginids occur in soft-, phytal-, and hard substrates in <20m water depth.

An adaptation (niche extension) of amphisteginids to the somewhat different 'Mediterranean conditions' than found in their native range is already observed in their abundance and dominance (see comments above) as well as in reproduction cycles and test weights. Aegean amphisteginids are shown to reproduce twice a year (summer and winter reproduction) sexually and asexually like their counterparts in the Red Sea, although combined environmental stressors (including low light levels, cold temperatures and reduced salinity) in the Aegean Sea will likely limit growth rates and reproductive success during winter (Triantaphyllou et al. 2012). Amphisteginid foraminifera from the Ionian and Aegean Sea sites investigated in this thesis contain both asexually and sexually reproduced individuals (although microspheric forms were the most abundant, building 80-95% of the assemblage) as observed in grinded specimens (Appendix 7.4.2). Sexual reproduction cycles observed in the Aegean and Ionian specimens in contrast to solely asexual reproducing counterparts in the eastern Mediterranean Sea may also reflect an adaptation of A. lobifera to central Mediterranean conditions. An adaptation of established populations to lower sea surface temperatures in winter (as observed in the Aegean and Marmara Sea) and a second yearly reproduction cycle in Aegean specimens (Triantaphyllou et al. 2012) underlines the invader success of Amphistegina in Mediterranean shallow-water habitats. Amphisteginid foraminifera in shallow-waters (1.5m water depth) off the eastern Mediterranean Sea (Israel) have shown to reproduce solely once a year asexually, so that a second reproduction cycle is limited due to sensitivity of amphisteginids to high light levels that occur in the investigated area during summer (Gruber et al. 2007). However, a subpopulation of amphisteginids has been observed by the authors, which seem to be well adapted to the high light intensities in shallow-waters in summer, reflecting also an adaptation mechanism within given local conditions. If the remaining Mediterranean amphisteginids in greater water depth (> 1.5-2m) reproduce twice a year (sexually or asexually) still requires examinations and is not resolved yet. The adaptation of amphisteginid foraminifera to Mediterranean conditions are likewise shown in test weight and temperature tolerance. It is interesting to notice that individuals from Israel are heavier by 15-25% than specimens from the Gulf of Eilat, suggesting an adaptation to higher wave energies in shallow-waters of the Mediterranean Sea (Gruber et al. 2007) and ,furthermore, reflects an increasing calcium carbonate production compared to the production of Red Sea dwellers (commented onn in Chapter 4.2.6). Another interesting aspect concerning the upper temperature limit and the success of eastern Mediterranean amphisteginids in average higher sea surface temperatures in summer is that of 'selective filtering' during invasion. As conducted by Fine et al. (2013) for coral larvae and Schmidt et al. (2016b) for Amphistegina lobifera, during postglacial re-colonization of the Red Sea from the Indian Ocean the larvae respectively propagules had to pass extremely hot shelf regions in the southern Red Sea, where 'selective filtering' of a heat-tolerant strain likely occurred.

These hypotheses imply that thermal tolerance in hermatypic corals and amphisteginids is a conservative trait and has been retained for thousands of years without an obvious functional benefit in the Gulf of Aqaba (Fine et al. 2013; Schmidt et al. 2016b). Mediterranean amphisteginids seem to take benefit of the conserved (heat-tolerance) trait during invasion of new habitats. Even when these exhibit substantially different temperature regimes as observed for eastern Mediterranean regions, where SST do not exceed 32°C in summer, whereas SST in the Gulf of Aqaba reach 29°C in summer (Schmidt et al. 2016a, b).

The invasion success of amphisteginids in the Mediterranean Sea may also be accompanied by propagule pressure. Propagule pressure has been shown to be positively related to the amount of genetic variation in the introduced population, improving the chances that the population will be able to adapt successfully to novel selection pressures in the recipient location (Ahlroth et al. 2003). The amount of different introduction pathways may increase genetic variability. If propagules are coming from different native source areas and if these native populations show spatial genetic structure, genetic diversity can be increased over that observed within any of the native or present populations (Lockwood et al. 2005). Such infusions of novel genetic material might provide the variation (genetic and phenotypic) for the non-native population to establish itself successfully and begin to expand its range (Lockwood et al. 2005). The increase in genetic variability that accompanies increased propagule pressure should also enhance establishment success as well as the potential for the non-native taxon to expand its range and cause ecological harm (Lockwood et al. 2005).

Until 2016, *A. lobifera* in the Mediterranean Sea was classified as a cryptogenic species, whose origin was not assessed. However, the presence of amphisteginids (especially *A. lobifera*) in the Indo-Pacific and Pacific realm and its spatial distribution in the Mediterranean Sea (Chapter 4.2., Fig. 2), suggests that established populations in the eastern Mediterranean Sea to be the result of 'newly arrived' Lessepsian migrants or stowaways transported via ballast ship water from the Red Sea, Indo-Pacific or Pacific Ocean respectively. This has been recently confirmed by Schmidt et al. (2016b), who conducted molecular investigations of Mediterranean (Crete and Eastern Mediterranean) and Red Sea amphisteginids and showed a genetic homogeneity between the host and endosymbionts, whereas a consistent divergence was observed in sequences from Australian amphisteginids.

# **4.2.6** *A. lobifera* as prolific calcium carbonate producing ecosystem engineer in the Mediterranean Sea

Amphisteginids are prolific producers of calcium carbonate and have substrate modifying capabilities. Their range shift has locally led to the establishment of amphisteginid monocultures (Abu Tair and Langer, 2010, Fig. 8A-C) and/or the accumulation of thick sandy layers (30-60 cm; Meric et al., 2008a) the so called "living sand" (Lee, 1995). Hyperabundances, mass occurrences and the appearance of invasive amphisteginids in monocultures were previously shown to lead to a homogenization of the foraminiferal fauna (Langer et al. 2012). At some sites along the coast of Turkey, amphisteginid foraminifera were reported to constitute 75 % of the sediment and up to 80 % of the 0.5–1 mm size fraction (Meric et al. 2008a). High numerical abundances of amphisteginid foraminifera with test sizes of 0.5-2mm (pers. observation; Hyams et al. 2002, 2008; Streftaris and Zenetos, 2006; Yokes and Meric, 2009), let them modify the grain size so that they have the capability to transform the composition, nature and chemistry of sediments from predominantly siliceous to carbonate deposits. Yokes and Meric (2004) have reported depositional rates of amphisteginid foraminifera to range between 2.5 and 4.0 cm year<sup>-1</sup> in shallow-waters off Turkey. With a frequency of 180 individuals/ g sediment amphisteginids lead to a deposition rate of approximately 200g CaCO<sub>3</sub>

 $m^2yr^{-1}$  in shallow-waters off Israel (Gruber et al. 2007). The large contribution of amphisteginid tests to the sediment resulted in sand accumulations, that "changed the habitat type and coastal structure" (Yokes and Meric, 2004) and thus, they have the potential to modify the structure of habitats and ecosystems (ecosystem engineers).

A positive effect of increasing (sand sizes) carbonate soft substrates provided by amphisteginids in future may be that on coastal erosion in the Mediterranean as a result of canalization, dams, irrigation works, storm events, sea level rise and increasing tourism (Özhan, 2002; Smith and Abdel-Kader, 1988; Alexandrakis et al. 2013; Gruda and Dollma, 2013; Phillips and Jones, 2006; Valdemoro and Jiménez, 2006).



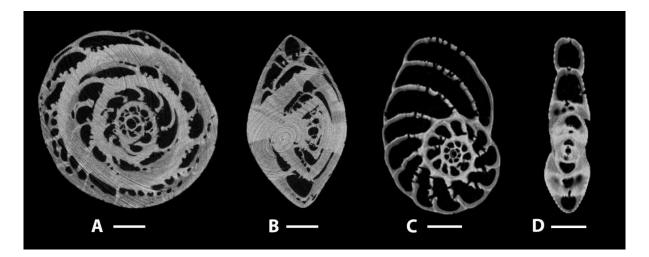
**Fig. 8** (A-C) 'Amphisteginid sands' from shallow-waters off Cyprus, A-B scale=2mm, C scale=1mm (D) Miocene amphisteginid monoculture from the Poland basin, scale=1mm (Fotos: G. Oleschinski).

As mentioned in the introduction (Chapter 1.8.2) as well as in the former Chapter (4.2.5), *Amphistegina lobifera* is the shallowest dwelling species among amphisteginid foraminifera, characterized by a massive and robust test, adapted to high energy conditions in shallow-water settings. Hansen and Reiss (1972) demonstrated that members of the family *Amphistegina* basically follow an identical scheme regarding both morphology and structure, so that all members are found to construct their chambers of two layers of calcite separated by an organic layer (Appendix, 7.4 Systematic description of *A. lobifera*). With the addition of a new chamber, the outer calcareous layer forms a continuous sheet of material covering all exposed ontogenically older shell parts (secondary lamellae, Chapter 6.5.2.1, Fig. 2), so that the umbilical regions receive secondary lamellae from all chambers (Hansen and Reiss, 1972; Hallock and Hansen, 1979).

The complex internal structure of the test (such as chambers with lobes complicated by secondary foulding, pustules covering the apertural face in rows radiating from the aperture, strongly lobulated

alar prolongations, pillars) as well as the thickened umbilical region due to secondary lamellation of all ontogenically older shell parts increases the amount of CaCO<sub>3</sub> production (visible in Appendix 7.5.1 and 7.5.2). As mentioned in Chapter 4.2.5 *A. lobifera* specimens observed in shallow-waters off Israel are up to 25% heavier compared to their counterparts from the Gulf of Elat, not only suggesting an adaptation to higher wave energies in shallow-waters of the eastern Mediterranean Sea (Gruber et al. 2007) but, furthermore, reflecting an increasing CaCO<sub>3</sub> production compared to Red Sea dwellers. This is confirmed through investigations made by Hallock and Hansen (1979) and Hallock et al. (1986), who have shown that secondary lamellar thickness in amphisteginids is influenced by water motion, light intensities and water depth. Therefore amphisteginids grown under water motion in shallow-waters have more inflated test shapes (high trochospiral) due to the ability to secrete more CaCO<sub>3</sub> with each chamber addition (resulting in an increasing rate of lamellar thickness on both spiral and umbilical test sides, Fig. 9A-B; Appendix 7.4.2.2), whereas deeper dwelling species are characterized by flatter test shapes with low trochospiral test morphology and a decreased rate of lamellar thickness (Hallock and Jansen, 1979; Hallock et al. 1986).

For example, larger symbiont-bearing peneroplids (*P. planatus* and *P. pertusus*) with porcellaneous wall structure, which likewise reach high numerical abundances and great test sizes in Mediterranean shallow-water environments show internally less complicated test morphology and thinner test walls (most probably due to the light requirements of the endosymbionts), so that  $CaCO_3$  production is decreased compared to amphisteginid foraminifera (Fig. 9C-D). As peneroplids decrease in the numerical abundances, when amphisteginids increases in percent abundances (Chapter 4.2.3), the amount of  $CaCO_3$  will most probably not decrease due to the displacement of important carbonate producing species sharing the same microhabitats, but increase due to the higher rates of  $CaCO_3$  production by amphisteginids in shallow-waters environments. But these observations need more examinations and quantitative analyes, to confirm this hypothesis (manuscript in preparation).



**Fig. 9** 2D sections of micro-CT scans of *Amphistegina lobifera* (A=equatorial section, B=axial section) and *Peneroplis planatus* (C= equatorial section, D=axial section), scale bar 200µm, (micro-CT scans: J. Könen).

### **4.2.7** Forecasting future range extensions of *A. lobifera* and invasion impacts on native foraminiferal assemblages in the Mediterranean Sea

It remains to be seen how far amphisteginid foraminifera will migrate into the Adriatic Sea. The elevated freshwater and terrigenous input due to rivers and erosion along the eastern coast will limit the distribution of amphisteginids locally. Weinmann et al. (2013a) mentioned that increasing

eutrophication and nutrient influx will locally impact the range expansion of Amphistegina spp., especially in the northern Adriatic, so that the total extend of the predicted future range expansion of this taxon may not be fully realized in future, even though the temperatures will become more suitable. However, the presence of larger symbiont-bearing species along the coastline of Croatia including Peneroplidae and Soritidae (Wiesner, 1913; Vatova 1928; Alfirevic 1964, 1998; Drobne and Cimerman, 1984; Vanicek et al. 2000; Cosovic et al. 2002, 2011; Vidovic et al. 2009; Cimerman and Langer, 1991) show that those species are able to overcome natural barriers such as rivers accompanied with massive terrigenous input. This is also shown in the distribution of foraminiferal species from the eastern and central Mediterranean Sea, where larger symbiont-bearing species (excluding stowaways) were able to overcome the Nile barrier now settling along the northern coastline of Egypt, Lebanon, Tunisia, the Pelagian Islands and Sicily (Blanc-Vernet et al. 1979; Samir et al. 2001; Samir et al. 2003; Elshanawany et al. 2011; Caruso and Cosentino, 2014). Sea surface currents will help to extend the distribution range of *Amphistegina* spp. by several hundred kilometers (Saidova, 1961; Todd, 1976; Lessard, 1980; Langer and Hottinger, 2000; Langer et al. 2012). Gastrointestinal transport (Ichthyoendochory) of amphisteginids in fishes has recently been suggested by Guy-Haim et al. (2016, 2017 in press) which eases and accelerates the dispersal and may be an explanation for increased dispersal rates of amphisteginids (determined in chapter 2.2.5). Gastrointestinal transport may, furthermore, also facilitate the breaching of natural barriers such as rivers. With current climate warming, amphisteginid foraminifera and several other NI foraminiferal species can be expected to invade shallow waters off Montenegro and Croatia, before the dispersal is getting limited through the eutrophic conditions and cooler sea surface temperatures in the Northern Adriatic Sea.

Species Distribution Models applied by Weinmann et al. (2013a) prognosticate an ongoing range expansion into the western Mediterranean Sea projected for the year 2050, with habitat suitability increasing around Italy (Chapter 1.8.2). Amphisteginid foraminifera already settle in rare occurrences along the southeastern coast of Sicily (Vendicari/Italy), which was confirmed by Caruso and Cosentino (2014). However, these sites are located in the Ionian Sea. The northwestward shift of the 14° winter isotherm (Coll et al. 2010; Chapter 1, Fig. 4) may already enable the migration of amphisteginids in the western Mediterranean Sea. But it remains to be seen, when amphisteginids will migrate further into the western Mediterranean Sea, namely the Tyrrhenian Sea. Langer and Hottinger (2000) argued that the entrance of thermophilic NI foraminiferal species into the Western Mediterranean Sea may be limited by the colder parts of the western Mediterranean which is influenced by colder water currents from the Atlantic Ocean. It appear to be difficult for amphisteginids to migrate into the Tyrrhenian Sea, due to colder sea surface currents leaving the Adriatic Sea and passing the Strait of Messina (Chapter 1.2.1, Fig. 1A) as well as through colder parts present in the Western Mediterranean Sea, exacerbating the migration and establishment of amphisteginids in these areas to date. Increasing sea surface temperatures in the Western Mediterranean Sea (Vargas-Yáñez et al. 2008, 2010; Bethoux et al. 2009; Nykjaer, 2009), however, favor increasing habitat suitability for amphisteginid foraminifera, so that their entrance in the Tyrrhenian Sea is probably just a matter of time.

# 4.3 Foraminifera and their use as bioindicators in impacted and non-impacted shallow-water marine sites

Foraminifera are unicellular organisms (Rhizaria) that form the most diverse and frequent group of shelled microorganisms (Sen Gupta, 1999; Debenay, 2012). Their biomineralized shells have high potential to get preserved, so that these widely distributed and highly abundant organisms constitute a great part of recent and fossil sediments and sedimentary rocks. Used as zonal indicators, even small sediment samples provide (palaeo)-ecological,- biological and environmental information, which make foraminifera the most widely used organisms utilized for biostratigraphy, age dating, paleoenvironmental interpretation and reconstructions (Loeblich and Tappan, 1987). In recent decades, studies of foraminiferal assemblages have contributed to our understanding of environmental problems in marine coastal ecosystems (Yanko et al. 1999; Debenay et al. 2000; Schafer, 2000), where they can be reliable indicators of environmental disturbance (Murray, 2000; Geslin et al. 2000, 2002) and pollution (Yanko et al. 1994, 1998, 1999; Alve, 1995a; Coccioni, 2000; Samir and El-Din, 2001; Murray and Alve, 2002; Armynot du Châtelet et al. 2004; Ferraro et al. 2006; Frontalini and Coccioni, 2008) as well as indicators for determining the suitability of benthic environments for communities dominated by calcifying organisms (FORAM- Index; Hallock et al. 2003).

### 4.3.1 Albanian foraminiferal assemblages in impacted and non-impacted sites

Albania is located in a peculiar position bordering three biogeographical regions (Eastern-, Western Mediterranean Sea, Adriatic) of the Mediterranean Sea. The shallow coastal waters off Albania are an environmentally sensitive region, which provide a wide range of habitats and comprise a high biodiversity, including rare, endemic and endangered species registered on the red list.

But many habitats are seriously endangered by human mediated impacts as they are most exposed and unprotected (Cullaj et al. 2005, 2007). Anthropogenic impacts include (e.g) maritime traffic, coastal pollution due to urban and industrial sewage discharges, building activities and forest mismanagement enhancing (coastal) erosion rates, tourism with uncontrolled activities, hydrocarbon exploration, agricultural overproduction and aquaculture accompanied with eutrophication. Natural mediated impacts concern geomorphology controlled erosion rates along the Adriatic coastline, which in combination with human forced erosion leads to massive deposition of solid material in the coastal areas, resulting in unfavorable conditions for life in rivers, lagoons and the marine coast (Cullaj et al. 2005). Current climate warming, the opening of the Suez Canal in 1869, ship fouling and ballast water transportation supplementary enhances the invasion of thermophilic NI species. The protection of Albania's coastal area and biota thus is of international significance, especially during times of current climate warming and increased pollution due to (uncontrolled) anthropogenic activities.

The samples collected show high species richness values (277 species, 112 Genera) with taxa known to be distributed in the Adriatic as well as in the Eastern and Western Mediterranean Sea. However, the performed hierarchical cluster analysis reveal the presence of two distinct clusters and biofacies characterized for the northern and southern coastline respectively. The disparity between the two biofacies and clusters along the northern and southern coastline is related to the above mentioned geomorphological and hydrological differences and intensified by anthropogenic influences. The two biofacies regimes are characterized by specific foraminiferal assemblages and differ in the composition of functional groups of foraminifera (heterotrophic, opportunistic, mixotrophic). The northern sample sites are characterized by the dominance of opportunistic and heterotrophic foraminifera, as they tolerate waters with high turbidity and nutrients as well as more stressful conditions such as high heavy metal concentrations and low oxygen conditions. The southern sample

stations contain a larger portion of mixotrophic and heterotrophic species, due to the absence of large rivers and oligotrophic water conditions.

Increasing anthropogenic pressure accompanied with pollution from sewage, urban wastes, maritime traffic, and building activities lead to partly degrading conditions within certain areas. The Gulf of Vlore and Sarande Bay were subjected to increasing anthropogenic pressure and have favored the establishment and accumulation of mainly opportunistic foraminiferal species. Mixotrophic foraminifera, which are well bioindicators for high water quality, underlines this, as they are only present in low abundances in Sarande Bay (30m) and are absent in the Gulf of Vlore. Foraminiferal assemblages along the northern coastline especially around Darezeze e Re (lowest species richness), as well as around Shengjin, Durres, and Divjaka show likewise increasing degradation rates traced back to human mediated impacts (urban and industrial sewages, hydrocarbon exploration, building activities) and natural forcing (river discharge, erosion rates).

The presence of benthic foraminiferal species of Indo-Pacific and Atlantic origin in the samples sites off Albania is generally low (4 species; 2.5% of the entire foraminiferal assemblage; excluding the locally high abundance of amphisteginids, chapter 3.1.3, Table 4). The local restriction of NI foraminiferal species (excluding *Amphistegina*) and their appearance in or near the principial ports of Albania suggests them to be transported via ballast ship water and a subsequent dispersal by currents. The distribution of amphisteginids along the southern coastline seems to be the result of enhanced sea surface temperatures and the dispersal by Ionian Sea surface currents.

The numbers of NI foraminiferal species will increase in the future as current climate warming facilitates the distribution of established populations in the Eastern Mediterranean Sea via natural expansion or human mediated (shipping, aquaculture). Climate models predicted that by 2041-2060, the major part of the Mediterranean Sea will become warmer except for the northern Adriatic, which is expected to become cooler (Coll et al. 2010). Continuing isotherm shifts and increasing maritime traffic thus will enhance the introduction of thermophilic species, especially in the southern and central Adriatic Sea. The presence of, most probably ballast ship transferred, NI foraminiferal species near the Port of Otranto (SW Adriatic Sea, see Appendix 7.3) support this hypothesis. It remains to be seen how invasion processes continue in the eutrophic northern Adriatic as cooling events may limit the establishment of thermophilic NI foraminiferal species. The northern Adriatic to date is inhabited by the largest amount of NI species of the whole Adriatic Sea (Zenetos et al. 2010). The introduction is mainly due to aquaculture, ship fouling and ship ballast water. NI species introduced via aquaculture, may well adapt to lower water temperatures, so that further invasions and establishment processes are quite possible.

The investigations made in chapter 3 represent the first survey of benthic foraminifera along nearly the entire seacoast of Albania with the atlas filling a knowledge gap on shallow-water benthic foraminifera from this region. Furthermore, the study serves as baseline for further assessment of environmental changes (human or natural induces) and ongoing range expansions of NI benthic foraminiferal species in this area.

#### 4.4 Concluding remarks

The results conducted in this phD thesis underline the impact of human activities on coastal marine systems. There is growing evidence that human activities directly or indirectly affect species diversity and ecosystem diversity in the continental shelf. Among those human activities are especially coastal development, fishing, pollution (nutrients, organic matter, heavy metals, turbidity, aquaculture facilities, dumping of solid waste) and increasing  $CO_2$  emissions that threaten the marine biota. Ocean

warming caused by anthropogenic climate change is already starting to impact the marine biota and, furthermore, facilitates the invasion and range expansion of NI species in new habitats, previously barren by lower sea surface temperatures. Biological invasions driven by global climate change are key processes modifying patterns of biodiversity. Ecological impacts of invasive species have shown to affect the entire ecosystem function. The restructuring of the whole Mediterranean and several other shallow marine ecosystems with potential consequences for ecosystem services may not just have serious impacts on many local, endangered and endemic species but may potentially lead to a homogenization (the replacement of local biotas with non-indigenous species) of the fauna in future.

Amphisteginid foraminifera have shown to be among the key species currently expanding their biogeographic range due to climate warming and the widening of the tropical belt. This makes them ideal bioindicators for climate induced invasions respectively changes in a 'natural laboratory' such as the Mediterranean 'miniature ocean'. Observations from the NW Mediterranean range front as well as from sites invaded by amphisteginid foraminifera decades ago, show that the invasion already outcompetes native species and finally leads to the homogenization of the foraminiferal fauna with severe consequences on ecosystem functioning. The substrate modifying capabilities further transform the composition, nature and chemistry of sediments from predominately siliceous to carbonate deposits. Invasive amphisteginid foraminifera must therefore be considered true ecosystem engineers in shallow-water habitats of the Mediterranean Sea, where their invasion and range front extension will require further monitoring studies in order to assess the impact on future ecosystems.

Future studies should further aim on questions or topics such as (1) the lower temperature tolerance of the most successful foraminiferal invader A. lobifera in the Mediterranean Sea (2) additional molecular investigations of Mediterranean amphisteginid populations to determine the source area and maybe to further explain invader success of amphisteginids (due to enhanced propagule pressure or novel genetic material infusion) (3) to check if the displacement of native species is just of local nature, and if natives due to the displacement persist in nearby uninvaded areas and (4) if amphisteginids displace any species than (native) for aminifera and what role they play in the food web of metacommunities. An additional examination topic may be that of (5) dominance and monoculture formation of amphisteginids in their native range (tropics) and when ecosystem disturbance occur in those areas to explain their invader success more accurately in new invaded areas (only observed marginally within this phD). Among larger-benthic foraminifera amphisteginids (hosting diatom endosymbionts) and soritids (hosting dinoflagellates) show the widest latitudinal extension worldwide. To investigate (6), if different endosymbiont requirements (such as higher temperature tolerances or potential depth ranges) of diatom and dinoflagellate species hosted by amphisteginids and soritids may affect the latitudinal distribution and settling success of the foraminifera in comparison to other endosymbiont requirements (such as those of Rhodophyceans or Chlorophyceans) and the settling success of their hosts may also be an interesting topic for future studies.

The diversity, assemblage structure and percent abundances of taxa such as *Amphistegina lobifer* may contain useful information for inferring the biogeographic course (i.e. shifting of the range expansion front) in species which are moving into new habitats as a result of changes (e.g. climate conditions). The use of bioindicators (such as *Amphistegina*) and increasing studies on biotic and abiotic factors, which are accompanied by human induced ecosystem changes, will increase our understanding and perception of changing ecosystems and will further provide an insight in prevention activities. The magnitude and effects that climate change and further human mediated impacts will have on the Mediterranean and generally in marine ecosystems will ultimately provide windows into processes of climate induced invasions and anthropogenic induced changes in past and future oceans.

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# 6 Index for figures and tables

## Chapter 1

**Fig. 1A** Biogeographic areas in the Mediterranean Sea. 1=Strait of Gibraltar, 2=Strait of Sicily, 3= Strait of Messina, 4=Strait of Otranto, 5=Dardanelles, 6=Bosporus, 7=Suez Canal, 8= Gulf of Suez, 9=Gulf of Aqaba, **1B** Strait of Gibraltar, **1C** Dardanelles and Bosporus, **1D** Suez Canal (NASA), **1E** Spatial distribution of annual average SST means over the 1982–2012 period (Shaltout and Omstedt, 2014).

Fig. 2 Sea surface circulation in the Mediterranean Sea (after Millot and Taupier-Letage, 2005).

**Fig. 3** Paleogeographic reconstruction of the Mediterranean and Paratethys region from Late Eocene (Priabonian) to Middle Miocene (Serravallian) (A) Lower Eocene (B) Early Oligocene (C) Aquitanian (D) Late Burdigalian (E) Langhian (F) Middle Serravallian, (Rögl, 1998b).

**Fig. 4** Recent northward shifting of February sea surface isotherms (°C) in the Mediterranean Sea (broken lines are the one-century climatological means, solid lines the means for 1985–2006: the 14°C and the 15°C "dividers" are highlighted by a thicker tract (modified after Coll et al. 2010).

**Fig. 5** (A) Contribution of marine alien taxa in the Mediterranean Sea (B) Species-area plot of the number of non-indigenous species (NIS) in the 4 Marine Strategy Framework Directive (MSFD) subregions of the Mediterranean Sea (C) Number of marine alien species per major groups in the MSFD subregions of the Mediterranean Sea (D) Percentages of marine NIS known or likely to be introduced by each of the main pathways by subregion. Percentages add to more than 100% as some species are linked to more than one pathway (all figures taken from Zenetos et al. 2012).

**Fig. 6** (A) Biogeographic distribution of *Amphisorus hemprichii* in the Mediterranean and Red Sea (B) *Amphisorus hemprichii* population on *Halophila stipulacea* Ascherson, Kas -Antalya, depth 26 m, scale bar = 6mm (Meric et al. 2014), (C) *Amphisorus hemprichii* population on *Cystoseira* sp., Kas - Antalya, depth 12m, scale bar = 2mm. (Meric et al. 2014), (D) *Amphisorus hemprichii* individuals on the sea bottom, scale bar = 0.85, (E) Dense *A. hemprichii* population on hard substrates, serving as a hiding place for a young individual of *Octopus vulgaris*, scale bar = 6mm (Photo: Baki Yokes; source: Cinar et al. 2010).

**Fig. 7** (A) Biogeographic distribution of *Amphistegina* spp. in the Mediterranean Sea, Red Sea and the Sea of Marmara, (B) *Amphistegina lobifera* population on a rock substrate, Üçadalar, Antalya, Mediterranean, 6.00m, scale bar = 20mm (Meric et al. 2014), (C) *Amphistegina lobifera* population on *Cystoseira* sp., Bodrum, Mugla, Aegean Sea, 9.00m, scale bar = 15mm (Meric et al. 2014), (D) *Amphistegina lobifera* population on algal mat, Arsuz, Iskenderun, Hatay, 8.00m, scale bar = 20mm. (Meric et al. 2014), (E) High accumulation rate of *A. lobifera* tests in shallow-waters off Cyprus. (F) Global biogeographic distribution of amphisteginid foraminifera ranging from 40°N to 31°S (Weinmann, unpubl. data).

**Fig. 8** (A) Species Distribution Models (SDM's) for *Amphistegina* spp. under current and future climates as projected by Maxent (modified after Weinmann et al. 2013b). Probability of presence is indicated by habitat suitability values ranging fromhigh (1, red areas) to very low (0.1813, light blue areas). Black stars indicate currently known distribution limits of *Amphistegina* spp. in Tunisia, Malta, Corfu and the northern Aegean Sea. Gray hatched areas indicate areas of possible extrapolation of the model due to predictor values being outside the training range (MESS). (B) Species Distribution Model under climate conditions projected for 2050. Note the ongoing range expansion into the western Mediterranean. Habitat suitability is increasing around Italy. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of Weinmann et al. 2013b).

Fig. 10 Map showing Mediterranean sample site locations (red lines and dots) investigated in this thesis.

### Chapter 2.1

**Fig. 1** Location of the collection areas in the eastern Mediterranean Sea with insets showing the position of the sampling sites at Ithaka, Lefkada and Cyprus (for details see Table 1).

**Fig. 2** Selected sample site locations (A) Ithaka, (B) Lefkada, (C) Aiya Thekla Beach (Cyprus), (D) Aegina Beach (Greece).

**Fig. 3** Quantitative foraminiferal assemblage analyses illustrating the impact of amphisteginid foraminifera on selected groups at shallow-water sites off Ithaka and Lefkada. A negative correlation exists between (A) amphisteginid percent abundances and total diversity (species richness) of associated benthic foraminifera, (B) percent abundances of other symbiont-bearing foraminifera, (C) abundance values (%) of peneroplid taxa among all LBF's, (D) percent abundances of other hyaline perforate benthic taxa, (E) occurrence values (%) of other trochspiral species, and (F) the amount of smaller non symbiont-bearing miliolid foraminifera.

**Fig. 4** Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in selected samples from the central and eastern Mediterranean Sea. Note the negative correlation and the decrease in species richness with increasing abundances of amphisteginid foraminifera.

#### Chapter 2.2

**Fig. 1** Location of the collection areas in the central Mediterranean and Adriatic Sea with insets showing the position of sampling sites in the northern Ionian, and southern Adriatic Sea at Corfu, Albania (black dots) and along the Salento Peninsula/Italy (squares, for details see Table 1). Star symbol shows the location of the sampling site from Aegina. Dashed line represents the range expansion front of amphisteginid foraminifera until summer 2010.

**Fig. 2** Selected sample site locations (A) Mpoukaris (Corfu), (B) Agnos Beach (Corfu), (C) Monastiri Bay (Albania), (D) Sarande Bay (Albania), (E) Porto Palermo (Albania), (F) Dermi Beach (Albania), (G) Otranto (Italy), (H) Tricase (Italy).

**Fig. 3** Quantitative foraminiferal assemblage analyses illustrating the impact of amphisteginid foraminifera on selected groups at shallow-water sites off Corfu and Albania. Locations listed in diagram **A**, **B** are identical for **C–H** A negative correlation exists between a amphisteginid percent abundances and species richness of associated benthic foraminifera, **B** percent abundances of other trochospiral foraminifera, **C** abundance values (%) of planispiral species, **D** percent abundances of peneroplid foraminifera, **E** occurrence values (%) of other elphidiid taxa, **F** the amount of smaller non symbiont-bearing miliolid foraminifera, **G** percent abundance values of temporary attached and **H** permanent attached epiphytic species.

**Fig. 4** Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in 124 selected samples from the central and eastern Mediterranean Sea (including the new material from the Adriatic Sea). Note the negative correlation and decrease in species richness with increasing abundances of amphisteginid foraminifera. The regression line is shown superimposed on the individual data points.

#### Chapter 3.1

Fig. 1 Location of the collection areas along the coastline of Albania located in the north eastern Ionian and south eastern Adriatic Sea.

**Fig. 2** Selected sample site locations (A) Port of Shengjin, (B) Beach of Durres, (C) Divjaka Beach, (D) Darezeze e Re (Dar) Beach, (E) Vlore, (F) Beach of Dermi, (G) Jala Beach, (H) Porto Palermo, (I) Sarande Bay, (J) Monastiri Bay.

**Fig. 3** Q-mode cluster dendogram (right) with two major clusters I and II (with two sub-clusters II1 and II2) and R-mode cluster dendogram (above) including species reaching at least 5% of the total foraminiferal assemblage (dominant taxa in bold characters) defines two biofacies (A and B) with four sub-biofacies (A1, A2, B1, B2). Distinct grey tones show q- and r-mode related relationships. Relative percent abundances for each species are indicated with individual symbols (see legend and Table 4).

#### Chapter 4

**Fig. 1** Contribution of alien and cryptogenic benthic foraminifera in the Mediterranean Sea (after Zenetos et al. 2008, 2010, 2012, EASIN 2016 and thesis data). (A) Numbers of alien and cryptogenic benthic foraminiferal taxa and percent abundances of miliolid, hyaline and agglutinated taxa in the 4 sub-regions (Western MS, Eastern MS, Central MS, Adria) of the Mediterranean Sea, (B) percentages of alien and cryptogenic benthic foraminifera known or likely to be introduced by each of the main pathways by sub-region (LM = Lessepsian migrant, SH = shipping, AQ = Aquaculture, unknown).

**Fig. 2** Map showing the current range extension of *A. lobifera* in the Mediterranean Sea (shaded in blue), red dots and lines mark the investigated areas in this thesis: coast of Albania, southern boot of Italy, sites in the Ionian (Corfu, Ithaka, Lefkada, Zakynthos), Aegean (Syros, Crete, Aegina) and Eastern Mediterranean Sea (Cyprus).

**Fig.3** Map showing the NW range expansion front of *A.lobifera* highlighted in yellow. Red squares show sample stations from the N Ionian and SE Adriatic Sea containing amphisteginid foraminifera (reaching 0.3-75% of the entire foraminiferal assemblage), black squares show sample stations along the Albania and Italian coast were amphisteginids are absent. Green square displays the Port of Otranto from the south-eastern boot of Italy inhabited by 3 NI foraminiferal species.

**Fig. 4**. Line diagram showing the relationship between percent abundances of *Amphistegina* spp. and the diversity of benthic foraminifera (species richness) in 110 selected samples from the central and eastern Mediterranean Sea (including the new material from the Adriatic Sea, Appendix 7.8). Note the negative correlation and decrease in species richness with increasing abundances of amphisteginid foraminifera. The regression line is shown superimposed on the individual data points.

**Fig. 5** Map showing the percent abundance of amphisteginid foraminifera in the eastern and central Mediterranean Sea. Percent abundances in the eastern Mediterranean Sea as well as some locations in the central Mediterranean Sea (A-C) show, that amphisteginid foraminifera become extreme abundant locally. The sample sites A-C represent exceptional localities with high percentages of amphisteginids contrary to the in general lower percent ages along the range front (A) Gjiri Monastiri Bay (76.1%), (B) Zakynthos 81%, (C) Linosa Island 79-97%.

**Fig. 6** Fossil distribution ranges of larger foraminifera (based on Adams et al. 1990, modified after Weinmann, 2014). Triangles indicate occurrence records from the middle Eocene (a), middle Miocene (b). For details, see Adams et al. (1990). Red areas display fossil distribution ranges in relation to recent latitudinal ranges of *Amphistegina* spp. (solid red lines).

**Fig. 7** Preferred macrohabitats of *A. lobifera* in the Mediterranean Sea. High percent abundances of amphisteginids occur in soft-, phytal-, and hard substrates in <20m water depth.

**Fig. 8**. (A-C) 'Amphisteginid sands' from shallow-waters off Cyprus, A-B scale=2mm, C scale=1mm (D) Miocene amphisteginid monoculture from the Poland basin, scale=1mm (Fotos: G. Oleschinski).

**Fig. 9** 2D sections of CT scans of *Amphistegina lobifera* (A=equatorial section, B=axial section) and *Peneroplis planatus* (C= equatorial section, D=axial section) (micro-CT scans: J. Könen).

#### Chapter 1

**Table 1.** Stratigraphic correlation chart of the standard scale with Central Paratethys and Eastern Paratethys regional stage systems, and the planktonic foraminifera and calcareous nannoplankton biozonation (according to Berggren et al. 1995; Popov et al. 1993; Rögl 1996, 1998b).

**Table 2:** Countries and coastal sectors included in the four sub-regions of the Mediterranean Sea (Zenetos et al. 2012).

#### Chapter 2.1

**Table 1** Sample site information for new collection locations from Ithaka, Lefkada and Cyprus (Mediterranean Sea).

**Table 2** Quantitative faunal analyses of foraminiferal assemblages from Ithaka and Lefkada, Greece (Mediterranean Sea). Numerical data include percent abundances of miliolid, hyaline and agglutinated foraminiferal specimens, relative amount of elphidiid and larger symbiont-bearing taxa (%) among foraminiferal biotas and other LBF's, and diversity and dominance indices of individual samples.

#### Chapter 2.2

 Table 1 Sample site information for collection locations from Albania, Greece (Corfu, Aegina) and Italy (Mediterranean Sea).

**Table 2** Numerical data include percent abundances of miliolid, hyaline and agglutinated foraminiferal specimens, number of species and genera, diversity and dominance indices, the relative amount of larger symbiont-bearing benthic foraminifera (including *Amphistegina* spp., *Peneroplis* spp., *Sorites* spp. and *Coscinospira hemprichii*), percent abundance values of *Amphistegina* spp. among LBF, abundance values (%) of symbiont-bearing foraminifera and *Amphistegina* spp. among symbiont-bearing taxa, percent abundance values of elphidiid, smaller non symbiont-bearing taxa, the relative amount of trochospiral and planispiral foraminifera as well as percent abundance values of temporary and permanent attached epiphytic species of individual samples.

#### Chapter 3.1

 Table 1. Sample site information for collection locations from shallow-waters off Albania.

Table 3. Functional groups of foraminifera included in the HCA.

**Table 2.** Quantitative faunal analysis of foraminiferal assemblages from Albania, including percent abundances of miliolid (Mil), perforate (Perf) and agglutinated (Agg) foraminifera, the number of species and genera, percent abundances of selected groups of foraminifera (Larger-benthic foraminifera = LBF, elphidiids, smaller miliolids, heterotrophic (h), opportunistic (o) and mixotrophic (m) foraminifers).

Table 4 Percent abundances of NI benthic foraminiferal species and the successful returnee *Sorites orbiculus* in shallow-waters off Albania.

**Table 5**. Abundance records of foraminiferal species reaching at least 5% of the foraminiferal assemblages. Dominant species (reaching at least 10%) were designated in bold characters.

# 7 Appendix

# 7.1. Sample site information for all samples studied in the Mediterranean Sea

Country	Collection Site	Sample Number	Wat er Dept h (m)	Latitude	Longitude	Collection Date	Amphistegina present
Cyprus	Cyprus 1/ Aiya Thekla	80/2009	2	34°58'36.59"N	33°55'22.61"E	09/March/2 009	yes
Cyprus	Cyprus 2/ Aiya Thekla	81/2009	3	34°58'36.59"N	33°55'22.61"E	09/March/2 009	yes
Greece	Ithaka 1	101/201 2	12	38°26'07.73"N	20°38'21.39"E	12/July/201 2	yes
Greece	Ithaka 2	102/201 2	20	38°26'07.73"N	20°38'21.39"E	12/July/201 2	yes
Greece	Lefkada/ Atherinos Bay	103/201 2	15	38°39'54.82"N	20°48'00.94"E	13/July/201 2	yes
Greece	Aegina	37	0.5	37°44'30.22"N	23°32'08.58" N	10/1967	yes
Greece	Corfu 1/ Mpoukaris	2	8	39°27'40.50"N	19°58'58.08"E	9/2014	yes
Greece	Corfu 2/ Mpoukaris	1	8	39°27'40.75"N	19°58'51.79"E	9/2014	yes
Greece	Corfu 3/ Agnos	3	10	39°47'58.02"N	19°46'39.65" E	9/2014	yes
Greece	Zakynthos/St. Nicolas	1	10	37°43'38.45"N	20°59'34.21"E	8/2016	yes
Greece	Zakynthos/Marathonisi	2	12	37°41'12.10"N	20°51'56.95"E	8/2016	yes
Greece	Syros /Galissas Beach	1	2	37°25'24.22"N	24°52'32.23"E	7/2014	yes
Greece	Syros / Galissas Beach	2	2-3	37°25'19.35"N	24°52'37.32"E	7/2014	yes
Greece	Syros /Lia Beach	3	2	37°29'23.33"N	24°54'02.73"E	7/2014	yes
Greece	Crete /Komos Beach	1	2	35°00'26.67"N	24°45'27.93"E	6/2014	yes
Greece	Crete /Kali Beach	2	2	34°56'02.94"N	24°48'23.89"E	6/2014	yes
Greece	Pacheia Ammos	3	1.5	35°06'35.93"N	25°48'39.52"E	8/2014	yes
Albania	Shengjin 1	Sh1	2	41°48'34.30"N	19°35'21.37"E	10/2015	no
Albania	Shengjin 2	Sh2	8	41°48'48.40"N	19°35'14.20"E	10/2015	no
Albania	Durres 1	D1	4	41°19'08.06"N	19°25'52.99"E	10/2015	no
Albania	Durres 2	D2	5	41°19'07.88"N	19°25'51.92"E	10/2015	no
Albania	Divjaka 1	Div	4	40°57'46.96"N	19°27'41.02"E	10/2015	no
Albania	Darezeze e Re	Dar	4	40°42'54.99"N	19°21'43.67"E	10/2015	no
Albania	Vlore 1	V1	0.5	40°27'11.06"N	19°28'40.20"E	10/2015	no
Albania	Vlore 2	V2	10- 12	40°27'05.01"N	19°28'38.51"E	10/2015	no
Albania	Vlore 3	V3	13- 14	40°27'03.20"N	19°28'37.31"E	10/2015	no
Albania	Vlore 4	V4	17	40°27'02.17"N	19°28'36.78"E	10/2015	no
Albania	Vlore 5	V5	18	40°27'00.09"N	19°28'34.87"E	10/2015	no
Albania	Vlore 6	V6	21	40°26'58.87"N	19°28'33.68"E	10/2015	no
Albania	Vlore 7	Vz	20- 22	40°26'58.18"N	19°28'36.36"E	10/2015	no
Albania	Dermi	Der	5	40°08'38.48"N	19°37'41.08"E	10/2014	yes
Albania	Jala 1	J	4	40°07'07.90"N	19°42'01.64"E	10/2015	yes
Albania	Porto Palermo 1	PP1	5	40°3'51.14"N	19°47'33.98"E	10/2014	yes
Albania	Porto Palermo 2	PP2	30	40°3'51.30"N	19°47'31.89"E	10/2014	no
Albania	Sarande Bay 1	SB1	5	39°52'23.04"N	20°0'29.19"E	10/2014	yes
Albania	Sarande Bay 2	SB2	30	39°52'20.82"N	20°0'28.16"E	10/2014	no
Albania Albania	Gjiri Monastiri Bay 1 Gjiri Monastiri Bay 2	MB1 MB2	5 30	39°48'49.79"N 39°48'51.71"N	20° 0'36.49"E 20° 0'34.89"E	10/2014 10/2014	yes
Italy	Otranto	11	10-	40°09'25.01"N	20 034.89 E 18°29'25.01"E	5/2013	yes No
Italy	Otranto	12	11 23	40°09'08.08"N	18°29'52.07"E	5/2013	No
Italy	Otranto	12	25	40°09'24.07"N	18°29'52.07 E 18°30'02.01"E	5/2013	No
Italy	Otranto	13	28	40°09'19.02"N	18°29'58.08"E	5/2013	No
Italy	Otranto	14	10	40°09'25.00"N	18°29'25.09"E	5/2013	No
Italy	Otranto	16	10	40°09'22.09"N	18°29'27.15"E	5/2013	No
Italy	Otranto	10	10	40°09'25.83"N	18°29'23.50"E	5/2013	No

Italy	Otranto	18	11	40°09'23.77"N	18°29'23.60"E	5/2013	No
Italy	Otranto	19	11	40°09'27.24"N	18°29'24.66"E	5/2013	No
Italy	Otranto	20	11	40°09'25.00" N	18°29'25.09"E	5/2013	No
Italy	Tricase /Porto di Gallipoli	21	1	39°55'49.01"N	18°23'42.42"E	5/2013	No
Italy	Tricase / Porto di Gallipoli	22	2-3	39°55'48.90"N	18°23'43.32"E	5/2013	No
Italy	Porto Santa Maria di	23	5-6	39°47'40.49"N	18°21'39.44"E	5/2013	No
	Leuca						
Italy	Porto Santa Maria di	24	3	39°47'41.80"N	18°21'43.31"E	5/2013	No
	Leuca						
Italy	Baia Verde (Gallipoli)	25	4	40°02'43.07"N	18°00'24.08"E	5/2013	No
Italy	Baia Verde (Gallipoli)	26	5	40°02'43.07"N	18°00'24.07"E	5/2013	No
Italy	Rada di Gallipoli	27	2	40°03'22.45"N	17°58'27.08"E	8/1990	No
Italy	Rada di Gallipoli	28	2	40°03'23.32"N	17°03'27.32"E	8/1990	No
Italy	Rada di Gallipoli	29	2	40°03'22.95"N	17°58'27.09"E	8/1990	No
Italy	Rada di Gallipoli	30	3	40°03'18.19"N	17°58'11.34"E	8/1990	No
Italy	Rada di Gallipoli	31	3	40°03'19.32"N	17°58'24.89"E	8/1990	No
Italy	Rada di Gallipoli	32	3	40°03'17.67"N	17°58'11.33"E	8/1990	No
Italy	Rada di Gallipoli	33	4	40°03'16.94"N	17°58'12.28"E	8/1990	No
Italy	Rada di Gallipoli	34	4	40°03'20.44"N	17°58'25.94"E	8/1990	No
Italy	Rada di Gallipoli	35	4	40°03'21.17"N	17°58'26.73"E	8/1990	No
Italy	Rada di Gallipoli	36	4	40°03'20.21"N	17°58'26.34"E	8/1990	No

# 7.2 Unpublished data

Unpublished data from Ionian and Aegean Sea sample sites. Percent abundances of wall structural types, number of species and genera, diversity indices: Fisher  $\alpha$  and Shannon (h), dominance factor, percent abundance of amphisteginids among the entire foraminiferal biota as well as among hyaline species, percent abundances of LBF foraminifera, morphogroups (trochospiral, planispiral, smaller miliolids), epiphytic foraminifera (temporary and permanent attached), water depth and substrate type.

	Zakynthos	Zakynthos 2	Syros 1	Syros 2	Syros 3	Kreta	Kreta 2	Kreta 3
Miliolid %	<u>1</u> 4,5	48,0	18,4	44,3	42,4	1 32,9	43,9	50,8
Hyaline %	88,0	52,0	76,3	55,7	56,0	66,8	55,5	47,2
Agglutinated	00,0	52,0	70,5	55,7	50,0	00,0	55,5	.,,2
%	7,4	0,0	5,3	0,0	1,7	0,3	0,7	1,7
Number of	- 1	- , -	22	48	39	- 7-	- 7 -	7 -
species	17	51				47	44	56
Number of			13	23	21			
genera	13	30				21	20	34
Fisher a	4,167	20,14	5,352	16,13	11,92	15,62	14,19	19,47
Shannon (H)	0,9619	2,924	1,815	3,057	2,57	2,892	2,573	3,26
Dominance	0,6542	0,1157	0,2962	0,08818	0,1253	0,09061	0,1435	0,06442
Amphistegina								
spp. %	80,6	27,1	66,0	4,0	31,5	16,9	19,3	6,6
Amphistegina								
% among								
hyaline	01.5	50.0	965	7.2	1.0	25.4	247	1 / 1
foraminifera	91,5	52,2	86,5	7,2	1,8	25,4	34,7	14,1
Peneroplis spp. %	1,3	22,2	15,3	11,3	31,8	12,6	25,9	27,2
Laevipeneroplis	1,5	22,2	0,0	0,0	0,0	12,0	23,9	0,3
karreri %	0,0	0,9	0,0	0,0	0,0	0,0	0,3	0,5
Sorites spp. %	0,0	0,9	0,9	0,0	1,0	0,0	1,3	4,3
Coscinospira	0,5	0,7	0,0	0,0	0,0	0,0	0,0	0,0
spp. %	0,0	1,8	0,0	0,0	0,0	0,0	0,0	0,0
LBF in %	83,2	52,5	82,2	16,3	65,2	29,9	46,8	38,5
Amphistegina	,	,	,	,	,	,	,	,
% among LBF	96,9	51,7	80,3	24,5	48,2	56,7	37,9	6,6
Amphistegina								
% among LBF								
(incl. elphidiid								
forams)	94,3	49,2	76,0	19,4	45,2	38,1	37,9	14,7
Elphidium					4.0		4.0	
spp. %	2,3	2,7	4,7	4,3	4,3	14,6	4,0	6,6
Smaller	2.0	22.2	2.2	9.6	22.2	10.0	16.2	10.0
miliolids % Trochospiral	2,9	22,2	2,2 5,6	8,6 24,0	32,2	19,9 33,6	16,3 30,2	18,9 25,0
foraminifera			3,0	24,0	20,2	55,0	50,2	23,0
101 annini ei a %	84,1	42,1						
Amphistegina	01,1	12,1						
% among								
trochospiral								
foraminifera	95,8	64,5	92,2	14,3	60,9	33,6	38,9	21,1
Planispiral			19,9	37,1	38,7	30,2	27,9	34,2
foraminifera								
%	3,9	29,4						
Epiphytic taxa								15,0
% (temp.	10.0			10-5	10.5			
attached) %	12,9	67,4	2,8	13,7	12,3	1,0	3,7	0.0
Epiphytic taxa	1.2	2.2	0,0	0.7	0,0	0,0	0,0	0,0
% (perm.	1,3	2,3						

attached)								
Epiphytes taxa								74,1
(temp. &								
perm. +								
smaller								
miliolids) %	14,2	69,7	26,9	60,3	58,2	48,2	53,5	
Water depth			2	2	2	2	2	1.5
( <b>m</b> )	10	12						
Substrate type	Coarse	Fine grained	Medium	Fine	Fine	Medium	Medium	Medium
	grained	sand	grained	grained	grained	grained	grained	grained
	sand		sand	sand	sand	sand	sand	sand

# 7.3 Non-indigenous foraminiferal species in shallow waters near the Port of Otranto

NI foraminiferal species present in shallow-waters near the Port of Otranto (*Euthymonacha polita*, *Spiroloculina antillarum* and *Loxostomina costulata limbata*) were found in 10-23m water depth in sand-algae and seagrass habitats.

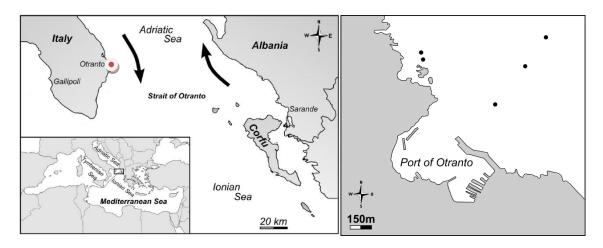


Fig 1 Left: study area in shallow-waters near the Port of Otranto/Italy (red dot), black arrows indicate the main directions of sea surface currents in the Adriatic Sea. Right map showing sample sites situated near the Port of Otranto.

Samples	18	19	20	34	35	36
Latitude	40°09'08.08"N	40°09'24.07''N	40°09'19.02"N	40°09'25.01''N	40°09'25.00''N	40°09'25.00"N
Longitude	18°29'52.07''E	18°30'02.01"E	18°29'58.08"E	18°29'25.01"E	18°29'25.09''E	18°29'25.09"E
Depth (m)	23	26	28	10-11	10-11	10-11
Individuals	1167	479	736	461	765	620
Species	106	87	90	63	82	68
Genera	54	43	42	36	53	42
Fisher a	28.32	31.10	26.91	19.73	23.28	19.48
Shannon (H)	3.942	3.896	3.749	3.364	3.318	3.204
% abundance of NI foraminiferal species	1.9%	-	-	1.6%	1.2%	-
NI species	Euthymonacha polita, Loxostomina limbata costulata			Spiroloculina antillarum	Spiroloculina antillarum	
Habitat	sand - algae	sand - algae	sand - algae	seagrass	seagrass	seagrass

Table: Sample site information and the number of NI foraminiferal species in the Port of Otranto

The non-indigenous species *Spiroloculina antillarum* has been found rarely (2 specimens) in seagrass assemblages within the Port of Otranto. This species have been reported in the northern Adriatic Sea (Wiesner, 1913) as well as from the eastern Mediterranean coastline (Gulf of Kalloni, Greece, Debenay et al. 2005 - cf. *S. antillarum*; along the Aegean and Levantine coast of Turkey, Meriç et al. 2008a, b; in shallow-waters off Israel, Hyams-Kaphzan et al. 2008 as well as along the coast of Egypt, Samir et al. 2003). *Spiroloculina antillarum* is, furthermore, distributed in the Indo-Pacific (Gulf of

Aqaba/Red Sea, Hottinger et al. 1993) Pacific (New Zealand, Hayward et al. 1999) and Atlantic Ocean (Caribbean, e.g. Culver and Buzas 1980). Zenetos et al. 2008 and the EASIN list classify *Spiroloculina antillarum* as a Lessepsian migrant, although a novel study conducted by Meric et al. (2015) state their presence in the Middle Pleistocene Mediterranean sequences, so that it should better be classified as both, a successful returnee (a foraminiferal species, which occurred in the fossil record from Pleistocene onwards and/or return/ed recently) as well as Lessepsian migrant. Its introduction via ballast ship water from the Atlantic of Pacific, however, can also be excluded.

Only one individual of *Euthymonacha polita* was observed in a sand-algae sample in shallow-waters near the Port of Otranto. This record here and its abundant occurrence records from around Kusadasi (Aydin), Ilica (Cesme-Izmir) Bays and NW Karaburun Peninsula (Meric et al. 2010) are the only evidences of its Mediterranean occurrence. The presence of *Euthymonacha polita* in the Port of Otranto, its local abundance in shallow-waters of Turkey and its absence in the remaining Mediterranean Sea especially around Isreal and Egypt, suggest it to be introduced via ballast ship water. To assess the source origin molecular investigations has to be conducted as its circumtropical distribution (Pacific Ocean: China, Zheng and Fu, 2008; Japan: Nomura, 1997; New Caledonia: Debenay, 2012; Indo-Pacific: Mozambique, Langer et al. 2013b; Altlantic Ocean: Culver and Buzas, 1980; Felder and Camp, 2009) impede a reliable origin.

*Loxostomina limbata costulata* (only one individual) has been found in a sand-algae habitat near the Port of Otranto. In the Mediterranean Sea it is solely documented in this study in the Port of Otranto and from shallow waters off Albania as well as from the coast of Israel (Hyams-Kaphzan et al. 2008). This species is reported to originate in the Indo-Pacific (Cushman, 1942), where it is additionally reported from the coast of Zanzibar (Thissen, 2014). Its presence in the Pacific Ocean is confirmed through Normura (1982, Japan) and Makled and Langer (2011, Timor Sea). Zenetos et al. 2012 as well as the EASIN list classify it as NI foraminiferal species, which is most probably introduced via shipping and as Lessepsian migrant.

#### Systematic of non-indigenous species in the Port of Otranto

Three non-indigenous species have been found in the sample sites located in the Port of Tranto (SE Itly) : *Spiroloculina antillarum* d'Obigny, *Euthymonacha polita* (Chapman) and *Loxostomina limbata* (Brady) *costulata* (Cushman).

#### Spiroloculina antillarum d'Orbigny 1839

Pl.1, figs. 3a-b

1839a Spiroloculina antillarum – d'Orbigny p. 166; pl. 9, figs 3,4.
1977b Spiroloculina antillarum d'Orbigny – Le Calvez, p. 91; pl. 17, figs 1-6.
1993 Spiroloculina antillarum d'Orbigny – Hottinger, et al., p. 45, pl. 24, figs. 15-17, pl. 25, figs. 1, 2.
2008a Spiroloculina antillarum d'Orbigny – Meriç et al., P. 2, fig. 19, Pl. 3,
2009 Spiroloculina antillarum d'Orbigny – Debenay, p. 341, figs 246 a-1, 247 a-1.
2012 Spiroloculina antillarum d'Orbigny – Meriç et al., p. 252, pl. 13, figs. 5-11

Euthymonacha polita (Chapman 1900)

Pl.1, figs. 1a-d

1900 Peneroplis (Monalysidium) polita – Chapman, p. 4, pl. 1, fig. 5 1987 Monalysidium polita Chapman – Baccaert, p. 61, pl. 110, fig. 8 1994 Euthymonacha polita (Chapman) – Loeblich and Tappan, p. 61, pl. 109, fig. 1-6 2009 Euthymonacha polita (Chapman) – Parker, p. 103, figs. 72 a-h, 73 a-j 2010 Euthymonacha polita (Chapman) – Meriç et al., p. 192, fig. 2 2013b *Euthymonacha polita* (Chapman) – Langer et al., p. 167, fig. 7.23-24 2014 *Euthymonacha polita* (Chapman) – Meriç et al., p. 296, pl. 36, fig. 8-15

#### *Loxostomina limbata* (Brady) *costulata* (Cushman) Pl.1, figs. 2a-b

1915 Bolivina limbata Brady – Heron-Allen & Earland, p. 646, pl. 50, figs. 1-4

- 1922c Bolivina limbata Brady var. costulata Cushman, p. 26, pl. 3, fig. 8
- 1942 Loxostoma limbata (Brady) var. costulatum (Cushman) Cushman, p. 36, pl. 10. figs. 2-4
- 1984 Brizalina (Parabrizalina) sp. A Reiss & Hottinger, fig. G 27 k, 1
- 1993 Loxostomina ? limbata (Brady) costulata (Cushman) Hottinger et al., p. 97, pl. 120, figs. 8-13
- 2009 Loxostomina limbata (Brady) Parker, p. 456, figs. 329 a-k, 330 a-h
- 2012 Loxostomina limbata (Brady) Debenay, p. 175, 302, pl. 12
- 2014 Loxostomina limbata (Brady) costulata (Cushman) Thissen, p. 71, pl. 13, figs. 19-21

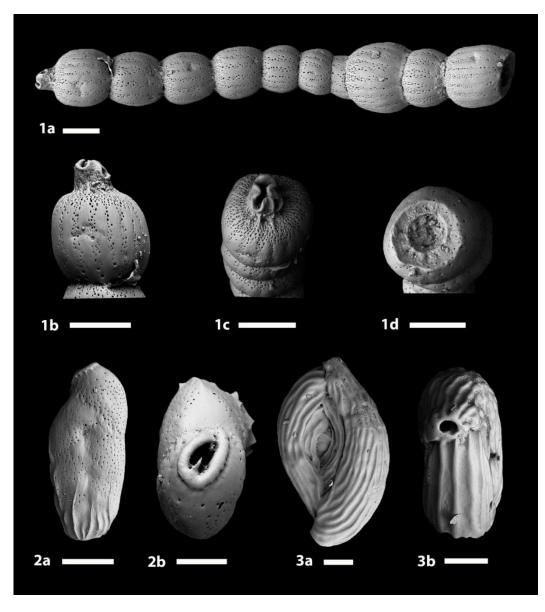


PLATE 1

**Plate 1**: 1a-d *Euthymonacha polita* (Chapman) a) side view 50mµ, b) side view aperture 50mµ, c) apertural view 50µm, d) basal view 50µm; 2a-d *Loxostomina limbata* (Brady) *costulata* (Cushman), a) side view 100µm, b) apertural view 50µm; 3a-b *Spiroloculina antillarum* d'Orbigny, a) side view 100µm, b) apertural view 100µm.

### 7.4. Systematic description of Amphistegina lobifera

Amphistegina lobifera LARSEN

### Appendix 7.4.1 - 7.4.2

"Coarsely perforate, lamellar, thick shelled, lenticular to subglobular, low trochospiral, involute test. Peripheral outline smooth, peripheral margin rounded. Dorsal chamber sutures flush, bent backwards in an unbroken, falciform arch. Sutures of alar prolongations strongly lobulated. Early chambers with lobes of about equal length; later, adult chambers with lobes of unequal length; later, adult chambers with lobes of unequal length, complicated by secondary foulding. The retral lobes of successive chambers (as seen by transparency of the walls) may be imbricated, covering each other like tiles on a roof. Radial, hemiseptular sutures longitudinally divide the lateral, alar chamber wall for a third or half of its radial extension. The hemiseptula are straight to moderately wavy, sometimes interrupted, never lobulated. The peripheral ending is independent of the position of the underlying periphery of the previous shell whorl. A large, transparent, sparcely perforated, flush umbo occupies the shell apex. Ventral chamber sutures sigmoidal-radial, strongly lobulated. In adult stellar chamberlets, retral chamber lobes of unequal length may cover umbilical parts of the previous chambers and obscure the early, transparent, nearly imperforate ventral umbo. The sutures of the stellar chamberlets (umbilical plate sutures) are long, faintly sigmoidal and, at low angles, oblique to the shell radius. Aperture in ventral, interiomarginal position forming a low but comparatively long slit with a notched or postulated lip extensing from the junction of the stellar chamberlet suture with the apertural face to the periphery of the shell. Areal supplementary apertures are irregularely spaced in between pustules covering the apertual face in rows radiating from the aperture. The internal, lateral wall surfaces of the stellar and the main chamber cavities including the retral lobes are covered with evenly spaced, polygonal, deep "eggholder" structures representing internal pore-pits. These structures house diatom symbionts of B2a-type ultrastructure (Leutenegger, 1984) responsible for the olive-greenish colour of the living animal." Description by Hottinger et al. (1993).

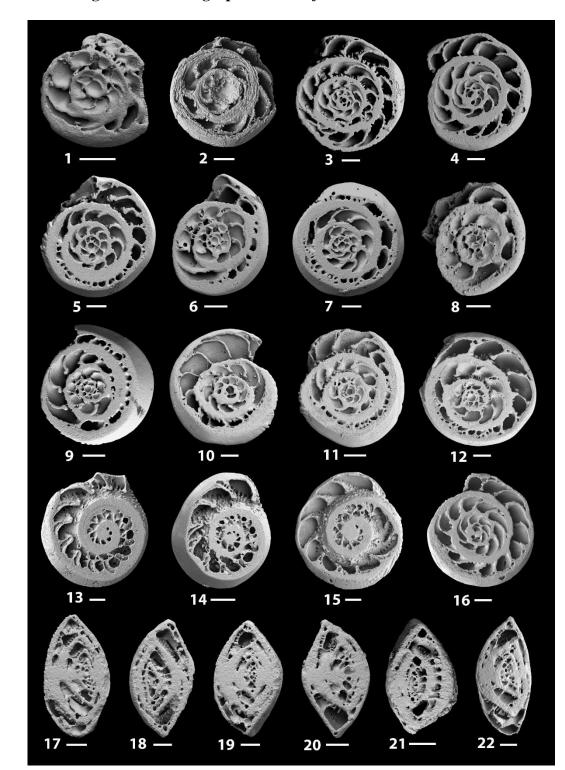
Members of the family *Amphistegina* were found to construct their chambers of two layers of calcite separated by an organic layer. With the addition of the outer calcareous layer forms a continuous sheet of material covering all exposed ontognetecically younger shell parts (Hallock and Hansen, 1987; Plate 1 fig. 2). The surface of the umbilico-lateral and peripheral dorsal lateral walls are covered with hemispherical to oval-elongate pustules (Plate 1, fig. 13-15). The endoskeletal shell elements may consist of linear elements (pillars) following the flux of the protoplasm along the foramenal axes without subdividing the chamber lumen into definite compartements (Plate 2, Fig 5-10). Hottinger (Larger foraminifera, Short course 1997).



# 7.4.1 Reflected light-images of A. lobifera individuals from the Mediterranean Sea.

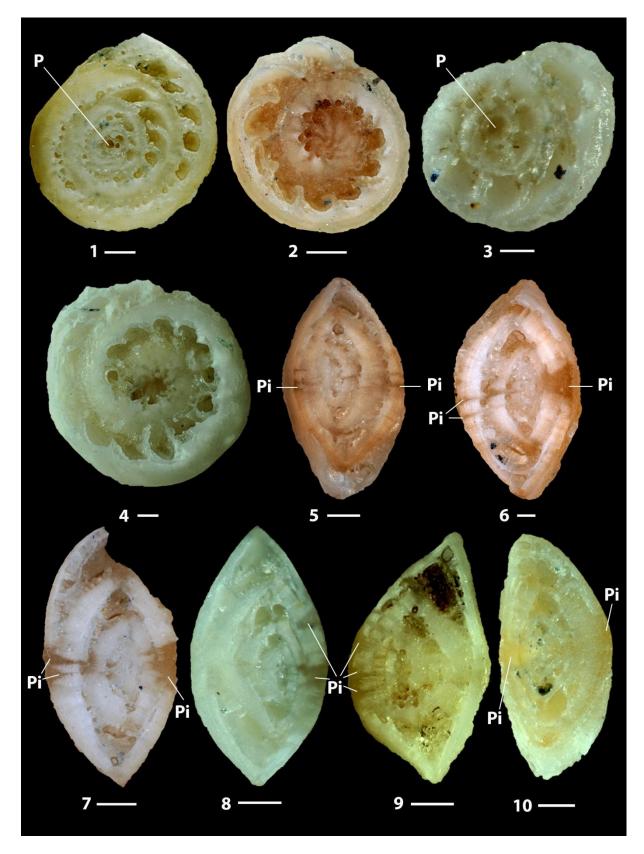
1, 3, 6, 7, 10, 12, 14, 16, 18, 22, 24, 25, 27, 29 ventral views. 2, 4, 5, 8, 9, 11, 13, 15, 17, 19, 20, 21, 23, 18, 30 dorsal views, scale bar= $200\mu$ m.

### 7.4.2 Micrographs of A. lobifera individuals from the Mediterranean Sea



# 7.4.2.1 Scanning electron micrographs of A. lobifera individuals

1-16. Polished equatorial sections of *A. lobifera* specimens; 17-22 Polished transversal axial sections of *A. lobifera* specimens. Specimens 1, 3, 5, 6, 7, 9, 11 with bilocular nucleonchs, specimens 8 and 12 with monolocular nucleoconchs, 4, 10, 13, 14, 15 transverse equatorial sections, scale bar =  $200\mu$ m.



7.4.2.2 Reflected light-micrographs of A. lobifera individuals from the Mediterranean Sea

1-4. Polished equatorial sections of *A. lobifera* specimens; 1 and 3 microspheres, 2 and 4 transversal equatorial sections, 5-10 transversal axial sections. P= proloculus, Pi= Pillar, scale bar= 200μm.

### 7.5 Non-indigenous foraminiferal species in the Mediterranean Sea

# 7.5.1 Contribution of NI foraminiferal species in the Mediterranean Sea and its subregions

**Table 1**: Contribution of NI foraminiferal species and numerical abundances in the Mediterranean Sea subbasins: EMS: Eastern Mediterranean Sea; CMS: Central Mediterranean Sea; WMS: Western Mediterranean Sea (after Zenetos et al. 2008, 2010, 2012; EASIN 2016 and data recorded in this thesis). Listed are numbers of species as well as percentages of wall structural types (miliolids, perforate and agglutinated) and of functional groups of foraminifera (LBF: Larger benthic foraminifera, pararotaliids and elphidiids) of the entire foraminiferal assemblage (783 species; Langer, 2008a; including 83 NI species).

	Number of NI foraminiferal species	% abundance among the whole foraminiferal fauna
Miliolids	47	56.6
perforates	31	37.3
agglutinated	6	7.2
LBF	17	20.4
elphidiids	2	2.4
EMS	79	95.2
CMS	9	10.8
Adriatic Sea	17	20.5
WMS	3	3.6

# 7.5.2 Numerical abundances of wall structural types and introduction pathways of NI foraminifera in the Mediterranean Sea

**Table 2:** Percent abundances of wall structural types and introduction pathways of NI foraminiferal species in the eastern Mediterranean (EMS), central Mediterranean (CMS), western Mediterranean (WMS) and Adriatic Sea, LM= Lessepsian Migrants, SH=Shipping/ballast water, AQU= Aquaculture.

	EMS	CMS	WMS	ADRIA
Agglutinated	7,6	11,1	0,0	5,9
Miliolid	57,0	55,6	33,3	52,9
Hyalin	35,4	33,3	66,7	41,2
LM	53,2	55,6	33,3	17,6
SH	13,9	0,0	33,3	47,1
LM+SH	13,9	22,2	0,0	23,5
SH+AQU	1,3	0,0	33,3	5,9
unknown	17,7	22,2	0,0	5,9

**7.6.** NI foraminiferal species in the Mediterranean Sea, year of first documentation/first literature evidence, status: A = Alien; cry= cryptogenic; unknown, vector: LM= Lessepsian migrant; Shipping= Sh; Atlantic= Atl, origin source, spatial distribution in Mediterranean sub-basins and occurrence records: C=casual; Est=Established; Alien data sources: Zenetos et al. 2008= Z8; Zenetos et al. 10 = Z10; Zenetos et al. 2012= Z12, EASIN (European Alien species information network, data from 2016) and thesis data= TD.

	Species	Year/Location	Status	Vector	Origin source	EMS	CMS	WMS	Adria	Origin	Alien data
1	Agglutinella compressa El- Nakhal, 1983	2003 Egypt	А	LM primary	Samir et al. 2003	cas				Indo-Pacific	sourcesZ10;EASIN
2	<i>Agglutinella robusta</i> El- Nakhal, 1983	2003 Egypt	А	LM primary	Samir et al. 2003	cas	X			Indo-Pacific	Z10; EASIN
3	AmphisorushemprichiiEhrenberg, 1840	1997Greece	А	LM primary	Hollaus & Hottinger, 1997	est	est			circumtropical	Z10; EASIN
4	Amphistegina lobifera Larsen, 1976	1959 Greece	cry	LM primary,	Emery & Neev, 1960	est	est		est	Indo- Pacific/circumtropical	Z10; EASIN; TD
5	Archaias angulatus (Fichtel and Moll, 1798)	1964 Croatia/ 1948	cry	Sh Primary	Alfirevic, 1964				cas	Atlantic	Z10; EASIN
6	Articulina alticostata Cushman, 1944	2004 Turkey	А	Sh Primary	Meric et al., 2004	est				Indo-Pacific	Z10; EASIN
7	Articulina mayori Cushman, 1922	2006 Turkey	А	unknown	Oflaz, 2006	Х				Atlantic	Z12; EASIN
8	Articulina pacifica Cushman, 1944	1970 Croatia	А	Sh Primary	v Daniels 1970a, b	Х			Х	circumtropical	Z12; EASIN
9	Astacolus insolitus (Schwager, 1866)	2004 Turkey	А	Sh Primary + LM	Meric et al., 2004	est				Indo-Pacific	Z10; EASIN
10	Astacolus sublegumen (Parr, 1950)	2004 Turkey	А		Meric et al., 2004	est				Indo-Pacific	Z10; EASIN
11	Borelis sp.	2002	А	LM primary	Hymas et al. 2002	est				Indo-Pacific	Z10; EASIN
12	Bolivina simpsoni Heron- Allen & Earland, 1915/ Brizalina simpsoni	2007 Turkey	A	LM	Meric et al. 2010	cas				Indo-Pacific	Z10
13	Cibicides mabahethi Said, 1949	2008 Israel /1996	А	LM	Hyams et al. 2008	Х				Indo-Pacific	Z12; EASIN
14	<i>Clavulina angularis</i> D'Orbigny, 1826	1979 Tunisia	А	LM	Blanc-Vernet et al., 1979	est			cas	Indo-Pacific /circumtropical	Z10; EASIN

15	<i>Clavulina</i> cf. <i>multicamerata</i> Chapman, 1907	2007 Turkey	А	LM	Meric et al. 2007	Est				Indo-Pacific	Z10; EASIN
16	Coscinospira acicularis(Batsch, 1791)/ Spirolina acicularis	2011 Turkey	A	LM	Meric et al. 2011	Est				Atlantic	
17	Coscinospira hemprichii Ehrenberg 1839	1911 Croatia	cry	Sh (Primary) + LM	Wiesner, 1911	est			cas	Indo-Pacific	Z10; EASIN
18	Cribromiliolinella milletti (Cushman, 1954)	Х	А	unknown	X	X?				Indo-Pacific, Pacific	EASIN
19	<i>Cushmanina striatopunctata</i> (Parker & Jones, 1865)	1913 Croatia	А	Sh Primary	Wiesner, 1913	cas			Х	Indo-Pacific	Z10; EASIN
20	Cycloforina quinquecarinata (Collins, 1958)	2008 Israel /1996	А	LM	Hyams-Kaphzan et al., 2008	Х				Indo-Pacific, Pacific	Z12; EASIN
21	Cycloforina sp.	1993 Israel	А	LM	Hottinger et al., 1993	est				Indo-Pacific	Z10; EASIN
22	Cyclorbiculina compressa (d'Orbigny, 1839)	2007 Turkey	А	LM	Meric et al. 2007	Est/cas				circumtropical	Z10; EASIN
23	Cymbaloporetta plana (Cushman, 1924)	1993 Italy	А	Sh Primary	Sgarrella & Moncharmont Zei, 1993	Cry/est		Cry/est	Cry/cas	Indo-Pacific	Z10; EASIN
24	Dendritina antillarum d'Orbigny, 1839	1999 Israel	А	LM	Hyams, 2000	Х					EASIN
25	<i>Edentostomina cultrata</i> (Brady, 1881)	1993 Israel	А	LM primary	Yanko et al., 1993	Est				Indo-Pacific	Z10; EASIN
26	<i>Elphidium</i> cf. <i>charlottense</i> (Vella, 1957)	2007 Turkey	А	Sh (Primary)	Meric et al., 2007	Est/				Indo-Pacific	Z10; EASIN
27	<i>Elphidium striatopunctatum</i> (Fichtel & Moll, 1798)	1911 Croatia	А	Sh + LM	Schaudinn, 1911	Est			est?	circumglobal	Z10; EASIN
28	Entosigmomorphina sp	2007 Turkey	А	LM	Meric et al. 2007	Est	est				Z8
29	Epistomaroides punctatus (Said, 1949)	2012 Israel /2005	A	LM primary	Almogi-Labin & Hyams-Kaphzan, 2012	est				Inod-Pacific, Pacific	Z12; EASIN
30	<i>Euthymonacha polita</i> (Chapman, 1900)	2007 Turkey	А	Sh primary	Meric et al., 2010	cas			est?	circumtropical	Z10; EASIN; TD
31	<i>Euuvigerina</i> sp	2004 Turkey	А	LM	Meric et al. 2004	est					Z8

32	Haddonia sp	2007 Turkey	А	LM	Meric et al., 2007	est			Z10;
									EASIN
33	Hauerina diversa Cushman, 1946	1993 Israel	A	LM	Yanko et al. 1993	est		Indo-Pacific, Pacific	Z10; EASIN
34	Heterocyclina tuberculata (Möbius, 1880)	1995 Israel	А	LM	Yanko, 1995	est		Indo-Pacific	Z10; EASIN
35	Heterostegina depressa d'Orbigny, 1826	1968 Lebanon	А	LM	Moncharmont-Zei, 1968	est		Indo-Pacific/ circumtropical	Z10; EASIN
36	Lagena oceanica Albani, 1974	2006 Israel /2003	А	LM	Hyams, 2006	Х		Indo-Pacific	Z12; EASIN
37	Loxostomina cf. L. africana (Smitter, 1955)	2008 Israel/ 1996	А	LM + Sh	Hyams-Kaphzan et al., 2008	Х			Z12; EASIN
38	Loxostomina costulata (Cushman, 1922)	2008 Israel/ 1998	А	unknown	Hyams-Kaphzan et al., 2008	Х		Pacific	Z12; EASIN
39	Loxostomina limbata (Brady) costulata (Cushman)	2013 Italy	А	Sh			Est?	Indo-Pacific, Pacific	TD
40	Miliolinella fichteliana (d'Orbigny, 1839)	2004 Turkey	А	Sh + LM	Meric et al., 2004	X		circumtropical	EASIN
41	Mimosina affinis Millet, 1900	2015 Albania	А	Sh	Mouanga and Langer (in prep.)		est?	Indo-Pacific, Pacific	TD
42	Monalysidiumacicularis(Batsch, 1791)	2007 Turkey	А	Sh primary	Meric et al. 2012	X		circumtropical	EASIN
43	Naxotia attenuata (Cushman and Todd, 1944) / Spiroloculina attenuata Cushman & Todd, 1944	2008 Israel	А	LM	Hyams et al. 2008	X		Indo-Pacific	EASIN
44	Nodopthalmidium antillarum (Cushman, 1922)	1995 Israel	А	LM	Yanko, 1995	est	est?	circumtropical	Z10; EASIN; TD
45	<i>Pararotalia calcariformata</i> McCulloch, 1877	2008 Turkey	А	Sh + LM	Meric et al., 2013	Х		Indo-Pacific	EASIN
46	Pararotalia cf. P. socorroensis McCulloch, 1977	2008 Israel/1996		LM	Hyams-Kaphzan et al., 2008	X		Pacific	Z12; EASIN
47	Pararotalia spinigera (Loeblich & Tappan, 1957 (ex. Le Calvez, 1949)	1995 Israel	А	not assessed	Bresler & Yanko, 1995	Х			Z12; EASIN
48	Paratrochammina madeirae	2008 Israel	А	LM	Hyams-Kaphzan	Х		Red Sea	Z10;

	Bronniman, 1979	1996			et al., 2008						EASIN
49	Pegidia lacunata McCulloch,	2008 Israel	А	LM	Langer, 2008a	est				Indo-Pacific	Z10;
	1977			primary							EASIN
50	Peneroplis antillarum	2002 Israel	А	LM	Hyams et al., 2002	cas				Carribean or SW	Z10
	d'Orbigny, 1839									Atlantic, Indo-Pacific	
51	Peneroplis arietinus (Batsch,	2006 Turkey	А	LM +	Oflaz, 2006	est	est			Pacific, Atlantic	Z8;
	1791) / Coscinospira			shipping?							EASIN
50	arietinus)/ Spirolina arietina	1011 Count's		C1. ''	W 1011.	V	-		V		710
52	Planispirinella exigua (Brady, 1879)	1911 Croatia	А	Shipping?	Wiesner, 1911a	Х			Х	circumtropical	Z12; EASIN
53	Planogypsina acervalis	1913 Croatia	cry	LM	Wiesner, 1913	X	X	X		circumtropical	Z10;
55	(Brady, 1884)	1915 Citatia	cry	primary	wieshei, 1915	Λ	Λ	Λ		encumuopicai	EASIN
54	Planogypsina squamiformis	2004 Turkey	А	LM	Meric et al., 2004a	est				circumtropical	Z10;
04	(Chapman, 1901)	2001 Turkey	11	primary	Mone et un, 200 lu	CSC				eneumuopieur	EASIN
55	Procerolagena oceanica	2003 Israel	А	LM	Hyams, 2006	Х				Indo-Pacific	EASIN
	(Albani, 1974)										
56	Pseudohauerinella dissidens	2008 Israel/	А	LM	Hyams-Kaphzan	Х				Indo-Pacific	Z12;
	McCulloch, 1977	1996		primary	et al., 2008						EASIN
57	Pseudolachlanella slitella	1979 Tunisia	А	unknown	Blanc-Vernet et	est				Indo-Pacific	Z10;
	Langer, 1992				al., 1979						EASIN
58	Pseudomassilina australis	2000	А	LM	Hyams, 2000	Х				circumtropical	Z12;
50	(Cushman, 1932)	Israel/1996	•	primary LM	A	4				Indo-Pacific	EASIN
59	<i>Pseudomassilina reticulata</i> (Heron-Allen & Earland)	2001 Turkey	А		Avsar et al., 2001	est				Indo-Pacific	Z10; EASIN
60	Pseudotriloculina	2008 Israel/	А	primary LM	Hyams-Kaphzan	X				Indo-Pacific, Pacific	Z12;
00	subgranulata	1996	Л	primary	et al., 2008	Λ				fildo-1 actric, 1 actric	EASIN
	(Cushman, 1918)	1770		printery	et ul., 2000						
61	Pyrgo denticulata (Brady,	1993 Israel	А	LM	Yanko et al. 1993	est		1		Indo-Pacific	Z10
-	1884)										
62	Quinqueloculina	1911 Italy	А	Sh + Aqu	Wiesner, 1911b	Х		Х	Х	Atlantic	EASIN
	carinatastriata (Wiesner,										
	1923)										
63	Quinqueloculina milletti	2006 Turkey/	А	Sh Primary	Oflaz, 2006	Х				Pacific, Atlantic	Z12;
<i>.</i> .	(Wiesner, 1923)	1988			11 17 1	N/					EASIN
64	Quinqueloculina cf. Q.	2008 Israel/	А	LM	Hyams-Kaphzan	Х				Pacific, Indo-Pacific	Z12;
	<i>multimarginata</i> Said, 1949	1996		primary	et al., 2008						EASIN
65	<i>Quinqueloculina</i> cf.	2007 Turkey	А	Sh primary	Meric et al., 2007	est		+		Indo-Pacific	Z10;
05	$\mathcal{L}^{\mu}$	2007 Turkey	17	1 Sh prinary	Meric et al., 2007	USI				mao-i acine	L10,

	mosharrafai Said, 1949									EASIN
66	Schlumbergerina alveoliniformis (Brady, 1879 )	2007 Turkey	Α	unknown	Meric et al., 2007	est			circumtropical	Z10; EASIN
67	<i>Septloculina rotunda</i> El-Nakhal, 1990	2006 Turkey/ 1988	А	Sh primary	Oflaz, 2006	Х			Red Sea	Z12; EASIN
68	<i>Septloculina tortuosa</i> El-Nakhal, 1990	2006 Turkey/ 1988	А	Sh primary	Oflaz, 2006	Х			Red Sea	Z12; EASIN
69	Sigmamiliolinella australis (Parr, 1932)	2015 Albania	А	Sh	Mouanga and Langer (in prep.)			est?	Indo-Pacific, Pacific	TD
70	Sigmoihauerina bradyi (Cushman, 1917)	2006 Turkey/ 1988	A	Sh primary	Oflaz, 2006	Х			Pacific, Atlantic	Z12; EASIN
71	Siphonaperta distorqueata (Cushman, 1954)	2008 Israel/ 1996	А	LM primary	Hyams-Kaphzan et al., 2008	Х			Pacific, Indo-Pacific	Z12; EASIN
72	Siphonaperta pittensis (Albani, 1974)	2008 Israel/ 1996	А	LM primary	Hyams-Kaphzan et al., 2008	Х			Indo-Pacific	Z12; EASIN
73	Sorites variabilis Lacroix, 1941	1997 Tunisia (France)	А	LM primary	Blanc-Vernet et al., 1979	est	est		Indo-Pacific	Z10; EASIN
74	Spirolina acicularis (Batsch, 1791) / Coscinospira acicularis(Batsch, 1791)	2007/ Turkey	Α	Shipping + LM?	Meric et al., 2011	est			circumtropical	Z12; EASIN
75	Spiroloculina angulata Cushman, 1917	1993	А	LM?	Yanko et al. 1993	cas	X		Pacific	Z10; EASIN
76	Spiroloculina antillarum D'Orbigny, 1839	1913 Croatia	А	Sh + LM	Wiesner, 1913	est	X	X	circumtropical	Z10; EASIN; TD
77	Spiroloculina aff. S. communis Cushman & Todd, 1944	2008 Israel/ 1996	А	LM primary	Hyams-Kaphzan et al., 2008	Х			Pacific , Atlantic	Z12; Easin
78	<i>Spiroloculina nummiformis</i> Said, 1949	2008 Israel/ 1996	А	LM primary	Hyams-Kaphzan et al., 2008	Х			Indo-Pacific, Pacific	Z12; EASIN
79	<i>Tretomphaloides clara</i> (Cushman, 1934)	2008 Israel/ 1996	А	LM primary	Hyams-Kaphzan et al., 2008	Х			Red Sea	Z12; EASIN
80	<i>Triloculina asymmetrica</i> Said, 1949	2006 Turkey/ 1988	А	Sh primary + LM	Oflaz, 2006	Х			Red Sea	Z12; EASIN
81	<i>Triloculina fichteliana</i> d'Orbigny, 1839	1911 Croatia	А	Sh + LM	Wiesner, 1911b	est		X	circumtropical	Z10

83	Vaginulinopsis	sublegum	en	2004 Tu	ırkey	А	LM	Meric et al., 2004	Х		circumtropical	EASIN
	Parr, 1950											
84	Varidentella	cf.	<i>V</i> .	2008	Israel/	А	LM	Hyams-Kaphzan	Х		Indo-Pacific, Pacific	Z12;
	neostriatula			1996			primary	et al., 2008				EASIN
	(Thalmann, 1950)	)										

# 7.6 Excluded foraminifera from Alien species lists (Zenetos et al. 2008; 2010; 2012).

Species	reasoning	Occurrence records/source	Excluded by
Acervulina inhaerens Schulze, 1854	?	Turkey: Meric et al. 2004	Zenetos et al. 2010
Agglutinella arenata (Said, 1949)	fossil record	Turkey: Yokes & Meric, 2009;Cinar et al. 2010	Zenetos et al. 2012
Amphistegina lessonii d'Orbigny in Guérin-Méneville, 1832	native	Israel: Hyams et al. 2002, Pelagian Islands: Caruso & Cosentino, 2014, Cyprus: Abu Tair & Langer, 2010; Mouanga & Langer, 2014, Ionian Islands:Mouanga & Langer, 2014	Zenetos et al. 2012
Amphistegina madagascariensis d'Orbigny, 1903	synonym /native	Tunisia: Blanc-Vernet, 1979,Turkey: Burrolet, 1981,Yokes & Meric, 2009, Egypt: Samir et al. 2003	Zenetos et al. 2012
Iridia diaphana Heron-Allen & Earland, 1914	?	Spain: Sanchez-Ariza, 1983, Turkey: Yokes & Meric, 2009; Meric et al., 2010	Zenetos et al. 2010
Cymbalporetta squammosa (d'Orbigny, 1839)	fossil record	l record Turkey: Meric et al., 2007; 2008a,b; Yokes & Meric, 2009, Pelagian Islands: Caruso & Cosentino, 2014, Italy:Caruso & Cosentino, 2014	
Miliolinella cf. M. hybrida (Terquem, 1878)	fossil record	Meric et al., 2007; 2008a,b, Yokes & Meric, 2009; Cinar et al. 2010	Zenetos et al. 2012
<i>Operculina ammonoides</i> Sidebottom, 1918	unsupported record	Croatia: Dezelic, 1896; Schaudinn, 1911; Vatova 1928, Turkey: Yokes & Meric, 2009; Yanko, 1995	Zenetos et al. 2012
Planorbulinella larvata (Parker & Jones, 1865)	unsupported record	Israel: Yanko 1995, Turkey: Yokes & Meric, 2009	Zenetos et al. 2012
Pyramidulina catesbyi (d'Orbigny, 1839)	fossil record	Israel: Yanko et al., 1993, Turkey: Avsar et al. 2001; Meric et al. 2007; Meric et al. 2008b; Yokes & Meric, 2009; Meric et al., 2010; Cinar et al. 2010	Zenetos et al. 2012
Pyramidulina perversa	fossil record	Turkey: Meric et al. 2007; Meric et al.	Zenetos et al. 2010

		2008b; Yokes & Meric, 2009	
Pulleniatina obliquiloculata	fossil record	Turkey: Meric et al. 2004b; Yokes & Meric, 2009; Cinar et al. 2010	Zenetos et al. 2012
Schackoinella imperatoria	fossil record	Lebanon: Blanc-Vernet, 1969	Zenetos et al. 2012
		(G.imperatoria), Adria :Cimerman &	
		Langer, 1991; Sgarrella & Moncharmont,	
		1993; Banchetti et al., 2009	
Triloculina affinis	?	Turkey: Meric et al., 2010	Zenetos et al. 2010
Sorites orbiculus	fossil record	Italy: Hofker, 1930, Israel: Hyams-	Zenetos et al. 2012
		Kaphzan et al., 2008; Yanko, 1995,	
		Egypt: Samir et al. 2001; Samir et al.	
		2003; Elshanawany et al. 2011, Greece:	
		Koukousioura et al. 2010; Zenetos et al.	
		2011; Mouanga & Langer, 2014, Pelagian	
		Islands: Caruso & Cosentino, 2014,	
		Cyprus : Mouanga & Langer, 2014; Abu	
		Tair & Langer, 2010, Croatia : Vanicek,	
		2000; Cosovic et al. 2002; Alfirević, S.,	
		1998; Vidovic et al. 2016, Italy: Crapon-	
		De Caprona & Benier, 1985; Caruso &	
		Cosentino, 2014; Cimerman & Langer,	
		1991; Sgarella & Moncharmont-Zei,	
		1993; Mateau-Vicens et al. 2014, Greece:	
		Cherif, 1970; France: Blanc-Vernet et al.	
		1979	

# 7.7. Selected sample data used for the line diagram (Conclusions, Fig. 4)

HK= Hyams Kapzhan; BV= Blanc-Vernet; Tri= Triantaphyllou

Country	Location/sample	Amphistegina %	Taxa_S	water depth (m)	Data source
Albania	Sarande Bay 1	9,2	53	5	thesis data
Albania	Sarande Bay 2	0,0	63	30	thesis data
Albania	Porto Palermo 1	0,6	59	5	thesis data
Albania	Porto Palermo 2	0,0	68	30	thesis data
Albania	Monastiri Bay 1	75,0	27	5	thesis data
Albania	Monastiri Bay 2	0,3	71	30	thesis data
Albania	Dermi	3,4	63	5	thesis data
Greece/Corfu	Mpoukaris	16,7	61	8	thesis data
Greece/Corfu	Mpoukaris	11,9	64	8	thesis data
Greece/Corfu	Agnos	6,6	53	10	thesis data
Greece/Ithaka	Ithaka Polis 1	11,4	55	12	thesis data
Greece/Ithaka	Ithaka Polis 2	0,3	40	20	thesis data
Greece/Meganisi	Atherinos Bay	16,7	48	15	thesis data
Greece/Zakynthos	St. Nicolas	80,6	17	8	thesis data
Greece/Zakynthos	Marathonisi	27,1	51	10	thesis data
Greece/Crete	Komos Beach	16,9	51	2	thesis data
Greece/ Crete	Kali Beach	19,3	49	2	thesis data
Greece/Crete	Pacheia Ammos	6,6	57	1,5	thesis data
Greece/Syros	Lia Beach	31,5	53	2	thesis data
Greece/Syros	Galissas Bay 1	66,0	39	2	thesis data
Greece/Syros	Galissas Bay 2	4,0	22	2,0	thesis data
Greece/Aegina	Aegina	1,4	45	0,5	thesis data
Cyprus	Aiya Thekla	18,9	33	2	thesis data
Cyprus	Aiya Thekla	60,1	12	3	thesis data
Israel	Haifa South A1	0,3	24	3	HK et al. 2008
Israel	Haifa South A2	1,6	29	6	HK et al. 2008
Israel	Haifa South A3	1,5	28	9	HK et al. 2008
Israel	Haifa South A4	39,4	65	15	HK et al. 2008
Israel	Haifa South A5	31,3	55	20	HK et al. 2008

Ianaal	Haifa South A6	28,3	48	25	HK et al. 2008
Israel	Halla South Ao	28,5	40	23	HK et al. 2008
Israel	Haifa South A7	15,4	33	30	HK et al. 2008
Israel	Bet-Yanai D2	0,4	29	6	HK et al. 2008
Israel	Bet-Yanai D3	0,3	32	9	HK et al. 2008
Israel	Akhziv M1	0,3	52	3	HK et al. 2008
Israel	Akhziv M3	0,3	67	9	HK et al. 2008
Israel	Akhziv M4	50,9	54	15	HK et al. 2008
Israel	Akhziv M5	16,4	67	20	HK et al. 2008
Israel	Akhziv M6	3,8	74	25	HK et al. 2008
Israel	Akhziv M7	0,3	85	30	HK et al. 2008
Israel	Rosh Hanikra Isles/TA1	0,8	67	30	Lazar, 2007
Israel	Rosh Hanikra Isles/SA7	2,2	59	25	Lazar, 2007
Israel	Rosh Hanikra Isles/NA20	3,4	41	20	Lazar, 2007
Israel	Rosh Hanikra Isles/NA21	22,4	35	15	Lazar, 2007
Israel	Rosh Hanikra Isles/NA23	37,1	14	5	Lazar, 2007
Israel	Rosh Hanikra Isles/NB24	32,5	21	5	Lazar, 2007
Israel	Rosh Hanikra Isles/SB14	91,3	10	10	Lazar, 2007
Israel	Rosh Hanikra Isles/TC4	1,0	28	5	Lazar, 2007
Israel	Rosh Hanikra Isles/SC17	0,8	25	0	Lazar, 2007
Tunisia	Gulf of Gabes/DRT28	14,0	26	18	BV et al. 1979
Egypt	Alexandria 18	53	15	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 19	73,5	13	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 35	15	17	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 36	31	23	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 37	25	30	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 38	31,5	25	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 39	37	26	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 40	60	27	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 41	36	28	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 42	30	27	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 43	25	17	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 44	70	33	5,0-16,0	Samir et al. 2003
L	1	100	_ L L		1

Egypt	Alexandria 45	16	32	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 46	17	31	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 47	49	34	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 48	29,5	35	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 49	27	17	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 50	58	35	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 51	45	29	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 52	27	22	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 53	29	23	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 54	11	35	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 55	30	32	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 56	27	22	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 57	2,5	29	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 58	24	29	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 59	46,5	26	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 60	30	25	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 66	54	24	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 67	46	24	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 72	60	22	5,0-16,0	Samir et al. 2003
Egypt	Alexandria 74	56	20	5,0-16,0	Samir et al. 2003
Greece	Korthi Gulf/KO1	35	32	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO2	40,6	21	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO3	29	24	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/ KO4	38	27	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO5	57,7	29	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO6	42,3	25	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO7	31,7	30	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO8	41	22	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO9	36,6	28	0,2-6,0	Tri et al. 2005
Greece	Korthi Gulf/KO10	40,3	29	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA1	32,7	22	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA3	53,5	33	0,2-6,0	Tri et al. 2005
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Greece	Kastro Gulf /KA4	42,6	23	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA7	47,3	32	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA9	42,6	28	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA11	51,3	28	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA12	44	24	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA13	26	28	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA14	36,6	31	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA15	38,3	21	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA16	12,1	21	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA18	42,6	34	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA19	28,3	25	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA21	29	28	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA22	33,3	21	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA23	23,7	31	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA25	41,6	30	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA27	38,3	21	0,2-6,0	Tri et al. 2005
Greece	Kastro Gulf /KA28	25,3	24	0,2-6,0	Tri et al. 2005

#### 7.8 Systematic descriptions of Albanian foraminiferal species

Suborder Allogromina Loeblich and Tappan, 1961 Family Saccamminidae Brady, 1884 Subfamily Saccaminae Brady, 1884

Lagenammina atlantica (Cushman, 1944)

Plate.1, figs. 1a-b

1944 *Proteonina atlantica* - Cushman, p. 5, pl. 1, fig. 4 (fide Ellis and Messina, 1940) 1970 *Saccammina atlantica* (Cushman) - v. Daniels, p. 65, pl. 1, fig. 1, Textfig. 39 1991 *Lagenammina atlantica* (Cushman, 1944) - Cimerman and Langer, p. 15, pl. 1, figs. 1-3

*Lagenammina* sp. 1 Plate 1, figs. 2a-b

*Saccammina difflugiformis* **Brady**, **1879** Plate 1, fig. 3

1879 Proteonina difflugiformis- Brady, p. 51, pl. 4, fig. 3 1913 Proteonina difflugiformis Brady - Rhumbler, p. 348, pl. 2, figs. 8-14 1970a Saccammina difflugiformis (Brady) - v. Daniels, p. 66, pl. 1, figs. 2a, 2c 1991 Lagenammina fusiformis (Williamson 1858) - Cimerman and Langer, p. 15, pl. 1, figs. 4-5

### Iridia diaphana Heron-Allen & Earland, 1914

Plate 1, fig 4

1914 *Iridia diaphana* - Heron-Allen & Earland, p. 371 1984 *Iridia diaphana* Heron-Allen & Earland - Loeblich and Tappan, p. 36, pl. 27, figs. 1-9 2014 *Iridia diaphana* Heron-Allen & Earland - Meric et al., p. 214, pl. 1, figs. 12-14

#### Daitrona sp. 1

Plate 1, figs 5a-c

Family Hippocrepinidae Rhumbler, 1895 Subfamiliy Hyperammininae Eimer and Fickert, 1899

#### *Hyperammina* sp. 1

Plate 1, figs 6a-b

1884 *Hyperammina elongata* - Brady, p. 257, pl. 23, figs. 4,7 1950 *Hyperammina cylindrica* Parr, p. 254, pl. 3, fig. 5 1994 *Hyperammina cylindrica* Parr - Jones, p. 33, pl. 23, figs. 4,7

Superfamily Ammodiscacea Reuss, 1862 Family Ammodiscidae Reuss, 1862 Subfamily Ammodiscinae Reuss, 1862

#### Ammodiscus planus Höglund, 1947

Plate 1, figs. 7a-b

1947 *Ammodiscus planus* - Höglund, p. 123, pl. 8, figs. 2-3, 8, pl. 28, figs. 17-18, Textfigs. 85-89, 105, 106, 109 1970a *Ammodiscus planus* Höglund - v. Daniels, p. 66, pl. 1, fig. 4 1991 *Ammodiscus planus* Höglund - Cimerman and Langer, p. 16, pl. 2, figs. 6-7

#### Ammodiscus sp. 1

Plate 1, figs. 8a-b

#### Ammodiscus sp. 2 Plate 1, figs. 9a-b

Ammodiscus sp. 3

Plate 1, figs. 10a-b

1970a Ammodiscus sp. - v. Daniels, p. 66, pl. 1, fig. 5b

Family Rzehakinidae Cushman, 1933

# Miliammina fusca (Brady, 1870)

Plate 1, figs. 11a-b

1870 *Quinqueloculina fusca* - Brady, p. 286, pl. 11, figs. 2 a-c, 3 a, b (fide Ellis and Messina, 1940) 1971 *Millammina fusca* (Brady) - Murray, p. 21, pl. 3, figs. 1-6 1991 *Millammina fusca* (Brady) - Cimerman and Langer, p. 17, pl. 3, figs. 11-13

*Trilocularena?* sp.1 Plate 1, figs. 12a-b

Family Hormosinidae Haeckel, 1894 Subfamily Reophacinae Cushman, 1910

#### Leptohalysis scotti, Chaster, 1892

Plate 1, figs. 14

1892 Reophax scotti - Chaster, p. 57, pl.1, fig.1
1947 Reophax catella Höglund, p.97; Od
1971 Reophax scotti Chaster, 1892 - Murray, p. 17, pl. 1, figs. 4-9
1984 Leptohalysis scotti Chaster, 1892 - Loeblich and Tappan, p. 57, pl. 44, fig.21
1992 Reophax scotti Chaster - Barmawidjaja et al., pl. 1, fig. 10
1993 Reophax scotti Chaster - Sgarella and Moncharmont Zei, p.156, pl. 2, fig. 5
2012 Reophax scotti Chaster - Debenay, p. 91, p. 255, pl. 1

#### Reophax fusiformis (Williamson, 1858)

Plate 1, figs. 13a-b

*Proteonina fusiformis* - Williamson, p. 1, pl. 1, fig. 1 *Reophax fusiformis* (Williamson) - Brady p.62, pl. 30, figs.7-11 *Reophax fusiformis* (Williamson) - Jones, p. 37, pl. 30, figs.7-11 *Reophax fusiformis* (Williamson) - Murray, p.17, pl. 1 figs. 1-3

#### Reophax nana (Rhumbler, 1913)

Plate 1, fig. 15a

*Reophax nana* - Rhumbler, p.471, pl. 8, fig. 6-12 *Reophax nana* Rhumbler - Parker, p.457, pl.1, fig.14-15 1970a *Reophax nanus* Rhumbler - v. Daniels, p. 67, pl. 1, figs. 9 *Reophax nana* Rhumbler - Barmawidjaja, p. 309, pl. 1, fig. 2 non 1 *Reophax nanus* Rhumbler - Sgarella and Moncharmont-Zei, p. 156, pl.2, fig.1

#### Reophax sp. 1

Plate 1, figs 16a-b

*Reophax* sp. 2 Plate 1, figs. 17a-b

*Reophax* sp. 3 Plate 1, figs. 18a-b

Subfamily Hormosinninae Haeckel, 1894

### Warrenia? sp.1

Plate 1, figs. 1a-b

Family Haplophragmoididae Maync, 1952

#### Labrospira sp. 1

Plate 1, figs 20a-e

1910 Haplophragmoides subglobosum (Sars) - Cushman, p. 105, figs. 162-164 1991 Labrospira subgloboca (Sars, 1910) - Cimerman and Langer, p.18, pl. 5, figs. 1-3 2014 Labrospira subglobosa Cushman - Meric et al., p. 214, pl. 2, figs. 1-2

Family Discamminidae Mikhalevich, 1980

Ammoscalaria pseudospiralis (Williamson, 1858) Plate 1, figs. 21 a-b

1858 *Proteonina pseudospiralis* - Williamson, p. 192, pl. 1. figs. 2, 3 1910 *Haplophragmium pseudospirale* (Williamson) - Sidebottom, p. 8, pl. 1, fig. 6 1947 Ammoscalaria pseudospiralis (Williamson) - Höglund, pl. 31, figs. 1 a-p 1971 Ammoscalaria pseudospiralis (Williamson) - Murray, p. 29, pl. 7, figs. 1-5 1991 Ammoscalaria pseudospiralis (Williamson) - Cimerman and Langer, p.18, pl. 5, figs. 4-6 1992 Ammoscalaria pseudospiralis (Williamson) - Barmawidjaja et al., p. 309, pl. 1, figs. 12-13 1993 Ammoscalaria pseudospiralis (Williamson) - Sgarella and Moncharmont-Zei, p. 160, pl. 2, fig. 7

#### Ammoscalaria tenuimargo (Brady, 1882)

Plate 1, figs 22a-b

1882 Haplophragmium tenuimargo - Brady, p.715 1932 Haplophragmium tenuimargo Brady - Hofker, p. 83-87, fig. 13 1960 Ammobaculites tenuimargo Brady - Hofker, p. 234, figs. 3-4 1970a Ammoscalaria tenuimargo Brady - v. Daniels, p. 69, pl.1, fig. 15 1993 Ammoscalaria tenuimargo Brady - Sgarella and Moncharmont Zei, p. 160, pl. 2, fig. 7

#### Ammoscalaria sp. 1

Plate 1, figs. 23a-b

Superfamily Spiroplectamminacea Family Spiroplectamminidae Cushman, 1927 Subfamily Spiroplectammininae Cushman, 1927

#### Spirolectinella earlandi Parker 1952

Plate 1, figs 24a-b

1971 *Textularia earlandi* (Parker) - Murray 1971, p.33, pl. 9, figs. 1-5 1993 *Spiroplectammina earlandi* (Parker) - Hottinger et al., p.31/32, pl. 6, figs. 5-10 1993 *Spirotectinella earlandi* (Parker) - Sgarella and Moncharmont Zei, p.161, pl. 3, figs. 1-3

Family Trochamminidae Schwager, 1877 Subfamily Trochammininae Schwager, 1877

#### Trochammina inflata (Montagu, 1808)

Plate 1, figs 25a-b

1803 Nautilus inflates - Montagu, p. 81 (fide Ellis and Messina, 1940)
1960 Trochammina inflata (Montagu) - Barker, p1. 41, fig. 4
1972 Trochammina inflata (Montagu) - Rosset- Moulinier, p. 122, pl. 3, figs. 11, 12
1971 Trochammina inflata (Montagu) - Murray, p. 35, pl. 10, figs. 3-6
1987 Trochammina inflata (Montagu) - Loeblich and Tappan, p. 122, pl. 129, figs. 20-23
1991 Trochammina inflata (Montagu) - Cimerman and Langer, p. 20, pl. 7, figs. 7-9

#### Jadammina macrescens (Brady, 1870)

Plate 2, figs. 1a-b

1870 Trochammina inflata (Montagu) var. macrescens - Brady, p. 290; pl. 11, fig. 5 1971 Jadammina macrescens Brady) - Murray, p. 41, pl. 13, figs. 1-5 1999 Jadammina macrescens (Brady) - Hayward et al., p. 83; pl. 1, figs 27-29 2006 Jadammina macrescens (Brady) - Debenay & Luan; pl. 1, figs 30, 31 2012 Jadammina macrescens (Brady) - Debenay, p. 53, pl. 3, p. 84, p. 259

*Trochamminula* **sp. 1** Plate 2, figs 2a-b

Subfamily Polystomammininae Brönnimann and Beurlen, 1977

*Deuterammina dubliensis* Brönniman and Whittaker, 1983 Plate 2, figs. 3a 1983 *Deuterammina dublinensis* - Brönnimann and Whittaker, p. 353, figs. 21-24, 28-30 1988 *Deuterammina dublinensis* Brönnimann and Whittaker-Loeblich and Tappan, p. 34, pl. 135, figs. 1-5 2012 *Deuterammina dublinensis* Broennimann and Whittaker-Milker and Schmiedl, p. 35, fig. 10.1-2

Superfamily Textulariacea Ehrenberg, 1838 Eggerellidae Cushman, 1937 Subfamily Eggerellinae Cushman, 1937

#### Eggerelloides advenus (Cushman, 1922)

Plate 2, figs. 4a

1922b Verneuffina advena - Cushman, p. 57, pl. 9, figs. 7-9 21 1974 Eggerella advena (Cushman) - Colom, p. 93, fig. 10 a 1970a Eggerella advena (Cushman) - v. Daniels, p. 70, pl.2, fig. 6 1991 Eggerelloides advenus (Cushman) - Cimerman and Langer, p. 20-21, pl. 8, figs. 5-6 2014 Eggerelloides advenus (Cushman) - Meric et al., p. 214, pl.3, figs. 15-17

#### Eggerelloides scabrus (Williamson, 1858)

Plate 2, figs. 5a

1858 Bulimina scabra - Williamson, p. 65, pl. 5, figs. 136, 137
1922b Verneuffina scabra (Williamson) - Cushman, p. 55
1937b Eggerella scabra (Williamson) - Cushman, p. 50. pl. 5, fig. 10
1960 Eggerella scabra (Williamson) - Barker, pl. 47, figs. 15-17
1987 Eggerelloides scabrus (Williamson) - Loeblich and Tappan, p. 170, pl. 189, figs. 5-7
1991 Eggerelloides scabrus (Cushman) - Cimerman and Langer, p. 21, pl. 8, fig. 7
1992 Eggereloides scabra (Williamson) - Barmawidjaja et al., p. 309, pl. 1, fig. 9

Family Textulariidae Ehrenberg, 1838 Subfamily Textularinae Ehrenberg, 1838

#### Textularia agglutinans d'Orbigny, 1839

Plate 2, figs 6a-b

1839b Textularia agglutinans - d'Orbigny, p. 136, pl. 1, figs. 17, 18, 32-34
1960 Textularia agglutinans d'Orbigny - Hofker, p. 237, suppl. A, fig. 18
1970a Textularia agglutinans d'Orbigny - v. Daniels, p. 69, pl. 2, figs. 1-2
1991 Textularia agglutinans d'Orbigny - Cimerman and Langer, p. 21, pl. 10, figs. 1-2
1993 Textularia agglutinans d'Orbigny - Hottinger et al., p. 36, pl. 13, figs. 1-9
2009 Textularia agglutinans d'Orbigny - Parker, p. 44, fig. 33a-k
2012 Textularia agglutinans d'Orbigny - Debenay, p. 95, p. 257, p. 52, pl. 2
2012 Textularia agglutinans d'Orbigny - Milker and Schmiedl, p. 38, figs. 10.15-16
2014 Textularia agglutinans d'Orbigny - Meric et al., p. 215, pl. 4, fig. 16

#### Textularia bocki Höglund, 1947

Plate 2, figs. 7a-b

1947 *Textularia bocki* - Höglund, p. 171, pl. 12, figs. 5, 6 1932a *Textularia agglutinans* d'Orbigny - Lacroix, p. 16, fig. 13 1958a *Textularia bocki* Höglund - Le Calvez, Y., p. 150, pl. 1, fig. 4 1991 *Textularia bocki* Höglund - Cimerman and Langer, p. 21, pl. 10, figs. 3-6 2014 *Textularia bocki* Höglund - Meric et al., p. 215, pl. 4, Figs. 17-21, pl. 5, figs. 1-10

#### Textularia conica d'Orbigny, 1839

Plate 2, figs. 8a-b

1839a *Textularia conica* - d'Orbigny, p. 143, pl. 1, figs. 19, 20 1899 *Textularia conica* d'Orbigny - Flint, p. 285, pl. 29, fig. 6 1932 *Textularia conica* d'Orbigny - Cushman, p. 11, p1. 2, figs. 8-10 1977a *Textularia conica* d'Orbigny - Le Calvez, Y., p. 18, figs. 1, 2 1991 *Textularia conica* d'Orbigny - Cimerman and Langer, p. 22, pl. 10, figs. 7-9

#### Textularia lateralis? Lalicker, 1935

Plate 2, figs. 9a-b

1935 *Textularia lateralis* - Lalicker, p.1, pl.1, figs.3-5 1994 *Textularia lateralis* Lalicker - Loeblich and Tappan, p. 28, pl. 33, figs. 13-1

#### Textularia porrecta Brady, 1884

Plate 2, figs. 10a-b

1884 *Textularia porrecta* - Brady, p. 363, pl. 43, fig. 4 1972a *Textularia porrecta* Brady - v. Daniels, p. 70, pl. 2, fig. 4 1991 *Textularia porrecta* Brady - Cimerman and Langer, p. 22, pl. 11, figs. 1-4

### *Textularia* sp. 1

Plate 2, figs. 11a-b

*Textularia* **sp. 2** Plate 2, figs. 12a-b

# Textularia sp. 3

Plate 2, figs. 13a-b

Subfamily Siphotextulariinae Loeblich and Tappan, 1985

#### Siphotextularia flintii (Cushman, 1911)

Plate 2, figs. 14a-b

*Textularia flintii* - Cushman, p. 21, Textfigs. 36a-b *Siphotextularia flintii* (Cushman) - Murray, p.33, pl. 9, figs. 6-8 *Siphotextularia flintii* (Cushman) - Milker and Schmiedl, p. 40, pl. 11, figs. 1-3 *Siphotextularia concava* (Cushman) - Meric et al., p 215, pl.6, figs. 11-17

#### Siphotextularia sp. 1

Plate 2, figs. 15a-b

Family Spirillinidae Reuss and Fritsch, 1861

#### Spirillina limbata Brady, 1884

Plate 2, figs. 16a-b

1879 Spirillina limbata - Brady, p. 278, pl. 8. fig. 26 (fide Ellis and Messina, 1940)
1960 Spirillina limbata Brady - Barker, pl. 85, figs. 18-22
1991 Spirillina limbata Brady - Cimerman and Langer, p. 24, pl. 14, figs. 1-3
2012 Spirillina limbata Brady - Milker and Schmiedl, p. 43, figs. 11.13-14
2014 Spirillina limbata Brady - Meric et al., p. 215, pl. 7, fig. 7

#### Spirillina vivipara Ehrenberg, 1841

Plate 2, figs. 17a-b

1841 Spirillina vivipara - Ehrenberg, p. 422, pl. 3, fig. 41 (fide Ellis and Messina, 1940)
1930 Spirillina vivipara Ehrenberg - Heron-Allen and Earland, p. 178
1958a Spirillina vivipara Ehrenberg - Le Calvez, Y., p. 181
1960 Spirillina vivipara Ehrenberg - Barker, pl. 85, figs. 1-5

*Spirillina vivipara* Ehrenberg - Colom, p. 139, figs. 23 c, d *Spirillina vivipara* Ehrenberg - Loeblich and Tappan, p. 304, pl. 318, figs. 4-7 *Spirillina vivipara* Ehrenberg - Cimerman and Langer, p. 24, pl. 14, figs. 4-6 *Spirillina vivipara* Ehrenberg - Sgarella and Moncharmont-Zei, p. 226, pl. 20, fig. 2 *Spirillina vivipara* Ehrenberg - Milker and Schmiedl, p. 43, fig. 11.15-16 *Spirillina vivipara* Ehrenberg - Meric et al., pl. 7, p. 215, figs. 8-9

Family Patellinidae Rhumbler, 1906 Subfamily Pattelininae Rhumbler, 1906

#### Patellina corrugata Williamson, 1858

Plate 2, figs. 18a-c

1858 Patellina corrugata - Williamson, p. 46, pl. 3, figs. 86-89
1958a Patellina corrugata Williamson - Le Calvez, Y., p. 181
1960 Patellina corrugata Williamson - Barker, pl. 86, figs. 1-7
1970 Patellina corrugata Williamson - v. Daniels, p. 86, pl. 7, fig. 4
1972 Patellina corrugata Williamson - Rosset- Moulinier, p. 173
1974 Patellina corrugata Williamson - Colom, p. 139, figs. 23 e, f
1987 Patellina corrugata Williamson - Loeblich and Tappan, p. 306, pl. 320, figs. 7-14
1991 Patellina corrugata Williamson - Cimerman and Langer, p. 24, pl. 14, figs. 7-12

Suborder Miliolina Delage and Hérouard, 1896 Superfamily Cornuspiracea Schultze, 1854 Family Cornuspiridae Schultze, 1854 Subfamily Cornuspirinae Schultze, 1854

#### Cornuspira foliacea (Philippi, 1844)

Plate3, figs. 1a-b

*Orbis foliaceus* - Philippi, p. 147, pl. 24, fig. 25 (fide Ellis and Messina, 1940) *Spirillina foliacea* (Philippi) - Williamson, p. 91, pl. 7, figs. 199-201 *Cornuspira foliacea* (Philippi) - Cushman, p. 24, pl. 1, fig. 1, pl. 2, Fig. 1 *Cyclogyra foliacea* (Philippi) - Colom, p. 211, figs. 69 a, b *Cornuspira foliacea* (Philippi) - Cimerman and Langer, p. 24, pl. 15, figs. 1-3 *Cornuspira foliacea* (Philippi) - Meric et al., p. 216, pl.7, figs. 13-14

*Cornuspira* **sp. 1** Plate 3, figs. 2a-b

*Cornuspira* **sp. 2** Plate 3, figs. 3a-b

Family Fischerinidae Millett, 1898 Subfamily Nodobaculariellinae Bogdanovich, 1981

#### Vertebralina striata d'Orbigny, 1826

Plate 3, figs 4 a-b, fig. 5a

1826 Vertebralina striata - d'Orbigny, p. 283, no. 1 1858 Vertebralina striata d'Orbigny - Williamson, p. 90, pl. 7, figs. 197, 198 1917 Vertebralina striata d'Orbigny - Cushman, p. 38, pl. 22, figs. 3, 4 1923 Vertebralina striata d'Orbigny - Wiesner, p. 93, pl. 19, figs. 274, 275 1929 Vertebralina striata d'Orbigny - Cushman, p. 96, pl. 22, figs. 6 a, b 1970 Vertebralina striata d'Orbigny - v. Daniels, p. 72, Textfig. 47 1979 Vertebralina striata d'Orbigny - Alfirevie, p. 68, pl. 5, fig. 2 1991 Vertebralina striata d'Orbigny - Cimerman and Langer, p. 25, pl. 16, figs. 1-5 2014 Vertebralina striata d'Orbigny - Meric et al., p 216, pl.8, figs. 1-9

#### Wiesnerella auriculata (Egger 1893)

Plate 3, figs. 6a-b

1893 Planispirina auriculata Egger - Egger p.245, pl. 3, figs. 13-15
1933 Wiesnerella auriculata Egger - Cushman, p. 33, fig. 8
1987 Wiesnerella auriculata Egger - Baccaert, p. 41, pl. 13, figs. 3-5
1993 Wiesnerella auriculata Egger - Hottinger et al., p. 43, pl. 24, figs. 1-4
2014 Wiesnerella auriculata Egger - Milker and Schmiedl, p. 46, fig. 12.4

Family Nubeculariidae Jones, 1875 Subfamily Nodophthalmidiinae Cushman, 1940

#### Nodophthalmidium antillarum (Cushman 1922)

Plate 3, figs. 7a-b

1922 Articulina antillarum Cushman - Cushman, pl. 71, pl. 12, fig. 5 1944 Nodophthalmidium antillarum Cushman - Cushman and Todd, p. 65, pl. 11, fig. 3 1949 Nodophthalmidium antillarum Cushman - Said, p.20, p. 2, fig. 3 1993 Nodophthalmidium antillarum Cushman - Hottinger et al., p.44, pl.23, Figs.4-7, Textfig. 2 2014 Nodophthalmidium antillarum Cushman - Meric et al., p.216, pl. 8, fig. 10

Subfamily Nubeculariinae Jones, 1875

#### Nubecularia lucifuga Defrance, 1825

Plate 3, figs. 8a-b

1825 Nubecularia lucifuga - Defrance, p. 210, pl. 44, fig. 3 (fide Ellis and Messina, 1940)
1917 Nubecularia lucifuga Defrance - Cushman, p. 41, pl. 8, fig. 6
1923 Nubecularia lucifuga Defrance - Wiesner, p. 94, pl. 17, figs. 278-281
1960 Nubecularia lucifuga Defrance - Barker, pl. 1, figs. 9-11, 13-16
1974 Nubecularia lucifuga Defrance - Colom, p. 174, figs. 47 a-e, 48 a-f
1987 Nubecularia lucifuga Defrance - Loeblich and Tappan, p. 324, pl. 332, figs. 1-3
1991 Nubecularia lucifuga Defrance - Cimerman and Langer, p.26, pl. 17, figs. 5-7
2014 Nubecularia lucifuga Defrance - Meric et al., p. 216, pl. 9, figs. 1-4

Family Ophthalmidiidae Wiesner, 1920

#### Spirophthalmidium sp. 1

Plate 3, figs. 9a-b

Superfamily Miliolacea Ehrenberg, 1839 Family Spiroloculinidae Wiesner, 1920

#### Adelosina aff. A. angulosa Wiesner 1923

Plate 3, figs. 10a-b

1923 Adelosina dubia var. angulosa - Wiesner, p. 78, pl. 14, fig. 196

#### Adelosina carinata-striata Wiesner, 1923

Plate 3, figs. 11a-c

1923 Adelosina milletti var. carinata-striata - Wiesner, p. 77, pl. 14, figs. 190, 191 1970 Quinqueloculina milletti var. carinata-striata (Wiesner) - v. Daniels, p. 74, pl. 2, figs. 17 a-c, Textfig. 49 1991 Adelosina carinala-striata Wiesner - Cimerman and Langer, p.28, pl. 20, figs. 1-4 1993 Adelosina carinala-striata Wiesner, Meric et al. 2014, p. 216, pl. 9, figs. 8-10

#### Adelosina cliarensis (Heron-Allen and Earland, 1930)

Plate 3, figs. 12a-c

1930 *Quinqueloculina cliarensis* - Heron-Allen and Earland, p. 58, pl. 3, figs. 26, 31 1958b *Quinqueloculina cliarensis* Heron-Allen and Earland - Le Calvez, J. and Y., p. 186, pl. 5, figs. 40- 41 1958a *Quinqueloculina cliarensis* Heron-Allen and Earland - Le Calvez, Y., p. 157, pl. 1, figs. 10- 11 1991 *Adelosina cliarensis* (Heron-Allen and Earland) - Cimerman and Langer, p. 26, pl. 18, figs. 1-4

#### Adelosina cf. A. cliarensis (Heron-Allen and Earland, 1930)

Plate 3, figs. 13a-c

1930 *Adelosina cliarensis* (Heron-Allen and Earland) - Heron-Allen and Earland, p. 58, pl. 3, figs. 26, 31 1991 *Adelosina cliarensis* (Heron-Allen and Earland) - Cimerman and Langer, p. 26, pl. 18, figs. 1-4 2014 *Adelosina cliarensis* (Heron-Allen and Earland) - Meric et al., p. 216, pl. 9, figs. 11-12

#### Adelosina dubia (d'Orbigny, 1826)

Plate 3, figs 15a-b

*Triloculina dubia* - d'Orbigny, p. 300, no. 24 *Adelosina dubia* (d'Orbigny) - Wiesner, p. 77, pl. 14, fig. 193 1958b *Triloculina dubia* (d'Orbigny) - Le Calvez, J. and Y., p. 197, pl. 14, figs. 164-166 *Adelosina dubia* (d'Orbigny) - Cimerman and Langer, p. 27, pl. 18, figs. 5-7 *Adelosina dubia* (d'Orbigny) - Milker and Schmiedl, p. 48, fig. 12.14

#### Adelosina mediterranensis (Le Calvez, J and Y., 1958)

Plate 3, figs. 16a-c

1958b *Quinqueloculina mediterranensis* - Le Calvez, J. and Y., p. 177, pl. 4, figs. 29-31 *Adelosina mediterranensis* Le Calvez, J and Y. - Cimerman and Langer, p. 28, pl. 19, figs. 1-16 *Adelosina mediterranensis* Le Calvez, J and Y. - Milker and Schmiedl, p. 48, figs. 12.22-28 *Adelosina mediterranensis* Le Calvez, J and Y. - Meric et al. p. 216, pl. 10, figs. 12-18, pl. 11, figs. 1-7

#### Adelosina pulchella d'Orbigny, 1846

Plate 3, figs. 17a-c, figs. 18a-b

1846 Adelosina pulchella - d'Orbigny, p. 203, pl. 20, figs. 25-30 1958b *Quinqueloculina pulchella* (d'Orbigny) - Le Calvez, J. and Y., p. 175, pl. 3, figs. 12-14 1991 Adelosina pulchella (d'Orbigny) - Cimerman and Langer, p. 28, pl. 20, figs. 9-10

#### Adelosina striata (Wiesner, 1923)

Plate 3, figs. 19 a-c, figs. 20a

1923 Adelosina longirostra d'Orbigny var. striata nom. nov.- Wiesner, p. 78, pl. 15, figs. 201-203

Adelosina sp. 1 Plate 4, figs. 1a-b

1991 *Adelosina* sp.1 - Cimerman and Langer, p. 28, pl. 21, figs. 2-3 *Adelosina* sp. 2 Plate 4, figs. 2a-c

*Adelosina* **sp. 3** Plate 4, figs. 3a-c

Adelosina? sp. 4 Plate 4, figs. 5a-c

*Spiroloculina angulosa* **Terquem, 1878** Plate 4, figs. 6a-b 1878 *Spiroloculina angulosa* - Terquem, p. 53, pl. 5, fig. 7 1958b *Spiroloculina angulosa* Terquem - Le Calvez, J. and Y., p. 204, pl. 8, fig. 92 1991 *Spiroloculina angulosa* Terquem - Cimermann and Langer, p. 29, pl. 21, figs. 10-13

#### Spiroloculina aff. S. antillarum d'Orbigny, 1839

Plate 4, figs. 7a-b

1839a Spiroloculina antillarum - d'Orbigny, p. 166; pl. 9, figs 3,4.

# Spiroloculina cf. Spiroloculina carinata, Wiesner 1923

Plate 4, figs. 8a-b

1969 Spiroloculina carinata nov. Wiesner - Wiesner, pl. 4, p.38, figs. 42, 43

#### Spiroloculina dilatata d'Orbigny, 1846

Plate 4, figs. 9a-b

1846 Spiroloculina dilatata - d'Orbigny, p. 271, pl. 16, figs. 16-18
1923 Spiroloculina dilatata d'Orbigny - Wiesner, p. 35, pl. 4, fig. 26
1991 Spiroloculina dilatata d'Orbigny - Cimerman and Langer, p. 30, pl. 22, figs. 5-8
2012 Spiroloculina dilatata d'Orbigny - Milker and Schmiedl, p. 48, fig. 13.1-2
2014 Spiroloculina dilatata d'Orbigny - Meric et al., p. 216, pl. 14, figs. 2-3

#### Spiroloculina krumbachi Wiesner, 1912

Plate 4, figs. 10a-b

1912 *Spiroloculina krumbachi* - Wiesner, p. 207, Fig. 1 1991 *Spiroloculina krumbachi* Wiesner - Cimerman and Langer, p.30, pl. 24, figs. 1-5 2014 *Spiroloculina krumbachi* Wiesner - Meric et al. 2012, p. 216, pl. 14, figs. 9-10

#### Spiroloculina ornata d'Orbigny

Plate 4, fig. 11

1839a *Spiroloculina ornata* - d'Orbigny, p. 167, pl. 12, fig. 7 1958b *Spiroloculina ornata* d'Orbigny - Le Calvez J. and Y., p. 207, pl. 8, fig. 83 1977a *Spiroloculina ornata* d'Orbigny - Le Calvez, Y., p. 94, pl. 18, figs. 1-4 1991 *Spiroloculina ornata* d'Orbigny - Cimerman and Langer, p.30, pl. 23, figs. 8-11

# Spiroloculina ornata d'Orbigny var. tricarinata Le Calvez, J. and Y., 1958

Plate 4, figs. 12a-b

1958b *Spiroloculina ornata* d'Orbigny var. *tricarinata* - Le Calvez, J. and Y., p. 207, pl. 8, figs. 84-85 1991 *Spiroloculina ornata* d'Orbigny var. *tricarinata* Le Calvez, J. and Y - Cimerman and Langer, p. 30, pl. 23, figs. 4-7

Family Hauerinidae Schwager, 1876 Subfamily Siphonapertinae Saidova, 1975

#### Siphonaperta agglutinans (d'Orbigny, 1839)

Plate 4, figs. 13a-b

1839a *Quinqueloculina agglutinans* - d'Orbigny, p. 195, pl. 12, figs. 11, 12 1958b *Quinqueloculina agglutinans* d'Orbigny - Le Calvez, J. and Y., p. 166, pl. 9, figs. 103, 104 1977 *Quinqueloculina agglutinans* d'Orbigny - Le Calvez, Y., p. 54, pl. 7, figs. 1-4 1991 *Siphonaperta agglutinans* (d'Orbigny, 1839) - Cimerman and Langer, p. 31, pl. 25, figs. 1-3

# Siphonaperta aff. S. aspera (d'Orbigny, 1826)

Plate 4, fig. 14a

1826 Quinqueloculina aspera - d'Orbigny, p. 301, no. 11

1958b *Quinqueloculina aspera* d'Orbigny - Le Calvez, J. and Y., p. 168, pl. 9, figs. 101, 102 1991 *Siphonaperta aspera* (d'Orbigny, 1826) - Cimerman and Langer, p. 31, pl. 25, figs. 4-6

#### Siphonaperta dilatata (Le Calvez, J. and Y, 1958)

Plate 4, figs. 15a-c, 16a-c

1958b *Quinqueloculina aspera* d'Orbigny var. *dilatata* - Le Calvez, J. and Y, p. 169, pl. 11, figs. 119-121 1991 *Siphonaperta dilatata* (Le Calvez, J. and Y.) - Cimerman and Langer, p. 31, pl. 26, figs. 1-3

#### Siphonaperta cf. S. dilatata (Le Calvez, J. and Y, 1958)

Plate 4, figs. 17a-b

1958 *Quinqueloculina aspera* d'Orbigny var. *dilatata* - Le Calvez, J. and Y, p. 169, pl. 11, figs. 119-121 1991 *Siphonaperta dilatata* (Le Calvez, J. and Y.) - Cimerman and Langer, p. 31, pl. 26, figs. 1-3

#### Siphonaperta cf. S. hauerina (Wiesner, 1923)

Plate 4, figs. 18a-b

1923 *Miliolina agglutinans* (d'Orbigny) var. *hauerina* - Wiesner, p. 44, pl. 5, fig. 48 1991 *Siphonaperta hauerina* (Wiesner, 1923) - Cimerman and Langer, p. 31, pl. 27, figs. 1-3

# Siphonaperta sp. 1

Plate 4, figs. 19a-b

1991 Siphonaperta sp. 2 - Cimerman and Langer, p. 32, pl. 26, figs. 7-9

*Siphonaperta* sp. 2 Plate 4, figs. 20a-b

# Siphonaperta sp. 3

Plate 4, figs. 21a-b

Subfamily Hauerininae Schwager, 1876

# Cycloforina juleana (d'Orbigny, 1846)

Plate 5, figs. 1a-b

*Quinqueloculina juleana* - d'Orbigny, p. 298, pl. 20, figs. 1-3 *Quinqueloculina juleana* (d'Orbigny) - Wiesner, p. 48, pl. 16, fig. 63 1958b *Quinqueloculina juleana* d'Orbigny - Le Calvez, J. and Y., p. 170, pl. 12, figs. 143-145 *Cycloforina juleana* (d'Orbigny, 1846) - Cimerman and Langer, p. 33, pl. 28, figs. 1-2

#### Cycloforina rugosa (d'Orbigny, 1826)

Plate 5, figs. 2a-b

1826 Quinqueloculina rugosa - (d'Orbigny), p. 302, no. 24
1923 Miliolina rugosa d'Orbigny - Wiesner, p. 46, pl. 6, fig. 54
1958b Quinqueloculina rugosa d'Orbigny - Le Calvez, J. and Y., p. 171, pl. 12, figs. 137-139
1991 Cycloforina rugosa (d'Orbigny) - Cimerman and Langer, p.33, pl. 28, figs. 3-4

*Cycloforina tenuicollis* (Wiesner, 1923) Plate 5, figs. 3a-c

1923 Miliolina tenuicollis - Wiesner, p. 48, pl. 6, fig. 66
1909 Miliolina ferussacii d'Orbigny - Sidebottom, p. 17, pl. 5, fig. 7
1970a Quinqueloculina tenuicollis (Wiesner) - v. Daniels, p. 75, pl. 3, fig. 5
1991 Cycloforina tenuicollis (Wiesner) - Cimerman and Langer, p. 33, pl. 28, figs. 5-6

#### Cycloforina aff. C. tenuicollis (Wiesner, 1923)

Plate 5, figs. 4a-b

1923 *Miliolina tenuicollis* - Wiesner, p. 48, pl. 6, fig. 66 1991 *Cycloforina tenuicollis* (Wiesner) - Cimerman and Langer, p. 33, pl. 28, figs. 5-6 2014 *Cycloforina tenuicollis* (Wiesner) - Meric et al., p. 217, pl. 17, figs. 16-17

#### Lachlanella planciana (d'Orbigny, 1839)

Plate 5, figs. 5a-c

1839a *Quinqueloculina planciana* - d'Orbigny, p. 186, pl. 10, figs. 24, 25, pl. 11, figs. 4-6 1977a *Quinqueloculina planciana* d'Orbigny - Le Calvez, Y., p. 79, pl. 13, figs. 1-3, 7-9, pl. 30, figs. 1-2 1991 *Lachlanella planciana* (d'Orbigny, 1839) - Cimerman and Langer, p. 34, pl. 30, figs. 1-2

#### Lachlanella undulata (d'Orbigny, 1826)

Plate 5, figs. 6a-c

1826 Quinqueloculina undulata - d'Orbigny, p. 302, no. 27
1893 Quinqueloculina undulata d'Orbigny - Schlumberger, p. 213, pl. 2, figs. 60, 61
1923 Miliolina undulata (d'Orbigny) - Wiesner, p. 53, pl. 7, fig. 81
1958b Quinqueloculina undulata d'Orbigny - Le Calvez, J. and Y., p. 179, pl. 13, figs. 146-148
1974 Quinqueloculina undulata d'Orbigny - Colom, p. 202, Figs. 58 h-k
1991 Lachlanella undulata (d'Orbigny) - Cimerman and Langer, p. 34, pl. 30, figs. 3-6

#### Lachlanella variolata (d'Orbigny, 1826)

Plate 5, figs. 7a-c

1826 Quinqueloculina variolata - d'Orbigny, p. 302, no. 26
1839a Trlloculina carinata - d'Orbigny, p. 179, pl. 10, figs. 15-17
1923 Millolina reticulata (d'Orbigny) - Wiesner, p. 52, pl. 7, fig. 78
1923 Miliolina reticulata (d'Orbigny) var. carinata d'Orbigny - Wiesner, p. 54, pl. 8, fig. 88
1970 Quinqueloculina reticulata d'Orbigny - Cherif, pl. 9, fig. I
1974 Quinqueloculina reticulata d'Orbigny - Colom, p. 201, figs. 56 a-d
1977a Quinqueloculina variolata d'Orbigny - Le Calvez, Y., p. 102, figs. 15-17
1991 Lachlanella variolata (d'Orbigny, 1826) - Cimerman and Langer, p. 35, pl. 31, figs. 1-12

#### Massilina gualteriana (d'Orbigny, 1839)

Plate 5, figs. 8a-c

1839a *Quinqueloculina gualtieriana* - d'Orbigny, p. 186, pl. 11, figs. 1-3 1932 *Quinqueloculina gualtieriana* d'Orbigny - Cushman, p. 23, pl. 6, figs. I a-c 1977a *Quinqueloculina gualtieriana* d'Orbigny - Le Calvez, Y. p. 75, pl. 12, figs. 4-8 1991 Massilina gualteriana (d'Orbigny, 1839) - Cimerman and Langer, p. 35, pl. 29, figs. 6-9

#### Massilina aff. M. secans (d'Orbigny, 1826)

Plate 5, figs. 9a-b, 10a-c

*Quinqueloculina secans* - d'Orbigny, p. 303, no. 43 1958b *Massilina secans* (d'Orbigny) - Le Calvez, J. and Y., p. 204, pl. 7, fig. 66 *Massilina secans* (d'Orbigny) - Murray, p. 67, pl. 25, figs. 1-6 *Massilina secans* (d'Orbigny) - Loeblich and Tappan, p. 335, pl. 344, figs. 1-3 *Massilina secans* (d'Orbigny) - Cimerman and Langer, p. 35, pl. 30, figs. 7-12

#### Massilina obliquistriata Cushman & Valentine, 1930

Plate 5, figs. 11a-c

1889*Sigmoilina secans* d'Orbigny var. *obliquistriata* - Halkyard, p.61, pl. 1, fig.7 1969 *Milionlina secans* d'Orbigny var. *obliquistriata* Halkyard - Wiesner, p.55, pl. 8, fig.93

#### Quinqueloculina adelaidensis (Howchin & Parr, 1938)

Plate 5, figs. 12a-c

1938 Quinqueloculina adelaidensis - Howchin & Parr, p. 293, pl. 15, figs. 5, 7 1970 Quinqueloculina adelaidensis (Howchin & Parr) - Cherif, p. 112, pl. 27, Figs. 4a-b, pl. 13, figs. 2a-b

#### Quinqueloculina berthelotiana d'Orbigny, 1839

Plate 5, figs. 13a-b

1839b Quinqueloculina berthelotiana - d'Orbigny, p. 142, pl. 3, figs. 25-27
1923 Quinqueloculina berthelotiana d'Orbigny - Wiesner, p. 48, pl. 6, fig. 67
1958b Quinqueloculina berthelonana d'Orbigny - Le Calvez, J. and Y., p. 173, pl. 10, figs. 115-117
1974 Quinqueloculina berthelotiana d'Orbigny - Colom, p. 188, figs. 59 e-g
1991 Quinqueloculina berthelotiana d'Orbigny - Cimerman and Langer, p.36, pl. 32, figs. 5-7

#### Quinqueloculina aff. Q. berthelotiana d'Orbigny, 1839

Plate 5, figs. 14a-b, 15a-b

1839b *Quinqueloculina berthelotiana* - d'Orbigny, p. 142, pl. 3, figs. 25-27 1991 *Quinqueloculina berthelotiana* d'Orbigny - Cimerman and Langer, p.36, pl. 32, figs. 5-7

#### *Quinqueloculina* cf. *Q. bicornis* Williamson var. *angulata* Wiesner, 1923 Plate 16, figs. 1a-c

1923 Miliolina bicornis Williamson var. angulata nov. - Wiesner, p. 54, pl.8, fig.86

#### Quinqueloculina bidentata? d'Orbigny, 1839

Plate 5, figs. 17a-c

1839a Quinqueloculina bidentata - d'Orbigny, p. 197, pl. 12, figs. 18-20
1929 Quinqueloculina bidentata d'Orbigny - Cushman, p. 22, pl. 1, fig. 2
1977a Quinqueloculina bidentata d'Orbigny - Le Calvez, Y., p. 64, 65, figs. 1, 2
1993 Quinqueloculina bidentata d'Orbigny - Cimerman and Langer, p.36, pl.32, figs.10-14

#### Quinqueloculina bosciana d'Orbigny, 1839

Plate 6, figs. 1a-c

1839a *Quinqueloculina bosciana* - d'Orbigny, p. 191, pl. 11, figs. 22-24 1977a *Quinqueloculina bosciana* d'Orbigny - Le Calvez, Y., p. 66, pl. 10, figs. 1-3 1991 *Quinqueloculina bosciana* d'Orbigny - Cimerman and Langer, p. 36, pl. 33, figs. 5-7

#### Quinqueloculina canaliculata Terquem, 1876

Plate 6, figs. 2a-c

1876 *Quinqueloculina canaliculata* - Terquem, p.74, pl. 8, figs. 23a-c 1969 *Adelosina canaliculata* Terquem - Wiesner, p. 82, pl. 16, fig. 224

#### Quinqueloculina carinata Wiesner, 1923

Plate 6, figs. 3a-b

1923 Adelosina miletti nom. nov. var. carinata - Wiesner, p.76, pl. 14, fig. 189

#### Quinqueloculina cf. Q. contorta (d'Orbigny, 1846)

Plate 6, figs. 5a-b, 6a-b

1846 Quinqueloculina contorta - d'Orbigny, p. 298, pl. 20, figs. 4-6
1923 Quinqueloculina contorta d'Orbigny - Wiesner, p. 46, pl. 6, fig. 56
1958b Quinqueloculina contorta d'Orbigny - Le Calvez, J. and Y., p. 171, pl. 12, figs. 140-142
1987 Cycloforina contorta (d'Orbigny) - Loeblich and Tappan, p. 33, pl. 342, figs. 4-9
1991 Cycloforina contorta (d'Orbigny) - Cimerman and Langer, p. 32, pl. 27, figs. 7-11

## Quinqueloculina disparilis d'Orbigny, 1826

Plate 6, figs. 7a-c

*Quinqueloculina disparilis* - d'Orbigny, p. 302, no. 21 *Quinqueloculina disparilis* d'Orbigny - Schlumberger, p. 212, pl. 2, figs. 55-57 *Quinqueloculina disparilis* d'Orbigny - Wiesner, p. 47, pl. 6. figs. 60, 61 1958b *Quinqueloculina disparilis* d'Orbigny - Le Calvez, J. and Y., p. 180, pl. 4, figs. 26, 27 *Quinqueloculina disparilis* d'Orbigny - Colom, p. 200, figs. 55 a-g *Quinqueloculina disparilis* d'Orbigny - Cimerman and Langer, p. 36, pl. 33, figs. 1-4

## Quinqueloculina irregularis d'Orbigny, 1878

Plate 6, figs. 8a-c

1878 *Quinqueloculina irregularis* - d'Orbigny, 302, no. 25 1923 *Miliolina irregularis* d'Orbigny - Wiesner, p. 48, pl. 6, fig.64

## Quinqueloculina italica, Terquem, 1878

Plate 6, figs. 9a-c

1878 Quinqueloculina italica - Terquem, p.69, pl. 7, figs.17a-c

#### Quinqueloculina laevigata d'Orbigny, 1839

Plate 6, figs. 10a-c

1839b *Quinqueloculina laevigata* - d'Orbigny, p. 143, pl. 3, figs. 32, 33 1923 *Miliollna laevigata* (d'Orbigny) - Wiesner, p. 55, pl. 8, figs. 94-96 1991 *Quinqueloculina laevigata* d'Orbigny - Cimerman and Langer, p. 37, pl. 33, figs. 8-11

#### Quinqueloculina longidentata Terquem, 1882

Plate 6, figs. 11a-b

1882 *Quinqueloculina longidentata* - Terquem, p. 176, pl. 18, figs. 29-30, pl. 19, fig. 1 1923 *Miliolina longidentata* (Terquem) - Wiesner, p. 64, pl. 11, fig. 139

## Quinqueloculina cf. Q. partschii d'Orbigny, 1846

Plate 6, figs. 12a-b

1846 Adelosina partschi - d'Orbigny, p. 293, pl. 19, figs. 4-6 1923 Adelosina partschi d'Orbigny - Wiesner, p.78, pl.14, fig. 200 1991 Adelosina partschi d'Orbigny - Cimerman and Langer, p. 28, pl. 20, figs.7-8

## Quinqueloculina parvula Schlumberger, 1894

Plate 6, figs. 13a-c

1894 *Quinqueloculina parvula* - Schlumberger, p. 255, pt. 3, figs. 8, 9 1958b *Quinqueloculina parvula* Schlumberger - Le Calvez, J. and Y., p. 184, pl. 10, figs. 131-133

## Quinqueloculina parvula? Schlumberger, 1894

Plate 6, figs. 14a-c

1894 Quinqueloculina parvula - Schlumberger, p. 255, pt. 3, figs. 8, 9
1991 Quinqueloculina parvula Schlumberger - Cimerman and Langer, p. 37/38, pl. 34, figs. 6-8
2014 Quinqueloculina parvula Schlumberger - Milker and Schmiedl, p. 59, figs. 15.25-27

## Quinqueloculina aff. Q. parvula Schlumberger, 1894

Plate 15a-c

1894 *Quinqueloculina parvula* - Schlumberger, p. 255, pt. 3, figs. 8, 9 1958b *Quinqueloculina parvula* Schlumberger - Le Calvez, J. and Y., p. 184, pl. 10, figs. 131-133

# Quinqueloculina aff. Q. planciana (d'Orbigny, 1839)

Plate 6, figs. 16a-c

1839 *Quinqueloculina planciana* - d'Orbigny, p. 186, pl. 10, fig. 24-25, pl. 11, fig. 6 1970 *Quinqueloculina planciana* (d'Orbigny) - Cherif, p. 72, pl. 8, figs2a-c

## Quinqueloculina aff. Q. pseudobuchiana Luczkowska, 1974

Plate 7, figs. 1a-b

1974 *Quinqueloculina pseudobuchiana* - Luczkowska, p. 58, p1. 4, fig. 5, pl. 5, figs. 1, 2 1991 *Quinqueloculina pseudobuchiana* - Cimerman and Langer, p. 38, pl. 35, figs. 1-4 2012 *Quinqueloculina pseudobuchiana* - Milker and Schmiedl, p. 59, pl. 15. figs. 28-29

## Quinqueloculina pygmaea Reuss, 1850

Plate 7, figs. 2a-b

1850 *Quinqueloculina pygmae* - Reuss, 1, S.384, pl.50, fig. 3a, b 1970 *Quinqueloculina pygmae Reuss* - v. Daniels, p. pl.3 figs. 2a-c 1993 *Quinqueloculina pygmae Reuss* - Sgarella and Moncharmont Zei, p. 174, Pl. 7 figs, 2 *Quinqueloculina rugosa* d'Orbigny, 1839 Plate 7, figs. 3a-b

1826 Quinqueloculina rugosa - (d'Orbigny), p. 302, no. 24

## Quinqueloculina stelligera Schlumberger, 1893

Plate 7, figs. 4a-c

1893 Quinqueloculina stelligera - Schlumberger, p. 210, pl. 2, figs. 58, 59
1923 Miliolina schlumbergeri - Wiesner, p. 49, pl. 6, fig. 73
1958b Quinqueloculina stelligera Schlumberger - Le Calvez, J. and Y., p. 174, pl. 11, figs. 125, 126
1970 Quinqueloculina schlumbergeri Wiesner - Haake, p. 196, pl. 1, fig. 3, 4
1991 Quinqueloculina stelligera Schlumberger - Cimerman and Langer, p. 38, pl. 34, figs 13-15

## Quinqueloculina aff. Q. tricarinella (Wiesner 1923)

Plate 7, figs. 5a-c

1923 Miliolina tricarinella Wiesner – p. 46, pl. 6, fig.53

## Quinqueloculina ungeriana d'Orbigny, 1846

Plate 7, figs. 6a-c

1846 *Quinqueloculina ungeriana* - d'Orbigny, p. 294, pl. 18, figs. 22-24 1958b *Quinqueloculina ungeriana* d'Orbigny - Le Calvez, J. and Y., p. 185, pl. 13, figs. 155-157 1993 *Quinqueloculina ungeriana* d'Orbigny - Cimerman and Langer, p.38, pl. 35, figs. 5-7

## Quinqueloculina viennensis

Plate 7, figs. 7a-c

1958b *Quinqueloculina viennensis* - Le Calvez & Le Calvez, p. 232, pl. 5, figs. 42,44,45 1993 *Quinqueloculina viennensis* Le Calvez and Le Calvez - Sgarrella and Moncharmont Zei, p. 176, pl. 7, fig. 8 2012 *Quinqueloculina viennensis* Le Calvez and Le Calvez - Milker and Schmiedl, p. 61, fig. 16.5-7

## Quinqueloculina aff. viennensis

Plate 7, figs. 8a-c

# Quinqueloculina cf. Cycloforina villafranca (Le Calvez, J. and Y., 1958)

Plate 7, figs. 9a-c

1958b *Quinqueloculina villafranca* - Le Calvez, J. and Y., p. 180, pl. 4. figs. 22, 23 1923 *Miliolina disparilis* forma *a* Wiesner (non d'Orbigny) - Wiesner, p. 47, pl. 6, fig. 60 1991 *Cycloforina villafranca* Le Calvez, J. & Y. - Cimerman and Langer, p. 33, pl. 28, figs. 7-9

# Quinqueloculina aff. Q. villafranca (Le Calvez, J. and Y., 1958)

Plate 7, figs. 10a-b

1958b *Quinqueloculina villafranca* - Le Calvez, J. and Y., p. 180, pl. 4. figs. 22, 23 1923 *Miliolina disparilis* forma *a* Wiesner (non d'Orbigny) - Wiesner, p. 47, pl. 6, fig. 60 1958b *Cycloforina villafranca* (Le Calvez, J. and Y) pl. 28, figs. 7-9 1993 *Cycloforina villafranca* (Le Calvez, J. and Y) - Cimerman and Langer, p.33, pl. 28, figs.7-9

# Quinqueloculina aff. Q. wiesneri (Parr, 1950)

Plate 7, figs. 11a-c

1950 Quinqueloculina anguina Terquem var. wiesneri - Parr, p. 290, pl. 6, figs. 9-10 1988 Quinqueloculina wiesneri Parr - Haig, pl. 8, figs. 29-31

# Quinqueloculina sp. 1

Plate 7, figs. 12a-c

# Quinqueloculina sp. 2

Plate 7, figs. 13a-c 2006a *Quinqueloculina* sp. 1 - Langer and Schmidt-Sinns, p. 20, pl. 7, fig. 17

#### *Quinqueloculina* sp. 3 Plate 7, figs. 14a-b

# *Quinqueloculina* sp. 4

Plate 7, figs. 15a 1923 *Miliolina gualteriana* - Wiesner, p. 50, pl. 7, figs. 75-76

# Quinqueloculina sp. 5

Plate 7, figs. 16a

# Quinqueloculina sp. 6

Plate 7, figs. 17a-b *Quinqueloculina* sp. 7 Plate 8, figs. 1a-b *Quinqueloculina* sp. 8 Plate 8, figs. 2a-b

# Quinqueloculina sp. 9

Plate 8, figs. 3a-c

Subfamily Miliolinellinae Vella, 1957

# Affinetrina planciana (d'Orbigny, 1839)

Plate 8, figs. 4a-c

1839 *Triloculina planciana* - d'Orbigny, p. 173, pl. 9, figs. 17, 18
1923 *Miliolina planciana* (d'Orbigny) - Wiesner, p. 59, pl. 9, fig. 106
1958 *Triloculina planciana* d'Orbigny - Le Calvez, J. and Y., p. 193, pl. 6, fig. 65
1970 *Quinqueloculina planciana* d'Orbigny - Cherif, p.72 pl. 8, fig. 2
1991 *Affinetrina planciana* - d'Orbigny - Cimerman and Langer, p. 39, pl. 37, figs. 1-

## Biloculinella labiata (Schlumberger, 1891)

Plate 8, fig. 5

1891 Biloculina Schlumberger - p. 556, pl. 9, figs. 60-62, Textfigs. 13, 14
1923 Biloculina labiata Schlumberger var. simplex - Wiesner, p. 89, pl. 18, fig. 261
1958a Biloculinella labiata (Schlumberger) var. simplex Wiesner - Le Calvez, J. and Y., p. 202, pl. 16, figs. 193-194
1987 Biloculinella labiata (Schlumberger) - Loeblich and Tappan, p. 337, pl. 348, figs. 1-4
1993 Biloculinella labiata (Schlumberger) - Cimerman and Langer, p. 40, pl. 36, fig. 12

#### Mesopateoris sp. 1

Plate 8, figs. 6a-b

#### Milionella dilatata (d'Orbigny, 1839)

Plate 8, figs. 7a-c, 8a-b

1839a *Quinqueloculina dilatata* - d'Orbigny, p. 192, pl. 11, figs. 28-30 1893 *Quinqueloculina dilatata* d'Orbigny - Schlumberger, p. 217, pl. 3, figs. 70-74 1977a *Pateoris dilatata* (d'Orbigny) - Le Calvez, Y., p. 72 1991 *Milionella dilatata* (d'Orbigny) - Cimerman and Langer, p. 41, pl. 37, figs. 9-11

#### Miliolinella grata (Terquem, 1878)

Plate 8, figs. 9a-c

1878 *Quinqueloculina grata* - Terquem, p. 75, pl. 9, figs. 4-7 1991 *Miliolinella grata* (Terquem) - Cimerman and Langer, p.41, pl. 37, figs. 12-14

#### Miliolinella labiosa (d'Orbigny, 1839)

Plate 8, figs. 10a-b, 11a-b

1839a *Triloculina labiosa* - d'Orbigny, p. 178, pl. 10, figs. 12-14 1923 *Miliolina labiosa* (d'Orbigny) - Wiesner, p. 71, pl. 134, fig. 171 1929 *Triloculina labiosa* d'Orbigny - Cushman, p. 60, pl. 15, fig. 3 1958b *Triloculina labiosa* d'Orbigny - Le Calvez, J. and Y., p. 196, pl. 14, figs. 168, 169 1991 *Milionella labiosa* d'Orbigny - Cimerman and Langer, p. 41, pl. 38, figs. 1-3

#### Miliolinella semicostata (Wiesner, 1923)

Plate 8, figs. 12a-c

1923 *Miliolina semicostata* - Wiesner - p. 72, pl. 14, figs. 177, 178 1958b *Triloculina semicostata* (Wiesner) - Le Calvez, J. and Y., p. 194, pl. 15, figs. 170-172 1991 *Miliolinella semicostata* (Wiesner) - Cimerman and Langer, p. 42, pl. 38, figs. 10-15

## Miliolinella trigonina (Wiesner 1923)

Plate 8, figs. 13 a-b

1923 Miliolina hybrida Terquem var. trigonina nov. - Wiesner, pl. 14, p. 72, fig. 176

## Miliolinella sp.1

Plate 8, figs. 14a-c

# Sigmamiliolinella australis (Parr, 1932)

Plate 8, figs. 15a-b

1932a Quinqueloculina australis - Parr, p. 7, pl. I, fig. 8 1954 Miliolinella australis (Parr) - Cushman, Todd & Post, p. 334, pl. 84, figs. 3, 4 1987 Miliolinella australis (Parr) - Baccaert, p. 13 8, pl. 60, figs. 6-8 1988 Miliolinella australis (Parr) - Haig, p. 224, pl. 2, fig. 14 1988 Sigmamiliolinella australis (Parr) - Zheng, S., p. 263, 234, pl. 20, figs. 5-7, pl. 33, figs. 16-19

1994 Sigmamiliolinella australis (Parr) - Loeblich & Tappan, p. 58, pl. 100, figs. 1-3 2001 Miliolinella australis (Parr) - Akimoto et al., p. 9, pl. 19, fig. 3 2009 Sigmamiliolinella australis - Parker, p.330, figs. 238a-k, 239a-j, 240a-j, 241 a-h

Pseudomassilina sp. 1 Plate 8, figs. 16a, Plate 9, figs. 1a-b

## Pseudomassilina sp. 2

Plate 9, figs. 2a-c

Pseudotriloculina laevigata (d'Orbigny, 1826)

Plate 9, figs. 3a-b

1826 Triloculina laevigata - d'Orbigny, p. 300, no. 15 1923 Miliolina laevigata (d'Orbigny) - Wiesner, p. 55, pl. 8, figs. 94-96 1958 Triloculina laevigata d'Orbigny - Le Calvez, J. and Y., p. 19, pl. 6, figs. 62-64 1991 Pseudotriloculina laevigata d'Orbigny - Cimerman and Langer, p. 43, pl. 39, figs. 8-12

# *Pseudotriloculina* sp. 1

Plate 9, figs. 4a-c

#### Pseudotriloculina sp. 2 Plate 9, figs. 5a-c

1991 Pseudotriloculina sp. 1 - Cimerman and Langer, p. 44, pl. 40, fig. 11

#### Pseudotriloculina sp. 3 Plate 9, figs. 6a

1923 Miliolina disciformis Terquem - Wiesner, p. 58, pl. 4, fig. 104

#### Pseudotriloculina sp. 4 Plate 9, figs. 7a-b

Pseudotriloculina sp. 5 Plate 9, figs. 8a-b

Pseudotriloculina sp. 6 Plate 9, figs. 9a-c

Pseudotriloculina sp. 7 Plate 9, figs. 10a-c

Pseudotriloculina sp. 8 Plate 9, figs. 11a-c

# Triloculina adriatica Le Calvez, J. and Y., 1958

Plate 9, figs. 12a-b, 13a

1923 Miliolina tricarinata (d'Orbigny) - Wiesner, p. 62, pl. 10, fig. 128 1958b Triloculina adriatica - Le Calvez, J. and Y., p. 188, pl. 14, figs. 158, 159 1991 Triloculina adriatica Le Calvez - Cimerman and Langer, p. 46, pl. 42, figs. 9-10

## Triloculina asymmetrica Said, 1949

Plate 9, figs. 14a-c, 15a-c

1949 Triloculina asymmetrica - Said, p. 18, pl.2, fig. 11 1993 Triloculina asymmetrica Said - Hottinger et al., p. 64, pl 66, figs. 4-9

# Triloculina plicata Terquem, 1878

Plate 9, figs. 16a-c

1878 Triloculina plicata - Terquem, p. 61, pl. 6, figs. 2 a, b
1923 Triloculina plicata Terquem - Wiesner, p. 62, pl. 11, figs. 129, 130
1958b Triloculina plicata Terquem - Le Calvez, J. and Y., p. 189, pl. 14, figs. 162, 163
1991 Triloculina plicata Terquem - Cimerman and Langer, p. 46, pl. 43, figs. 8-10

#### Triloculina terquemiana (Brady, 1884)

Plate 10, figs. 1a-c

1884 *Miliolina terquemiana* - Brady, p. 114, fig. 1 1917 *Triloculina terquemiana* (Brady) - Cushman, p. 72 1959 *Triloculina terquemiana* (Brady) - Graham and Militante, p. 57, pl. 8, fig. 12

#### Triloculina tricarinata d'Orbigny, 1826

Plate 10, figs. 2a-b

1826 *Triloculina tricarinata* - d'Orbigny, p. 299 no. 6 1923 *Miliolina angularis* (d'Orbigny) - Wiesner, p. 63, pl. 11, fig. 133 1991 *Triloculina tricarinata* (d'Orbigny) - Cimerman and Langer, p. 46, pl. 44, figs. 3-4

#### Triloculinella sp. 1

Plate 10, figs. 3a-c

# Varidentella sp. 1

Plate 10, figs. 4a-b

Subfamily Sigmoilinitinae Luczkowska, 1974

## Sigmoilinita costata (Schlumberger, 1893)

Plate 10, figs. 5a-b

1893 *Sigmoilina costata* - Schlumberger, p. 203, pl. 1, figs. 51, 52 1958 *Sigmoilina costata* Schlumberger - Le Calvez, J. and Y., p. 20, pl. 7, figs. 69, 70 1991 *Sigmoilinita costata* Schlumberger - Cimerman and Langer, p. 47, pl. 45, figs. 1-6

## Sigmoilinita var. S. costata (Schlumberger, 1893)

Plate 10, figs. 6a-c

Sigmoilinita grata (Terquem, 1878)

Plate 10, figs. 7a-b

1878 Spiroloculina grata - Terquem, p. 55, pl. 5, figs. 14, 15 1958 Sigmoilina grata (Terquem) - Le Calvez, J. and Y., p. 209, pl. 8, fig. 91 1993 Sigmoilinita grata (Terquem) - Cimerman and Langer, p. 47, pl. 45, figs. 11-14

## Sigmoilinita sp. 1

Plate 10, figs. 8a-c

1991 Sigmoilinita sp. 2 - Cimerman and Langer, p.48, pl. 46, figs. 6-8

#### *Sigmoinella* sp. 1 Plate 10, figs. 9a-b, 10a-b

*Sigmoinella* sp. 2 Plate 10, figs. 11a-b

#### Subfamily Tubinellinae Rhumbler, 1906

#### Articulina carinata Wiesner, 1923

Plate 10, figs. 14a-b

1923 *Articulina sagra* d'Orbigny var. *carinata* - Wiesner, p. 74, pl. 19, fig. 188 1970a *Articulina pacifica* Cushman - v. Daniels, p. 78, Textfig. 53 1991 *Articulina carinata* Wiesner - Cimerman and Langer, p.48, pl. 47, figs. 1-5

#### Parrina bradyi (Milieu, 1898)

Plate 10, figs. 15a-b, 16a

1898 Nubecularia bradyi - Milieu, p. 261, pl. 5, figs. 6 a, b (fide Ellis and Messina, 1940)
1923 Miliolina hibrida (Terquem) - Wiesner, p. 71, pl. 14, figs. 172-175
1960 Parrina bradyi (Milieu) - Barker, pl. 1, figs. 5, 6
1970 Parrina bradyi (Milieu) - v. Daniels, p. 78, pl. 4, fig. 3
1987 Parrina bradyi (Milieu) - Loeblich and Tappan, p. 351, pl. 358, figs. 16-18
1991 Parrina bradyi (Milieu) - Cimerman and Langer, p. 49, pl. 47, figs. 6-7

Family Peneroplidae Schultze, 1854

#### Laevipeneroplis karreri (Wiesner, 1923)

Plate 10, figs. 17a-b

1923 *Peneroplis karreri* Wiesner - Wiesner, p. 96, pl. 20, fig. 285 1991 *Peneroplis karreri* Wiesner - Cimerman and Langer, p.49, pl. 48, figs. 1-7

#### Peneroplis pertusus (Forskal, 1775)

Plate 10, figs. 18a-b, 19a-b

1775 Nautilus pertusus - Forskal, p. 125 (fide Ellis and Messina, 1940)
1917 Peneroplis pertusus (Forskal) - Cushman, p. 86, pl. 36, fig. 1, pl. 37, Figs. 1, 2, 6
1974 Peneroplis pertusus (Forskal) - Colom, p. 219, fig. 64 j
1991 Peneroplis pertusus (Forskal) - Cimerman and Langer, p. 49, pl. 49, figs. 1-8

#### Peneroplis planatus (Fichtel and Moll, 1798)

Plate 10, figs. 20a-b

1798 Nautilus planatus - Fichtel and Moll, p. 91, pl. 16, figs. a-h
1826 Peneroplis planatus (Fichtel and Moll) - d'Orbigny, p. 285, no. 1
1858 Peneroplis planatus (Fichtel and Moll) - Williamson, p. 45, pl. 3, figs. 84, 85
1960 Peneroplis planatus (Fichtel and Moll) - Barker, pl. 13, fig. 15
1974 Peneroplis planatus (Fichtel and Moll) - Colom, p. 219, figs. 64 h-i, k
1987 Peneroplis planatus (Fichtel and Moll) - Baccaert, p. 58, pl. 17, figs. 1-4, pl. 18, fig. 1
1987 Peneroplis planatus (Fichtel and Moll) - Loeblich and Tappan, p. 371, pl. 391, figs. 7, 8
1991 Peneroplis planatus (Fichtel and Moll) - Cimerman and Langer, p.50, pl. 50, figs. 1-6

Family Soritidae Ehrenberg, 1839 Subfamily Soritinae Ehrenberg, 1839

#### Sorites orbiculus Ehrenberg, 1839

Plate 10, figs. 221a-b

1775 Nautilus orbiculus - Forskal, p. 125 (fide Ellis and Messina, 1940)
1839 Sorites orbiculus - Ehrenberg, p. 134
1852 Orbiculina complanata - Williamson, p. 115
1961 Sorites orbiculus Ehrenberg - Lehman, p. 641, pl. 8, figs. 1-8
1991 Sorites orbiculus Ehrenberg - Cimerman and Langer, p. 117, pl. 51, figs. 1-5

Suborder Lagena Delage and Hérouard, 1896 Superfamily Nodosaricea Ehrenberg, 1838 Family Nodosariidae Ehrenberg, 1838 Subfamily Nodosariinae Ehrenberg, 1838

# Botuloides? sp. 1

Plate 11, figs. 1a-b

## Dentalina subarcuata (Montagu, 1803)

Plate 11, figs. 2a-b

1803 Nautilus subarcuatus - Montagu, p. 198, pl. 6, fig. 5 1971 Dentalina subarcuata (Montagu) - Murray, p. 79, figs. 4-5

## Laevidentalina filiformis (d'Orbigny, 1826)

Plate 11, figs. 3a-b, 4a-b

1826 Nodosaria filiformis - d'Orbigny, p. 253, no. 14.
1884 Nodosaria (D.) filiformis d'Orbigny - Brady, p. 500, pl. 63, figs 3-5.
1995 Laevidentalina filiformis (d'Orbigny) - Yassini & Jones, p. 99, figs 257-258.
1999 Laevidentalina filiformis (d'Orbigny) - Hayward et al., p. 109, pl. 6, figs 18-19.
2012 Laevidentalina filiformis (d'Orbigny) - Debenay, p. 165, p. 284, p.62, pl. 11

Laevidentalina sp. 1

Plate 11, figs. 5a-b

*Laevidentalina* sp. 2 Plate 11, figs. 6a-b

# Dentalinoides ? sp. 1

Plate 11, figs. 7a-c

Family Vaginulinidae Reuss, 1860 Subfamily Lenticulinidae Chapman, Parr and Collins, 1934

## Lenticulina gibba (d'Orbigny, 1826)

Plate 11, figs. 8a-b, 9a-b

1826 Cristellaria gibba - d'Orbigny, p. 292, no. 17
1839a Cristellaria gibba - d'Orbigny, p. 40, pl. 7, figs. 20, 21
1913 Cristellaria gibba d'Orbigny - Cushman, p. 105, pl. 25, fig. 4
1974 Robulus gibbus (d'Orbigny) - Colom, p. 96, fig. 11 g
1977b Lenticulina gibba (d'Orbigny) - Le Calvez, Y., p. 25, fig. 1
1991 Lenticulina gibba (d'Orbigny) - Cimerman and Langer, p. 51, pl. 53, figs. 7-11
2014 Lenticulina gibba (d'Orbigny) - Meric et al., p. 220, pl. 45, figs. 6-7

# Lenticulina orbicularis (d'Orbigny, 1826)

Plate 11, figs. 10a-b

1826 Robulina orbicularis - d'Orbigny, p. 288, pl. 15, figs. 8, 9 1974 Robulus orbicularis (d'Orbigny) - Colom, p. 97, figs. 11 a-e 1982 Lenticulina orbicularis (d'Orbigny) - Foraminiferi padani (AGIP, S.p.A.), pl. 10, figs. 5, 5a 1991 Lenticulina orbicularis (d'Orbigny) - Cimerman and Langer, p. 51/52, pl. 53, fig. 12 2014 Lenticulina orbicularis (d'Orbigny) - Meric et al., p. 220, pl. 45, fig. 8

Lenticulina sp. 1

Plate 11, figs. 11a-b

7 Appendix

*Lenticulina* sp. 2

Plate 11, figs. 12a-b

Family Lagenidae Reuss, 1862

## Lagena striata (d'Orbigny, 1839)

Plate 11, figs. 13a-b, 14a

1839c Oolina striata - d'Orbigny, pl. 5, Fig. 12
1923 Lagena substriata Williamson - Cushman, p. 56, pl. 10, fig. 11
1970 Lagena striata (d'Orbigny) - v. Daniels, p. 79, pl. 4, fig. 9 a1839
1991 Lagena striata (d'Orbigny) - Cimerman and Langer, p. 53, pl. 55, figs. 6-7
1993 Lagena striata - Sgarella and Moncharmont Zei, p.198/199, pl. 12, fig. 3, non 2

#### Lagena strumosa Reuss, 1858

Plate 11, figs. 15a-b

1858 Lagena strumosa - Reuss, p. 434 1863 Lagena strumosa Reuss - Reuss, p. 328, pl. 4, fig. 49 1987 Lagena strumosa Reuss - Baccaert, p. 157, pl. 67, Figs. 5,6, pl. 68, fig. 1 1993 Lagena strumosa Reuss - Hottinger et al., p. 79, pl. 90, figs. 18-25 2012 Lagena strumosa Reuss - Milker and Schmiedl, p. 75, fig. 18.34 2014 Lagena strumosa Reuss - Meric et al., p. 221, pl. 47, figs. 10-13

# Lagena sp. 1

Plate 11, figs. 16a

2014 Lagena doveyensis Haynes 1973 - Meric et al., p.221, pl. 47, fig. 2

## *Pygmaeoseistron?* sp. 1

Plate 11, figs. 17a-b

1993 Pygmaeoseistron? sp. 1 - Hottinger et al., p. 79, pl. 91, figs. 1-5

Family Polymorphinidae d'Orbigny, 1839 Subfamily Polymorphininae d'Orbigny, 1839

#### Polymorphina sp. 1

Plate 11, figs. 18a-b

1991 Polymorphina sp. 4 - Cimerman and Langer, p. 54, pl. 56, figs. 8-11

## Sigmoidella sp. 1

Plate 11, figs. 19a-c

1987 Sigmoidella kagaensis- Loeblich and Tappan, p. 421/422, pl. 459, fig. 5

Family Ellipsolagenidae A. Silvestri, 1923 Subfamily Ellipsolageninae A. Silvestri, 1923

# Fissurina lucida (Williamson, 1858)

Plate 11, figs. 20a-b

1858 *Entosolenia marginata* var. *lucida* - Williamson, p. 10, pl. 1, figs. 22, 23 1991 *Fissurina lucida* (Williamson) - Cimerman and Langer, p. 55/56, pl. 59, fig. 1 2012 *Fissurina lucida* (Williamson) - Debenay, p. 147, p. 292, p. 60, pl. 9 7 Appendix

*Fissurina* sp. 1 Plate 11, figs. 21a-b

Subfamily Parafissurinae R.W. Jones, 1984

#### Parafissurina sp. 1

Plate 11, figs. 22a-b

Family Bolivinidae Glaessner, 1937

# Bolivina pseudoplicata Heron-Allen and Earland, 1930

Plate 11, figs. 23a-b

1930 Bolivina pseudoplicata - Heron-Allen and Earland, p. 81, pl. 3, figs. 36-40 1937c Bolivina pseudoplicata Heron-Allen and Earland - Cushman, p. 166, pl. 19, figs. 12-20 1970a Bolivina pseudoplicata Heron-Allen and Earland - v. Daniels, p. 81, pl. 5, figs. 2a-c 1971 Bolivina pseudoplicata Heron-Allen and Earland - Murray, p. 107, pl. 43, figs. 1-7 pl. 61 1991 Bolivina pseudoplicata Heron-Allen and Earland - Cimerman and Langer, p.58, pl. 61, figs. 1-3 1992 Bolivina pseudoplicata Heron-Allen and Earland - Barmawidjaja et al., pl. 4, fig.8

#### Brizalina dilatata (Reuss, 1850)

Plate 12, figs. 1a-b, 2a-b

1850 Bolivina dilatata - Reuss, p. 381, pl. 48, fig. 15
1970a Bolivina dilatata Reuss - v. Daniels, p. 81, pl. 5, fig.3
1991 Brizalina dilatata (Reuss) - Cimerman and Langer, p. 59, pl. 62, fig.2
1992 Bolivina dilatata Reuss - Barmawidjaja et al. p., 310, pl. 2, figs. 5-7

#### Brizalina aff. B. pygmaea (Brady, 1881)

Plate 11, figs. 24a-b

1881 Bolivina pygmaea - Brady, p. 406 1994 Brizalina pygmaea Brady - Jones, p. 58, pl.53, figs.5-6

#### Brizalina spathulata (Williamson, 1858)

Plate 11, figs. 25a-b

*Textularia variabilis* var. *spathulata* - Williamson, p. 76, pl. 6, figs. 164, 165 1937c *Bolivina spathulata* (Williamson) - Cushman, p. 162, pl. 15, figs. 20-24 1970a *Brizalina spathulata* (Williamson) - v. Daniels, p. 81, pl. 5, fig. 4, a-b *Brizalina spathulata* (Williamson) - Colom, p. 121, figs. 18 h, i *Brizalina spathulata* (Williamson) - Cimerman and Langer, p. 60, pl. 62, figs. 3-5 *Bolivina spathulata* (Williamson) - Barmawidjaja et al., p. 310, pl. 2, figs. 15-17 *Bolivina spathulata* (Williamson) - Sgarella and Moncharmont-Zei, p. 210, pl. 14, fig. 3 *Brizalina spathulata* (Williamson) - Meric et al., p. 222, pl. 50, figs. 2-5

## Brizalina striatula (Cushman, 1922)

Plate 12, figs. 3a-b, 4a-b
1922a *Bolivina striatula* - Cushman, p. 27, pl. 3, fig. 10 (fide Ellis and Messina, 1940)
1922b *Bolivina striatula* Cushman - Cushman, p. 43
1937c *Bolivina striatula* Cushman - Cushman, p. 154, pl. 18, figs. 30, 31
1970a *Brizalina striatula* (Cushman) - v. Daniels, p. 82, pl. 5, fig 5
1974 *Bolivina striatula* Cushman - Colom, p. 120, figs. 17 a-g
1991 *Brizalina striatula* (Cushman) - Cimerman and Langer, p. 60, pl. 62, figs.6-9
1993 *Bolivina striatula* Cushman - Sgarella and Moncharmont-Zei, p. 210, pl. 14, fig. 16
2012 *Brizalina striatula* (Cushman) - Milker and Schmiedl, p. 82, fig. 20.3

# Brizalina aff. B. striatula (Cushman, 1922)

Plate 12, figs. 5a-c

1922a *Bolivina striatula* - Cushman, p. 27, pl. 3, fig. 10 (fide Ellis and Messina, 1940) 1992 *Bolivina dilatata* Reuss *striatula* type - Barmawidjaja et al. p. 310, pl.2, fig.10 2014 *Brizalina striatula* Cushman - Meric et al., p. 222, pl.50, fig. 6

*Brizalina* **sp. 1** Plate 12, figs. 6a

Superfamily Cassidulinacea d'Orbigny, 1839 Family Cassidulinidae d'Orbigny, 1839 Subfamily Cassidulininae d'Orbigny, 1839

## Cassidulina laevigata d'Orbigny, 1826

Plate 12, figs. 7a

*Cassidulina laevigata* - d'Orbigny, p. 282, pl. 6, figs. 4-5 *Cassidulina laevigata* d'Orbigny - Vénec-Peyré (in Ecomed), p. 79, pl. 8, fig. 4 *Cassidulina laevigata* d'Orbigny - Loeblich and Tappan, p. 504, pl. 555, figs. 1-5 *Cassidulina laevigata* d'Orbigny - Cimerman and Langer, p. 61, pl. 63, figs. 1-3 *Cassidulina laevigata* d'Orbigny - Milker and Schmiedl, p.84, fig. 20.5-6

#### Globocassidulina subglobosa (Brady, 1884)

Plate 12, figs. 8a-b

*Cassidulina subglobosa* - Brady, p. 430, pl. 54, figs. 17 a-c 1922b *Cassidulina subglobosa* Brady - Cushman, p. 127, pl. 24, fig. 6 *Cassidulina subglobosa* Brady - Rosset-Moulinier, p. 185, pl. 11, fig. 20 *Globocassidulina subglobosa* (Brady) - Cimerman and Langer, p. 61, pl. 63, figs. 4-6 *Globocassidulina subglobosa* (Brady) - Sgarella and Moncharmont-Zei, p. 23, pl. 24, figs. 1-2 *Globocassidulina subglobosa* (Brady) - Milker and Schmiedl, p. 85, fig. 20.13-14

#### Family Stainforthiidae Reiss, 1963

# Stainforthia concava (Höglund, 1947)

Plate 12, figs. 9a-b

1947 Virgulina concava n. sp. - Höglund, p. 237, pl. 23, fig. 3-4
1987 Stainforthia concava - Loeblich and Tappan, p. 148, pl. 565, figs. 9-12
1970a Stainforthia concava - v. Daniels, p. 83, pl. 6, fig. 1
1992 Stainforthia fusiformis (Williamson) - Barmawidjaja et al., pl. 3, fig. 5, non 1-4
2012 Stainforthia complanata - Milker and Schmiedl, p. 86, fig. 20.16
2014 Fursenkoina acuta (d'Orbigny) - Meric et al., p. 223, pl. 52, figs. 19-23

Superfamily Buliminacea Jones, 1875 Family Siphogenerinoididae Saidova, 1981 Subfamily Siphogenerinoridinae Saidova, 1981

## Loxostomina? limbata (Brady, 1881) costulata (Cushman, 1922)

Plate 12, figs. 10a-b

1922a Bolivina limbata Brady var. costulata Cushman - Cushman, p. 26, pl. 3, fig. 8
1968 Loxostomina limbata (Brady) var. costulata (Cushman) - Sellier de Civreux, pl. 7, figs. 3-5
1974 Bolivina limbata Brady - Lutze, p. 27, pl. 5, figs. 90-91
1975 Brizalina (Parabrizalina) sp. A. - Zweig-Strykowski and Reiss, p. 109, pl. 6, figs. 7-11
1984 Brizalina (Parabrizalina) sp. A. - Reiss and Hottinger, fig. G27 k-1
1993 Loxostomina? limbata (Brady) costulata (Cushman) - Hottinger et al., p. 97, pl. 120, figs. 8-13

# Loxostomina sp. 1

Plate 12, figs. 11a-b

# Loxostomina sp. 2

Plate 12, figs. 12a-b

Subfamily Tubulogenerininae Saidova, 1981

## Rectuvigerina phlegeri Le Calvez 1958

Plate 12, figs. 13a-b

1958a *Rectuvigerina phlegeri* - Berthois and Le Calvez, p. 363, pl. 1, fig. 11 *Rectuvigerina phlegeri* Le Calvez - Schiebel, p. 55, pl. 3, fig. 10 *Rectuvigerina phlegeri* Le Calvez - Milker and Schmiedl, p. 86-87, fig. 20.18 *Rectuvigerina phlegeri* Le Calvez - Meric et al., p. 222, pl. 50, fig. 19

Family Buliminidae Jones, 1875

## Bulimina aculeata d'Orbigny, 1826

Plate 12, figs. 14

1826 Bulimina aculeata - d'Orbigny, p. 269, no. 7
1922a Bulimina aculeata d'Orbigny - Cushman, p. 96, pl. 22, figs. 1, 2
1960 Bulimina aculeata d'Orbigny - Barker, pl. 51, figs. 7-9
1974 Bulimina aculeata d'Orbigny - Colom, p. 115, fig. 16 g
1970a Bulimina aculeata d'Orbigny - v. Daniels, p. 82, pl. 5, fig. 8
1991 Bulimina aculeata d'Orbigny - Cimerman and Langer, p. 61 pl. 63, figs. 10-11
1993 Bulimina aculeata d'Orbigny - Sgarella and Moncharmont-Zei, p. 211, pl. 15, fig. 1
2012 Bulimina aculeata d'Orbigny - Milker and Schmiedl, p. 87, fig. 20.19
2014 Bulimina aculeata d'Orbigny - Meric et al., p. 327, pl. 50, figs. 20 a-b, 21 a-b

#### Bulimina elongata d'Orbigny, 1846

Plate 12, figs. 15

1846 Bulimina elongata - d'Orbigny, p. 187, pl. 11, figs. 19, 20
1922a Bulimina elongata d'Orbigny - Cushman, p. 107
1960 Bulimina elongata d'Orbigny - Barker, pl. 51, figs. 1, 2
1972 Bulimina elongata d'Orbigny - Rosset-Moulinier, p. 163, pl. 9, fig. 18
1974 Bulimina elongata d'Orbigny - Colom, p. 116, fig. 16 n

*Bulimina elongata* d'Orbigny - Cimerman and Langer, p. 62, pl. 64, figs. 3-8 *Bulimina elongata* d'Orbigny - Hottinger et al., p. 99, pl. 124, figs.3-7 *Bulimina elongata* d'Orbigny - Sgarella and Moncharmont-Zei, p. 211, pl. 15, figs. 10-11 *Bulimina elongata* d'Orbigny - Milker and Schmiedl, p. 88, fig. 20.21

## Bulimina marginata d'Orbigny, 1826

Plate 12, figs. 16
1826 Bulimina marginata - d'Orbigny, p. 269, pl. 12, figs. 10-1
1970 Bulimina marginata d'Orbigny - v. Daniels, p. 83, pl. 5, fig.9
1979 Bulimina marginata d'Orbigny - Hageman, p. 90, pl. 2, fig. 7
1984 Bulimina aculeata - Vénec-Peyré (not d'Orbigny), in Ecomed, pl. 6, fig. 2
1987 Bulimina marginata forma marginata d'Orbigny - Jorissen, p. 46, pl. 4, figs. 6 a, b
1988 Bulimina marginata forma marginata d'Orbigny - Jorissen, p. 75, pl. 4, fig. 6, pl. 12, figs. 7, 14-17, pl. 13, figs. 5, 10, 11, 13-15, pl. 14, figs. 1-3, 7, 9-11, pl. 15,figs. 1, 2, 5-6
1991 Bulimina marginata d'Orbigny - Cimerman and Langer, p. 62, pl. 64, figs. 9-11
1993 Bulimina marginata d'Orbigny - Sgarella and Moncharmont-Zei, p. 212, pl.15, figs. 5-7

## Bulimina sp. 1

Plate 12, figs. 17a-b

#### Praeglobobulimina sp. 1

Plate 12, figs. 18a

## Protoglobobulimina pupoides (d'Orbigny, 1846)

Plate 12, figs. 19a

1846 *Bulimina pupoides* - d'Orbigny, p. 185, pl. 11, figs. 11-12 1987 *Protoglobobulimina pupoides* (d'Orbigny) - Loeblich and Tappan, p. 522, pl. 572, figs. 1-6 1991 *Protoglobobulimina pupoides* (d'Orbigny, 1846) - Cimerman and Langer, p. 62, pl. 65, figs. 1-3

Family Buliminellidae Hofker, 1951

## Buliminella elegantissima, d'Orbigny, 1839

Plate 12, figs. 20a-c

1839c Buliminella elegantissima - d'Orbigny, p. 51, pl. 7, figs. 13-14 1960 Buliminella elegantissima (d'Orbigny) - Hofker, p. 248, Beilage C, fig. 83 1970a Buliminella elegantissima d'Orbigny - v. Daniels, p. 80, pl. 5, figs. 1a-b 1971 Buliminella elegantissima d'Orbigny - Murray, p. 105, pl. 42, figs.1-4 1987 Buliminella elegantissima d'Orbigny - Loeblich and Tappan, p. 522, pl. 572, figs. 7-11 2012 Buliminella elegantissima d'Orbigny - Debenay, p. 303, p. 188

Family Uvigerinidae Haeckel, 1894 Subfamily Uvigerininae Haeckel, 1894

# Uvigerina mediterranea Hofker, 1932

Plate 12, figs. 21a-b

1932 Uvigerina mediterranea - Hofker, p. 118, Textfigs. 32a-g
1974 Uvigerina mediterranea Hofker - Colom, p. 122, figs. 19 h-n
1987 Uvigerina mediterranea Hofker - Jorissen, p. 214, pl. 1, fig. 2
1991 Uvigerina mediterranea Hofker - Cimerman and Langer, p. 63, pl. 65, figs. 7-9
1993 Uvigerina mediterranea Hofker - Sgarella and Moncharmont-Zei, p. 214, pl. 16, figs. 1-2
2012 Uvigerina mediterranea Hofker - Milker and Schmiedl, p. 90, fig. 20.28

Subfamily Angulogerininae Galloway, 1933

## Angulogerina angulosa (Williamson, 1858)

Plate 12, figs. 22a-c

1858 Uvigerina angulosa - Williamson, p. 67, pl. 5, fig. 140
1958a Angulogerina angulosa (Williamson) - Le Calvez, Y., p. 180
1960 Trifarina angulosa (Williamson) - Barker, pl. 74, figs. 15, 16
1970a Trifarina angulosa (Williamson) - v. Daniels, p. 83, pl. 6, fig. 4
1979 Trifarina angulosa (Williamson) - Alfirevic, p. 121, pl. 25, fig. 3
1987 Angulogerina angulosa (Williamson) - Loeblich and Tappan, p. 525, pl. 574, figs. 5-9
1991 Angulogerina angulosa (Williamson) - Cimerman and Langer, p. 63, pl. 66, figs. 3-4

Family Reussellidae Cushman, 1933

## Reussella spinulosa (Reuss, 1850)

Plate 12, figs. 23a-c

1850 Verneuilina spinulosa - Reuss, p. 374, pl. 47, fig. 12
1970a Reussella spinulosa (Reuss) - v. Daniels, p. 83, pl. 6, fig. 2
1979 Reussella spinulosa (Reuss) - Alfirevic, p. 117, pl. 25, fig. 2
1987 Reussella spinulosa (Reuss) - Loeblich and Tappan, p. 527, pl. 575, figs. 9-12
1991 Reussella spinulosa (Reuss) - Cimerman and Langer, p. 63, pl. 66, figs. 5-8
1993 Reussella spinulosa (Reuss) - Sgarella and Moncharmont-Zei, p. 214, pl. 15, fig. 14

2012 Reussella spinulosa (Reuss) - Debenay, p. 182, p. 305, pl. 13

Family Trimosinidae Saidova, 1975

#### Mimosina affinis Millett, 1900

Plate 13, figs. 1a-b

1900 *Mimosina affinis* - Millett, Part 4, p. 548, pl. 4, fig. 11, 1901, Part x, pl. 1, fig. 1 1993 *Mimosina affinis* Millett - Hottinger et al., p. 104, pl. 133, figs. 9-12, pl. 134, figs. 1-3 2012 *Mimosina affinis* Millett - Debenay, p. 180, p. 64, pl. 13, p. 305

Superfamily Fursenkoinacea Loeblich and Tappan, 1961 Family Fursenkoinidae Loeblich and Tappan, 1961

## Fursenkoina aff. F. pauciloculata (Brady, 1884)

Plate 13, figs. 2a-c

1884 Virgulina pauciloculata - Brady, p. 414, pl. 52, figs 4-5 1960 Virgulina squammosa d'Orbigny - Hofker, p. 249, Beilage D, fig. 100-101 1994 Fursenkoina pauciloculata (Brady) - Loeblich & Tappan, p. 131; pl. 256, figs 1-5 2012 Fursenkoina pauciloculata (Brady) - Debenay, p. 174, p. 63, pl. 12, p. 306

# Fursenkoina sp. 1

Plate 13, figs. 3a-b

Family Bagginidae Cushman, 1927

# Valvulineria bradyana (Fornasini, 1900)

Plate 13, figs. 4a-c

1900 Discorbina bradyana - Fornasini, p. 393, Textfig. 43 (fide Ellis and Messina, 1940)
1984 Valvulineria bradyana (Fornasini) - Bizon (in Ecomed), p. 91, fig. 13
1984 Valvulineria bradyana (Fornasini) - Vénec-Peyré (in Ecomed), p. 78, pl. 7, fig. 2
1988 Valvulineria bradyana (Fornasini) - Jorissen, p. 26, pl. 4, figs. 1- 2
1991 Valvulineria bradyana (Fornasini) - Cimerman and Langer, p. 64, pl. 67, figs. 8-10
1993 Valvulineria bradyana (Fornasini) - Sgarella and Moncharmont Zei, p. 220, pl. 18, figs. 1-2

Family Pleurostomellidae Reuss, 1860 Subfamily Pleurostomellinae Reuss, 1860

## Pleurostomella ? sp. 1

Plate 13, figs. 5a-b Family Eponididae Hofker, 1951

# Eponides concameratus (Williamson, 1858)

Plate 13, figs. 6a-b

1858 Rotalina concameratus - Williamson, p. 52, pl. 4, figs. 101-102
1960 "Eponides repandus (Fichte) and Molly var. concamerata (Williamson) - Barker, pl. 104, fig. 19
1979 Eponides repanda (Fichtel and Moll) var. concamerata (Williamson) - Barker, pl. 104, fig. 19
1984 Eponides repandus (Fichtel and Moll) - Rögl and Hansen, pl. 3, Fig. 4, pl. 4, figs. 1-2
1991 Eponides concameratus (Williamson) - Cimerman and Langer, p. 64, pl. 67, figs. 11-14

Family Rosalinidae Reiss, 1963

*Gavelinopsis praegeri* (Heron-Allen and Earland, 1913) Plate 13, figs. 7a-b 1913 Discorbina praegeri - Heron-Allen and Earland, p. 122, pl. 10, figs. 8-10 (fide Ellis and Messina, 1940)
1971 Gavelinopsis praegeri (Heron-Allen and Earland) - Murray, p. 133, pl. 55, figs. 1-5
1972 Gavelinopsis praegeri (Heron-Allen and Earland) - Rosset-Moulinier, p. 167, pl. 9, figs. 27- 28
1977 Gavelinopsis praegeri (Heron-Allen and Earland) - Haake, p. 66, pl. 2, fig. 4
1987 Gavelinopsis praegeri (Heron-Allen and Earland) - Loeblich and Tappan, p. 560, pl. 608, figs. 6-12
1987 Gavelinopsis praegeri (Heron-Allen and Earland) - Jorissen, pl. 3, fig. 13
1991 Gavelinopsis praegeri (Heron-Allen and Earland) - Cimerman and Langer, p. 66, pl. 70, figs. 3-4
1993 Gavelinopsis praegeri (Heron-Allen and Earland) - Sgarella and Moncharmont-Zei, p. 28, pl. 17, figs. 1-2
2012 Gavelinopsis praegeri (Heron-Allen and Earland) - Milker and Schmiedl, p. 97, figs. 22.3-4
2014 Gavelinopsis praegeri (Heron-Allen and Earland) - Meric et al., p. 224, pl. 55, figs. 1a-b

#### Neoconorbina terquemi (Rzehak, 1888)

Plate 13, figs. 8a-c, 9a-b

1876 Rosalina orbicularis - Terquem, p. 75, pl. 9, figs. 4 a, b (fide Ellis and Messina, 1940)
1908 Discorbina orbicularis (Terquem) - Sidebottom, p. 13, pl. 4, figs. 7a-c
1970a Neoconorbina terquemi (Rzehak) - v. Daniels, p. 186, pl. 9, figs. 29, 30
1974 Discorbis orbicularis (Terquem) - Colom, p. 125, fig. 21 k
1987 Neoconorbina terquemi (Rzehak) - Loeblich and Tappan, p. 560, pl. 609, figs. 8-10
1991 Neoconorbina terquemi (Rzehak) - Cimerman and Langer, p. 66, pl. 70, figs. 5-7
1993 Neoconorbina terquemi (Rzehak) - Sgarella and Moncharmont-Zei, p. 218, pl. 16, fig. 13
2012 Neoconorbina terquemi (Rzehak) - Milker and Schmiedl, p. 97, fig. 22.5-6
2014 Neoconorbina terquemi (Rzehak) - Meric et al., p. 224, pl. 55, figs. 3-4

#### Rosalina cf R. anomala Terquem, 1875

Plate 13, figs. 10a-c

1875 *Rosalina anomala* - Terquem, p. 438, pl. 5, fig. 1 2012 *Rosalina anomala* Terquem - Milker and Schmiedl, p. 98, figs. 22.9-10

#### Rosalina bradyi (Cushman, 1915)

Plate 13, figs. 11a-c

1884 Discorbina globularis - Brady (not d'Orbigny), p. 178, pl. 86, figs. 8a-c
1915 Discorbis globularis (d'Orbigny) var. bradyi - Cushman, p.12
1951 Discopulvinulina bradyi (Cushman) Hofker, p. 452, figs. 310 a, b
1960 Rosalina bradyi (Cushman) - Barker, pl. 86, figs. 8a-c
1979 Rosalina globularis bradyi (Cushman) - Blanc-Vernet et al. pl. 22, fig. 12
1987 Rosalina bradyi (Cushman) - Jorissen, pl. 3, figs. 6a-b
1991 Rosalina bradyi (Cushman) - Cimerman and Langer, p. 66, pl. 71, figs. 1-5
1993 Rosalina bradyi (Cushman) - Hottinger et al., p. 110, pl. 143, figs. 1-6
1993 Rosalina bradyi (Cushman) - Sgarella and Moncharmont-Zei, p. 218, pl. 17, figs. 4-5
2012 Rosalina bradyi (Cushman) - Milker and Schmiedl, p. 98, figs. 22.11-14
2014 Rosalina bradyi (Cushman) - Meric et al., p. 224, pl. 55, figs. 6-13

#### Rosalina floridensis (Cushman, 1931)

Plate 13, figs. 12a-c

1931 Rosalina bertheloti (d'Orbigny) var. floridensis- Cushman, p. 17, pl. 3, figs. 5 a-c 1960 Discopulvinulina bertheloti (d'Orbigny) - Hofker, p. 253, pl. 4, figs. 127 a-c 1991 Rosalina floridensis (Cushman) - Cimerman and Langer, p. 67, pl. 70, figs. 8-10 2014 Rosalina floridensis (Cushman) - Meric et al., p. 224, pl. 56, figs. 1-5

#### Rosalina macropora (Hofker, 1951)

Plate 13, figs. 13a-b

1951 *Discopulvinulina macropora* - Hofker, p. 460, figs. 312, 313 1960 *Discopulvinulina macropora* - Hofker, p. 253, pl. D, figs. 122 a-c 1970a *Rosalina bradyi* (Cushman) - v. Daniels, p. 84, pl. 6, fig. 8 *Rosalina globularis semiporata* (Egger 1983) - Wenger, p. 305, pl. 15, figs. 10-12 *Rosalina macropora* Hofker - Cimerman and Langer, p. 67, pl. 71, figs. 6-7 *Rosalina macropora* Hofker - Milker and Schmiedl, p. 99, figs. 22.17-18 *Rosalina macropora* Hofker - Meric et al., p. 224, pl. 56, figs. 10-14

#### Rosalina obtusa? d'Orbigny, 1846

Plate 13, figs. 14a-b

1846 Rosalina obtusa - d'Orbigny, p. 179, pl. 11, figs. 4-6 1985 Rosalina obtusa d'Orbigny - p. 67-68, pl. 61, figs. 7-12 1993 Rosalina obtusa d'Orbigny - Sgarella and Moncharmont-Zei, p. 219, pl. 17, figs. 9-10 2014 Rosalina obtusa d'Orbigny - Meric et al. p. 224, pl. 57, figs. 1a-b, 2

#### Rosalina orientalis (Cushman, 1925)

Plate 13, figs. 15a-b

1925 Discorbis orientalis - Cushman, p. 130 1987 Rosalina orientalis (Cushman) - Baccaert, p. 201, pl. 79, figs. 5-6 1993 Rosalina orientalis (Cushman) - Hottinger et al., p.11, pl. 143, figs. 7-9, pl. 144, figs.1-2

## Rosalina vilardeboana d'Orbigny, 1839

Plate 13, figs. 16a-c

1839c *Rosalina vilardeboana* - d'Orbigny, p. 44, pl. 6, figs. 13-15 *Rosalina vilardeboana* d'Orbigny - Barker, pl. 86, fig. 9 *Rosalina vilardeboana* d'Orbigny - Cimerman and Langer, p. 67, pl. 72, figs. 1-2 *Tretomphalus* sp. 1 - Milker and Schmiedl, p. 100, figs. 23.1-2

## Tretomphalus bulloides (d'Orbigny, 1839)

Plate 13, figs. 17a-c

1839a *Rosalina bulloides* - d'Orbigny, p. 98, pl. 3, figs. 2 - 5 *Rosalina (Tretomphalus) bulloides* (d'Orbigny) - Banner, Pereira and Desai, p. 164, pl. 1, figs. 1-5 *Tretomphalus bulloides* (d'Orbigny) - Loeblich and Tappan, p. 262, pl. 612, figs. 1-11 *Tretomphalus bulloides* (d'Orbigny) - Cimerman and Langer, p. 67, pl. 72, figs. 3-5 *Tretomphalus bulloides* (d'Orbigny) - Hottinger et al., p. 112, pl. 146, figs. 1-7 *Tretomphalus bulloides* (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 219, pl. 17, figs. 11-12 *Tretomphalus bulloides* (d'Orbigny) - Meric et al. pl. 224, pl. 57, figs. 5-6

## Conorbella imperatoria (d'Orbigny, 1846)

Plate 13, figs. 18a-c

1846 Rosalina imperatoria - d'Orbigny, p. 176, pl. 190, figs. 16-18
1908 Discorbna imperatoria (d'Orbigny) - Sidebottom, p. 13, pl. 5, figs. 1, 2
1985 Schackoinella imperatoria (d'Orbigny) - Papp and Schmid, p. 226, pl. 60, figs. 2-5
1991 Conorbella imperatoria (d'Orbigny) - Cimerman and Langer, p. 68, pl. 72, figs. 9-11
1993 Schakoinella imperatoria (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 222, pl. 18, figs. 5-6
2012 Schakoinella imperatoria (d'Orbigny) - Milker and Schmiedl, p. 103, figs. 23.20-21
2014 Conorbella imperatoria (d'Orbigny) - Meric et al., p. 224, pl. 57, figs. 10-14

Superfamily Glabratellacea Loeblich and Tappan, 1964 Family Glabratellidae Loeblch and Tappan, 1964

## Conorbella patelliformis (Brady, 1884)

Plate 14, figs. 1a-c

1884 Discorbina patelliformis - Brady, p. 647, pl. 88, fig. 3, pl. 89, fig. 1 1960 Pileolina? patelliformis (Brady) - Barker, pl. 89, fig. 1 1974 Glabratella patelliformis (Brady) - Colom, p. 137, figs. 22 d-g 1991 Conorbella patelliformis (Brady) - Cimerman and Langer, p. 68, pl. 73, figs. 1-3 2009 *Glabratella lauriei* (Heron and Allen, 1924) - Parker, p. 610, figs. 431 a-k 2012 *Glabratella patteliformis* (Brady, 1884) - Milker and Schmiedl, p. 102, figs. 23.16-17

#### Glabratella erecta (Sidebottom, 1908)

Plate 14, figs. 2a-b

1908 Discorbina erecta - Sidebottom, p. 16, pl. 5, Figs. 6, 7
1991 Conorbella erecta (Sidebottom) - Cimerman and Langer, p.68, pl. 73, figs. 6-8
1993 Glabratella erecta (Sidebottom) - Sgarella and Moncharmont-Zei, p. 220, pl. 18, figs. 7-8
2012 Glabratella erecta (Sidebottom) - Milker and Schmiedl, p. 102, figs. 23.12-13
2014 Conorbella erecta (Sidebottom) - Meric et al., p. 224, pl. 57, figs. 7-9

#### Glabratella hexacamerata Seiglie and Bermudez, 1965

Plate 14, figs. 3a-c *Glabratella hexacamerata* - Seiglie and Bermudez, p. 31, pl. 1, figs. 6-7 *Glabratella hexacamerata* Seiglie and Bermudez - Sgarella and Moncharmont-Zei, p. 222, pl. 18, figs. 9-10 *Glabratella hexacamerata* Seiglie and Bermudez - Parker, p. 611, figs. 430a-b *Glabratella hexacamerata* Seiglie and Bermudez - Milker and Schmiedl, p. 102, figs. 23.14-15

Family Siphoninidae Cushman, 1927

#### Siphonina reticulata (Czjzek, 1848)

Plate 14, figs. 4a-b

1848 Rotalina reticulata - Czjzek, p. 145, pl. 13, figs. 7-9
1850 Siphonina fimbriata - Reuss, p. 372, pl. 47, fig. 6
1931 Siphonina reticulata (Czjzek) - Cushman, p. 68, pl. 14, figs. 1 a-c
1971 Siphonina reticulata (Czjzek) - Murray, p. 139, pl. 58, figs. 5-7
1987 Siphonina reticulata (Czjzek) - Loeblich and Tappan, p. 571, pl. 624, figs. 4-6
1991 Siphonina reticulata (Czjzek) - Cimerman and Langer, p. 69, pl. 73, figs. 11-13
1993 Siphonina reticulata (Czjzek) - Sgarella and Moncharmont Zei, p. 222, pl. 19, figs. 7-8

Family Pseudoparrellidae Voloshinova, 1952 Subfamily Pseudoparrellinae Voloshinova, 1952

#### Eilohedra aff. E. vitrea Parker, 1953

Plate 14, figs. 5a-b 1953 *Epistominella vitrea* - Parker, p. pl. fig. 1970a *Epistomella vitrea* - v. Daniels, p. 84, pl. 6, figs. 6a-b 1971 *Epistomella vitrea* - Murray, p. 131, pl. 54, figs. 1-6 1992 *Epistomella vitrea* - Barmawidjaja et al., pl. 3, figs. 12-14

Family Discorbinellidae Sigal, 1952 Subfamily Discorbinellinae Sigal, 1952

#### Discorbinella bertheloti (d'Orbigny, 1839)

Plate 14, figs. 6a-c

1839b Rosalina bertheloti - d'Orbigny, p. 135, p1. 1, figs 28-30 1974 Discorbinella bertheloti (d'Orbigny) -Le Calvez, p. 59, pl. 14, figs. 1-4 1991 Discorbinella bertheloti (d'Orbigny) - Cimerman and Langer, p. 70, pl. 86, figs. 1-4 1993 Discorbinella bertheloti (d'Orbigny) - Hottinger et al., p. 114, pl. 150, figs. 1-4 2012 Discorbinella bertheloti (d'Orbigny) - Milker and Schmiedl, p. 104, figs. 23.29-30 2014 Discorbinella bertheloti (d'Orbigny) - Meric et al., p. 224, pl. 59, figs. 2-6

Family Cibicidae Cushman, 1927 Subfamily Cibicidinae Cushman, 1927

## Cibicides advenum (d'Orbigny, 1839)

Plate 14, figs. 7a-b, 8a-b

1839a *Truncatulina advena* - d'Orbigny, p. 87, p1. 6, figs. 3-5 1958a *Cibicides advenum* (d'Orbigny) - Le Calvez, Y., p. 187 1977b *Cibicides advenum* (d'Orbigny) - Le Calvez, Y., p. 122, figs. 1-5 1991 *Cibicides advenum* (d'Orbigny) - Cimerman and Langer, p. 70, pl. 74, figs. 8-10 2014 *Cibicides advenum* (d'Orbigny) - Meric et al., p. 225, pl. 59, figs. 15-18

#### Cibicides refulgens Montfort, 1808

Plate 14, figs. 9a-c

1808 Cibicides refulgens - Montfort, p. 123, fig. p. 122 (fide Ellis and Messina, 1940)
1896 Truncatulina refulgens (Montfort) - Dezelic, p. 86
1931 Cibicides refulgens Montfort - Cushman, p. 116, pl. 21, fig. 2
1958a Cibicides refulgens Montfort - Le Calvez, Y., p. 189
1960 Cibicides refulgens Montfort - Barker, pl. 92, figs. 7-9
1974 Cibicides refulgens Montfort - Colom, p. 150, figs. 31 o-t
1987 Cibicides refulgens Montfort - Loeblich and Tappan, p. 582, pl. 634, figs. 1-3
1991 Cibicides refulgens Montfort - Cimerman and Langer, p. 70, pl. 75, figs. 5-9

## Cibicides? mayori (Cushman, 1924)

Plate 14, figs. 10a-c

1924 *Truncatulina mayori* - Cushman, p. 39, pl. 12, figs. 3-4 1965 cf. *Cibicides mayori* (Cushman) - Todd, p. 53, pl. 22, figs. 3-4 1975 *Cibicides* (?) *mayori* (Cushman) - Perelis and Reiss, p. 77, pl. 3, figs. 1-7 1993 cf. *Cibicides? mayori* (Cushman) - Hottinger et al., p.116, pl. 152, figs. 1-6 2012 cf. *Cibicides mayori* (Cushman) - Milker and Schmiedl, p. 106, figs.24.10-11

#### Lobatula lobatula (Walker and Jacob, 1798)

Plate 14, figs. 11a-c

1798 Nautilus lobatulus - Walker and Jacob (in Kanmacher), p. 642, pl. 14, fig. 36 (fide Ellis and Messina, 1940)
1896 Truncatulina lobatula (Walker and Jacob) - Dezelic, p. 87
1958a Cibicides lobatulus (Walker and Jacob) - Le Calvez, Y., p. 188
1960 Cibicides lobatulus (Walker and Jacob) - Barker, pl. 92, fig. 10, pl. 93, figs. I, 4, 5, pl. 95, figs. 4,-5
1970a Cibicides lobatulus (Walker and Jacob) - v. Daniels, p. 89, pl. 8, fig. 3
1974 Cibicides lobatulus (Walker and Jacob) - Colom, p. 147, figs. 29 a-g, i, fig. 30
1984 Cibicides lobatulus (Walker and Jacob) - Reiss and Hollinger, fig. G. 29 d.
1979 Cibicides lobatulus (Walker and Jacob) - Alfirevic, p. 148, pl. 33, fig. 3
1987 Lobatula lobatula (Walker and Jacob) - Loeblich and Tappan, p. 583, pl. 637, figs. 10-13
1991 Lobatula lobatula (Walker and Jacob) - Cimerman and Langer, p. 71, pl. 75, figs. 1-4

#### Paracibicides sp. 1

Plate 14 figs. 12a-c

## Cyclocibicides vermiculatus (d'Orbigny, 1826)

Plate 14, figs. 13a-b

1826 Planorbulina vermiculata - d'Orbigny, p. 280, no. 3
1927 Cyclocibicides vermiculatus (d'Orbigny) - Cushman, p. 93
1960 Cyclocibicides vermiculatus (d'Orbigny) - Barker, pl. 115, figs. 2a, b
1987 Cyclocibicides vermiculatus (d'Orbigny) - Loeblich and Tappan, p. 586, pl. 640, figs. 15-17
1991 Cyclocibicides vermiculatus (d'Orbigny) - Cimerman and Langer, p. 71, pl. 76, figs. 2-7
1993 Cyclocibicides vermiculatus (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 234, pl. 23, fig. 1
2014 Cyclocibicides vermiculatus (d'Orbigny) - Meric et al., p. 225, pl. 61, figs. 1-4

Family Planorbulinidae Schwager, 1877 Subfamily Planorbulininae Schwager, 1877

#### Planorbulina mediterranensis d'Orbigny, 1826

Plate 14, figs. 14a-c

1826 Planorbulina mediterranensis - d'Orbigny, p. 280, no. 2
1931 Planorbulina mediterranensis d'Orbigny - Cushman. p. 129, pl. 24, figs. 5-8
1960 Planorbulina mediterranensis d'Orbigny - Barker, pl. 92, figs. 1-3
1974 Planorbulina mediterranensis d'Orbigny - Colom, p. 158, figs. 39-40
1991 Planorbulina mediterranensis d'Orbigny - Cimerman and Langer, p. 71, pl. 78, figs. 1-8
1993 Planorbulina mediterranensis d'Orbigny - Sgarella and Moncharmont-Zei, p. 235, pl. 23, fig. 4

## Cibicidella variabilis (d'Orbigny, 1839)

Plate 14, figs. 15a-b, 16a-b

1839b *Truncatulina variabilis* - d'Orbigny, p. 135, pl. 2, fig. 29 *Cibicidella variabilis* (d'Orbigny) - Colom, p. 150, figs. 33, 34 *Cibicidella variabilis* (d'Orbigny) - Le Calvez, Y., p. 96, pl. 26, figs. 1-4 *Planorbulina variabilis* (d'Orbigny) - Loeblich and Tappan, p. 588, pl. 645, figs. 5-6 *Cibicidella variabilis* (d'Orbigny) - Cimerman and Langer, p. 72, pl. 77, figs. 1-10 *Cibicidella variabilis* (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 234, pl. 23, figs. 2-3

Family Cymbaloporidae Cushman, 1927

#### Cymbaloporetta sp. 1

Plate 14, figs. 17a-b

1991 *Cymbaloporetta* sp. 1 - Cimerman and Langer, p. 72, pl. 80, figs. 1-5 1993 *Cymbaloporetta* sp. A - Hottinger et al., p. 120, pl. 160, fig.1

Family Homotrematidae Cushman, 1927

#### Miniacina miniacea (Pallas, 1766)

Plate 14, figs. 18a-b
1766 Millepora miniacea - Pallas, p. 251 (fide Ellis and Messina, 1940)
1960 Miniacina miniacea (Pallas) - Barker, pl. 100, figs. 5-9, pl. 101, fig. 1
1974 Miniacina miniacea (Pallas) - Colom, p. 161, fig. 43
1979 Miniacina miniacea (Pallas) - Alfirevic, p. 151, pl. 35, fig. 1
1987 Miniacina miniacea (Pallas) - Loeblich and Tappan, p. 599, pl. 664, figs. 1-5
1991 Miniacina miniacea (Pallas) - Cimerman and Langer, p. 73, pl. 81, figs. 1-6
1993 Miniacina miniacea (Pallas) - Hottinger et al., p. 122, pl. 175, figs, 9-10, pl. 176, figs. 1-6, pl. 177, figs. 1-7
1993 Miniacina miniacea (Pallas) - Sgarella and Moncharmont-Zei, p. 235, pl. 23, fig. 5
2012 Miniacina miniacea (Pallas) - Milker and Schmiedl, p. 110, figs. 25.5-6

Superfamily Asterigerinacea d'Orbigny, 1839 Family Asterigerinatidae Reiss, 1963

#### Asterigerinata adriatica Haake, 1977

Plate 15, figs. 1a-b

1970a Asterigerinata sp.2 - v. Daniels, p. 86, pl. 7, fig. 4 1977 Asterigerinata adriatica - Haake, p. 69, pl. 3, figs. 1-5 1991 Asterigerinata sp. 1 - Cimerman and Langer, p. 73, pl. 82, figs. 5-6 1993 Asterigerinata adriatica Haake - Barmawidjaja, pl. 4, figs. 5-6 1993 Asterigerinata adriatica - Sgarella and Moncharmont-Zei, p. 224, pl. 19, figs. 11-12 2012 Asterigerinata adriatica - Milker and Schmiedl, p. 111, figs. 25.7-9

#### Asterigerinata mamilla (Williamson, 1858)

Plate 15, figs. 2a-c

1858 Rotalina mamilla - Williamson, p. 54, pl. 4, figs. 109-111
1931 Discorbis mamilla (Williamson) - Cushman, p. 23, pl. 5, fig. 11
1958a Discorbis mamilla (Williamson) - Le Calvez, Y., p. 182
1960 Asterigerinata mamilla (Williamson) - Hofker, p. 252, fig. 111
1970a Asterigerinata mamilla (Williamson) - v. Daniels, p. 86, pl. 6, fig. 11
1971 Asterigerinata mamilla (Williamson) - Murray, p. 141, pl. 59, figs. 1-6
1972 Asterigerinata mamilla (Williamson) - Rosset-Moulinier, p. 172, pl. 10, figs. 6, 7, pl. 13, figs. 1-9
1974 Discorbis mamilla (Williamson) - Colom, p. 124, figs. 21 x, y
1979 Asterigerinata mamilla (Williamson) - Jorissen, pl. 3, fig. 1
1991 Asterigerinata mamilla (Williamson) - Jorissen, pl. 3, fig. 1
1991 Asterigerinata mamilla (Williamson) - Milker and Schmiedl, p. 111, figs. 25.10-13
2014 Asterigerinata mamilla (Williamson) - Meric et al., p. 225, pl. 67, figs. 2-13

Family Amphisteginidae Cushman, 1927

#### Amphistegina lobifera Larsen, 1976

Plate 15, figs. 3a-d

1880 Amphistegina lessonii dOrbigny - Möbius p. 99, pl. 10, figs. 11-14, pl. 11, figs. 1-3 1972 Amphistegina cf. A. radiata Terquem - Hansen and Reiss, pl. 10, figs. 3-4 1976 Amphistegina lobifera - Larsen, p. 4, pl. 3, figs. 1-5, pl. 7, fig. 3, pl. 8. fig.3 1977 Amphistegina lobifera Larsen - Larsen and Drooger, p. 225, fig. 1-1b 1984 Amphistegina lobifera Larsen - Reiss and Hottinger, p. 217, figs G11, G12a-c 1988 Amphistegina lobifera Larsen - Morariu and Hottinger, p. 695, figs. 1a-B, fig. 2 2001 Amphistegina lobifera Larsen - Avsar et al., p.109, pl. 3, figs. 5-8 2002 Amphistegina lobifera Larsen - Hyams et al., p. 174, pl. 1, figs. 2-4 2007 Amphistegina lobifera Larsen - Yokes et al., fig. 2 A-E 2008 Amphistegina lobifera Larsen - Yalcin et al., p. 369, pl. 4, figs. 6-7 2008 Amphistegina lobifera Larsen - Meric et al., p. 321, pl. 9, figs. 5-8 2009 Amphistegina lobifera Larsen - Triantaphyllou et al., pl. 1, figs1-6 2009 Amphistegina lobifera Larsen - Yokes and Meric, pl. 5, figs. 1-3 2011 Amphistegina lobifera Larsen - Koukouisoura et al., p. 493, pl. 1, figs. 1-2 2012 Amphistegina lobifera Larsen - Triantaphyllou et al., fig. 2 2014 Amphistegina lobifera Larsen - Caruso and Cosentino, p. 44, fig. 5.1-2 2014 Amphistegina lobifera Larsen - Meric et al., p. 226, pl. 67, figs. 15-20, pl. 68, figs. 1-8, pl. 69, figs. 1-2, pl. 70, figs. 1-2

Family Nonianidae Schultze, 1854 Subfamily Nonioninae Schultze, 1854

#### Haynesina depressula (Walker and Jacob, 1798)

Plate 15, figs. 4a-b

1798 Nautilus depressulus - Walker and Jacob, p. 641, pl. 14, fig. 33 (fide Ellis and Messina, 1940)
1970a Nonion umbiculatum (Walker and Jacob, 1798) - v. Daniels, p. 90, pl. 8, fig. 10
1971 Nonion depressulus (Walker and Jacob) - Murray, p. 195, pl. 82, figs. 1-8
1972 Nonion depressulum (Walker and Jacob) - Rosset-Moulinier, p. 186, pl. 21, figs. 1-4, pl. 22, figs. 1, 2
1976 Nonion depressulum (Walker and Jacob) - Hansen and Lykke-Andersen, p. 21, pl. 19, figs. 3. 6
1978 Haynesina depressulu (Walker and Jacob) - Banner and Culver, p. 200, pl. 10, figs. 1-8
1987 Nonion depressulum (Walker and Jacob) - Jorissen, pl. 2, figs. 7a-b
1991 Haynesina depressula (Walker and Jacob) - Cimerman and Langer, p. 81, pl. 83, figs. 1-4
1993 Nonion depressulum (Walker and Jacob) - Sgarella and Moncharmont-Zei, p. 238, pl. 24, figs. 3-4
2012 Haynesina depressula (Walker and Jacob) - Milker and Schmiedl, p. 112, figs. 25.17-18
2014 Nonion depressulum (Walker and Jacob) - Meric et al. p. 226, 71, figs. 9-13

## Haynesina sp. 1

Plate 15, figs. 5a-b

1839 Nonionina grateloupi - d'Orbigny, p. 46, pl. 6, figs.6-7
1939 Nonion grateloupi (d'Orbigny) - Cushman, p. 21, pl. 6, figs. 1-7
1974 Nonionella cf. grateloupi (d'Orbigny) - Lutze, p. 42, pl. 10, figs. 160-161
1975 Nonionoides grateloupi (d'Orbigny) - Saidova, p. 248
1993 Nonionoides grateloupi (d'Orbigny) - Hottinger et al., p. 138, pl.195, figs. 4-13
2012 Nonionoides grateloupi (d'Orbigny) - Debenay, p. 66, pl. 15p. 227, p. 320

## Haynesina sp. 2

Plate 15, figs. 6a-c

#### Nonionella stella (Cushman and Moyer, 1930)

Plate 15, figs. 7a-b

1991 Nonionella opima Cushman - Cimerman an Langer, p. 74, pl. 84, figs. 1-3 1993 Nonionella stella (Cushman and Moyer) - Sgarella and Moncharmont-Zei, p. 240, pl. 24, fig. 6

#### Nonionella turgida

Plate 15, figs. 8a-b

1858 *Rotalina turgida* - Williamson, p. 50, pl. 4, figs. 95-97 1960 *Nonionella turgida* (Williamson) - Barker, pl. 109, figs. 17-19 1971 *Nonionella turgida* (Williamson) - Murray, p. 193, pl. 81, figs. 1-5, Plate 15, figs. 8a-b

#### Nonionoides grateloupi (d'Orbigny, 1839)

Plate 15, figs. 9a-c

Subfamily Astrononioninae Saidova, 1981 Genus Astrononion Cushman and Edwards

## Astrononion stelligerum (d'Orbigny, 1839)

Plate 15, figs. 10a-b

1839b Nonionina stelligera - d'Orbigny, p. 128, pl. 3, fig. 12 1930 Nonion stelligerum (d'Orbigny) - Cushman, p. 7, pl. 8, figs. 8-12, pl. 3, figs. 1-3 1937 Astrononion stelligerum (d'Orbigny) - Cushman and Edwards, P. 31, pl. 3, fig. 7 a 1960 Astrononion stelligerum (d'Orbigny) - Barker, pl. 109, figs. 3, 4 1974 Astrononion stelligerum (d'Orbigny) - Le Calvez, Y., p. 37, pl. 9, figs. 1-4 1991 Astrononion stelligerum (d'Orbigny) - Cimerman and Langer, p. 74, pl. 84, figs. 13-15 2012 Astrononion stelligerum (d'Orbigny) - Milker and Schmiedl, p. 113, figs.26.7-8 2014 Astrononion stelligerum (d'Orbigny) - Meric et al., p. 216, pl. 71, figs. 9-13 Subfamily Pulleniinae Schwager, 1877

# Melonis pompilioides (Fichtel and Mall, 1798)

Plate 15, figs. 11a-c

1798 Nautilus pompilioides - Fichtel and Moll, p. 31, pl. 2, figs. a-c (fide Ellis and Messina, 1940)
1808 Meloi's etruseus (Fichte] and Moll) - Montfort, p. 66
1959 Nonion pompilioides (Fichtel and Moll) - Norvang, p. 145, figs. 1-6
1976 Melonis pompilioides (Fichtel and Moll) - Hansen and Lykke-Andersen, p. 24, pl. 22, figs. 10-13
1984 Melonis barleanus (Fichtel and Moll) - Bizon (in Ecomed), p. 93, fig. 17
1984 Melonis pompilioides (Fichte! and Moll) - ROegel and Hansen, p. 30, pl. 2, figs. 1-2 (lectotype)
1987 Melonis pompilioides (Fichtel and Mall) - Loeblich and Tappan, p. 621, pl. 696, figs. 7, 8
1991 Melonis pompilioides (Fichtel and Moll) - Cimerman and Langer, p. 74, pl. 85, figs. 1-4

7 Appendix

Family Trichohyalidae Saidova, 1981

#### Aubignyna planidorso (Atkinson, 1969)

Plate 15, figs. 12a-c, 13a-c

1969 Buccella planidorso - Atkinson, p. 535, pl. 6, figs. 3 a-c 1970 Aubignyna cf. A. mariei (Margerel, 1970) - v. Daniels, p.85, pl. 7, figs. 6a-c 1972 Buccella planidorso Atkinson - Rosset- Moulinier, p. 166, pl. 9, figs. 21, 22, pl. 12, figs. 1-5 1987 Ammonia perlucida (Heron-Allen & Earland, 1913) - Jorissen, p. 47, pl. 2, figs. 11-12 1988 Ammonia perlucida (Heron-Allen & Earland, 1913) - Jorissen, p. 46, pl. 11, figs. 4-5 1991 Aubignyna planidorso Atkinson - Cimerman and Langer, p. 75, pl. 86, figs. 5-6

## Buccella sp. 1

Plate 15, figs. 14a-c

1991 Buccella sp. 1 - Cimerman and Langer, p. 75, pl. 87, figs. 1-2

Family Rotaliidae Ehrenberg, 1839 Subfamily Rotaliinae Ehrenberg, 1839

#### Ammonia beccarii (Linnaeus, 1758)

Plate 16, figs. 1a-c

1758 Nautilus beccarii - Linnaeus, p. 710 (fide Ellis and Messina, 1940)
1858 Rotalina beccarii (Linnaeus) - Williamson, p. 48, pl. 4, figs. 90-92
1931 Rotalia beccarii (Linnaeus) - Cushman, p. 58, pl. 12, figs. 1-7, pl. 13, figs. 1, 2
1979 Ammonia beccarii (Linne) - Alfirevic, p. 126, pl. 27, fig. 1
1980 Ammonia beccarii (Linne) - Billman et al., p. 85, pl. 1, figs. 1-10, pl. 2, figs. 1-6
1987 Ammonia beccarii (Linne) - Loeblich and Tappan, p. 664, pl. 767, figs. 1-7
1991 Ammonia beccarii (Linne) - Cimerman and Langer, p. 76, pl. 87, figs. 3-4
1993 Ammonia gaimardi (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 228, pl. 20, figs. 7-8
2004 Ammonia beccarii (Linne) - Hayward et al., pl. 2, fig. B, pl. 3, fig B, pl. 4, fig. B
2014 Challengerella bradyi (Billman, Hottinger and Oesterle, 1980) - Meric et al., p. 226, pl. 77, figs. 18-21, pl. 78, figs. 1-5

#### Ammonia inflata (Seguenza, 1862)

Plate 16, figs. 2a-c

1862 Rosalina inflata- Seguenza, p. 106, pl. 1, fig. 6
1960 Streblus beccarii (Linné) - Hofker, p. 255, suppl. E, figs. 134a-b
1988 Ammonia beccarii (Linné) forma inflata - Jorissen, p. 52, pl. 6, figs. 1-4
1991 Ammonia inflata (Seguenza) - Cimerman and Langer, p. 76, pl. 87, figs. 5-6
1992 Ammonia beccarii (Linné) - Barmawidjaja et al., pl. 4, fig. 1
2004 Ammonia inflata (Seguenza) - Hayward, pl. 2, fig. T3Y, pl. 3, fig. T3Y, pl. 4, fig. T3Y
2012 Ammonia beccarii (Linné) - Milker and Schmiedl, p. 117, figs. 27.1-2
2014 Ammonia compacta Hofker - Meric et al., p. 226, pl. 75, fig. 16-17 non 8-15, non 18, pl. 76, figs. 1-4

# Ammonia parkinsoniana (d'Orbigny, 1839)

Plate 16, figs. 3a-c

1839a Rosalina parkinsoniana - d'Orbigny, p. 99, pl. 4, figs. 25-27

1960 Streblus parkinsonianus (d'Orbigny) - Hofker, p. 254, suppl. E, fig. 130-132

1977b Ammonia parkinsoniana (d'Orbigny) - Le Calvez, Y., p. 92, pl. 11, figs. 1-3

1988 Ammonia parkinsoniana (d'Orbigny) forma parkinsoniana - Jorissen, p. 46, pl. 9, figs. 1-5

1991 Ammonia parkinsoniana (d'Orbigny) - Cimerman and Langer, p. 76, pl. 87, figs. 7-9

1993 Ammonia parkinsoniana (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 228, pl. 20, figs. 3-4

2004 ? Ammonia parkinsoniana (d'Orbigny) - Hayward et al., pl. 2, fig. T9, pl. 3, fig. T9, pl. 4, fig. T9

2012 Ammonia parkinsoniana (d'Orbigny) - Milker and Schmiedl, p. 119, figs. 27.3-4

2014 Ammonia parkinsoniana (d'Orbigny) - Meric et al., p. 226, pl. 76, figs. 10-22, pl. 77, figs. 1-5

## Ammonia tepida (Cushman, 1926)

Plate 16, figs. 4a-c

1926 Rotalia beccarii (Linne) var. tepida - Cushman, p. 79, pl. 1 (fide Ellis and Messina, 1940)
1931 Rotalia beccarii (Linnaeus) var. tepida Cushman - Cushman, p. 61, pl. 13, figs. 3 a-c
1965 Streblus becearii tepida (Cushman) - Todd, p. 29, pl. 6, fig. 1, pl. 7, fig. 2
1972 Ammonia beccarii (Linne) var. tepida Cushman - Rosset-Moulinicr, p. 174
1987 Ammonia beccarii tepida (Cushman) - Jorissen, pl. 2, figs. 8a-b
1988 Ammonia parkinsoniana (d'Orbigny) forma tepida - Jorissen, pl. 7, figs. 1.4
1991 Ammonia tepida (Cushman) - Cimerman and Langer, p. 76, pl. 87, figs. 10-12
1993 Ammonia beccarii (Linne) var. tepida - Sgarella and Moncharmont-Zei, p. 226, pl. 20, figs. 5-6
2004 Ammonia tepida (Cushman) - Hayward et al., pl. 2. fig. T, pl. 3, fig. T, pl. 4, fig. T

#### Ammonia sp. 1

Plate 16, figs. 5a-c

1970 Ammonia beccarii (Linné) - v. Daniels, p. 86, pl. 7, figs. 5a-c 1988 Ammonia parkinsoniana (d'Orbigny) forma tepida - Jorissen, p.62, pl. 10, figs. 1-3 1993 Ammonia beccarii (Linné) var. tepida - Sgarella and Moncharmont-Zei, p. 226, pl. 20, figs. 5-6

Family Elphidiidae Galloway, 1933 Subfamily Elphidiinae Galloway, 1933

## *Elphidium aculeatum* (d'Orbigny, 1846)

Plate 16, figs. 6a-b

1846 Polystomella aculeata - d'Orbigny p. 131, pl. 6, figs. 27, 28
1972 Elphidium aculeatum d'Orbigny -Rosset-Moulinier, p. 175
1979 Elphidium aculeatum d'Orbigny - Alfirevic, p. 127, pl. 27, fig. 2
1991 Elphidium aculeatum d'Orbigny - Cimerman and Langer, p. 77, pl. 89, figs. 1-4
2012 Elphidium aculeatum d'Orbigny - Milker and Schmiedl, p. 119, figs. 27.5-6
2014 Elphidium aculeatum d'Orbigny - Meric et al. p. 227, pl. 79, figs. 6-16

## Elphidium cf. E advenum (Cushman, 1922)

Plate 16, figs. 7a-b

1922 Polystomella cf. P. advena - Cushman, p. 56, pl. 9, figs. 11-12
1970a Cribononion advenum (Cushman) - v. Daniels, p. 87, pl. 7, fig.10
1991 Elphidium cf. E advenum Cushman - Cimerman and Langer, p.77, pl. 89 figs. 5-7
1993 Elphidium cf. E advenum Cushman - Hottinger et al., p. 146, pl. 207, figs. 1-7

#### Elphidium crispum (Linnaeus, 1758)

Plate 16, figs. 8a-b

1758 Nautilus crispus - Linnaeus, p. 709 (fide Ellis and Messina, 1940)
1960 Elphidium crispum (Linnaeus) - Barker, pl. 110, figs. 6, 7
1970 Elphidium crispum (Linnaeus) - v. Daniels, p. 87, pl. 7, fig. 7
1971 Elphidium crispum (Linnaeus) - Murray, p. 155, pl. 64, figs. 1-6
1974 Elphidium crispum (Linnaeus) - Colom, p. 143, figs. 26 e-j, m, n
1976 Elphidium crispum (Linnaeus) - Hansen and Lykke-Andersen, p. 6, pl. 1, figs. 10-12, pl. 2, figs. 1, 2
1991 Elphidium crispum (Linnaeus) - Cimerman and Langer, p. 77, pl. 90, figs. 1-6
2001 Elphidium crispum (Linnaeus) - Hottinger et al., p. 28, pl. 10, figs. 4-7
2004 Elphidium crispum (Linnaeus) - Meric et al., p. 211/212, pl. 33, figs. 3.6
2012 Elphidium crispum (Linnaeus) - Milker and Schmiedl, p. 120, figs. 27.13-14
2014 Elphidium crispum (Linnaeus) - Meric et al., p. 227, pl.81, figs. 5-16, pl. 82, figs. 1-10

## Elphidium cf. E. gerthi van Voorthuysen, 1957

Plate 16, figs. 9a-b

1957 *Elphidium gerthi* - van Voorthuysen, p. 32, pl. 23, fig. 12 (fide Ellis and Messina, 1940) 1971 *Elphidium gerthi* van Voorthuysen - Murray, p. 161, pl. 67, figs. 1-7 1976 *Elphidium gerthi* van Voorthuysen - Hansen and Lykke-Andersen, p. 10, pl. 5, figs. 7-12 1991 *Elphidium gerthi* van Voorthuysen - Cimerman and Langer, p. 78, pl. 91, figs. 1-2 1993 *Elphidium gerthi* van Voorthuysen - Hottinger et al., p. 148, pl. 211, figs. 1-7

#### Elphidium jenseni (Cushman, 1924)

Plate 16, figs. 10a-c, 11a-b

1924b Elphidium jenseni - Cushman, p. 49, pl. 16, figs. 4, 6
1933 Elphidium jenseni Cushman - Cushman, p. 48, pl. 11, figs. 6-7
1939 Elphidium jenseni Cushman - Cushman, p. 62, pl. 17, figs. 14, 15
1970a Elphidium lessonii (d'Orbigny, 1826) - v. Daniels, p. 87, pl. 7, fig. 9
1991 Elphidium jenseni Cushman - Cimerman and Langer, p. 78, pl. 92, figs. 1-3
1993 Elphidium jenseni Cushman - Hottinger et al., p. 148, pl. 211, figs. 8-14
1993 Elphidium complanatum (d'Orbigny) - Sgarella and Moncharmont-Zei, p. 228, pl. 20, figs. 9-10
2014 Elphidium complanatum (d'Orbigny) - Meric et al., p. 227, pl. 80, Figs. 14-17, pl. 81, figs. 1-10

#### Elphidium macellum (Fichtel and Moll, 1798)

Plate 16, figs. 12a-c, 13a-b, 14a-b, 15a-b, 16a-b

*Nautilus macellus* var. beta - Fichtel and Moll, p. 66, pl. 10, figs. h-k *Elphidium macellum* (Fichtel and Moll) - Rögl and Hansen, p. 50, pl. 14, fig. 4, pl. 15, figs. 1-2 (lectotype) *Elphidium macellum* (Fichtel and Moll) - Cimerman and Langer, p. 78, pl. 89 fig. 9 *Elphidium macellum* (Fichtel and Moll) - Milker and Schmiedl, p. 122, figs. 27.21-22

#### Elphidium advenum (Cushman, 1922)

Plate 16, figs. 17a-b

1922 Polystomella cf. P. advena - Cushman, p. 56, pl. 9, figs. 11-12
1909 Polystomella subnodosa Münster - Sidebottom, p. 16, pl. 5, figs. 6a-b
1991 Elphidium sp. 1 - Cimerman and Langer, p. 79, pl. 89, figs. 8
1993 Elphidium punctatum (Terquem) - Sgarella and Moncharmont-Zei, p. 230, pl. 21, figs. 3-4
2012 Elphidium advenum (Cushman) - Milker and Schmiedl, p. 119, figs. 27.7-8
2014 Elphidium charlottense (Vella) - Meric et al., p. 227, pl. 80, figs. 10-13

## Elphidium translucens Natland, 1938

Plate 17, figs. 1a-b

1938 Elphidium translucens - Natland, p. 144, pl. 5, figs. 3, 4
1970a Cribrononion translucens (Natland) - v. Daniels, p. 88, pl. 7, figs. 13 a, b
1976 Elphidium translucens Natland - Hansen and Lykke-Andersen, p. 11, pl. 7, figs. 1 - 11
1987 Elphidium poeyanum forma decipiens Costa - Jorissen, pl. 2, fig. 6
1988 Elphidium poeyanum (d'Orbigny) - Jorissen, p. 116, pl. 2, figs.4-6, pls.20-23
1991 Elphidium translucens Natland - Cimerman and Langer, p. 78, pl. 92, figs. 7-11
1993 Elphidium cuvilleri (Levy, 1966) - Sgarella and Moncharmont-Zei, p. 229, pl. 20, fig. 13
2014 Criboelphidium poeyanum (d'Orbigny, 1826) - Meric et al., p. 226, pl. 78, figs. 6-12

#### Elphidium williamsoni Haynes 1973

Plate 17, figs. 2a-b

*Elphidium williamsoni* - Haynes, p. 207, pl. 24, fig. 7, pl. 25, figs, 6,9, pl. 27, figs. 1-3 *Elphidium williamsoni* Haynes - Hansen and Lykke-Andersen, p. 9, pl. 5, figs. 1-6 *Elphidium williamsoni* Haynes - Alexander and Banner, p. 167, pl. 4 *Elphidium williamsoni* Haynes - Hottinger et al., p. 150, pl. 215, figs. 1-5 *Elphidium williamsoni* Haynes - Hottinger et al., p. 28, pl. 11, figs. 1-7

Elphidium sp. 1

Plate 17, figs. 3a-b

# *Elphidium* sp. 2

Plate 17, figs. 4a-b

1991 Elphidium margaritaceum (Cushman) - Cimerman and Langer, p.79, pl. 92, figs.4-6

# Elphidium sp. 3

Plate 17, figs. 5a-b

## Porosononion granosum (d'Orbigny, 1846)

Plate 17, figs. 6a-b

1857 Nonionina subgranosa - d'Orbigny, p. 110, pl. 5, figs. 19-20 1936 Elphidium lidoense (Cushman, 1936) - p. 86, pl. 15, figs. 6a-b 1988 Elphidium granosum (d'Orbigny) - Jorissen, p. 112, pl. 18, figs. 1-18 1991 Porosononion sp. 2 - Cimerman and Langer, p. 81, pl. 84, figs. 4-5 1993 Elphidium granosum (d'Orbigny) -Sgarella and Moncharmont-Zei, p. 229, pl. 21, figs. 1-2 2012 Elphidium granosum (d'Orbigny) - Milker and Schmiedl, p. 121, figs. 27.17-18 2014 Porosononion subgranosum (Egger, 1956) - Meric et al., p. 227, pl. 78, figs. 1-4

## Porosononion aff. P. granosum (d'Orbigny, 1846)

Plate 17, figs. 7a-b, 8a-b

1857 Nonionina subgranosa - d'Orbigny, p. 110, pl. 5, figs. 19-20 1988 Elphidium granosum forma granosum (d'Orbigny) - Jorissen, p. 104, pl. 2, figs. 1-3, pl. 16, figs. 1-5

## Porosononion aff. P. simplex (Cushman, 1933)

Plate 17, figs. 9a-b

1933 Elphidium simplex - Cushman, p. 52, pl. 12, figs. 8-9 1993 Elphidium sp. A - Sgarella and Monchramont- Zei, p. 230, pl. 21, figs. 8-9 2012 Haynesina simplex (Cushman) - Milker and Schmiedl, p. 112, figs. 25.19-20

## Porosononion sp. 1

Plate 17, figs. 10a-b, 11a-b

1991 Haynesina sp. 2 - Cimerman and Langer, p. 82, pl. 83, figs. 5-8 1993 Elphidium pauciloculum (Cushman, 1944) - Sgarella and Moncharmont-Zei, p. 229, pl. 22, figs. 1-3

# Porosononion sp. 2

Plate 17, figs. 12a-b

# 7.9 Selected Oral Presentations

**Gloria H. Mouanga** & Martin R. Langer (2013). Environmental-Driven Trends in shallow-water Foraminiferal Assemblages from Fetovaia Bay (Elba Island, Mediterranean Sea), Berichte, MARUM – Zentrum für Marine Umweltwissenschaften, Fachbereich Geowissenschaften, Universität Bremen, No. 292, 134 pages, Bremen 2013. ISSN 0931-0800, p. 36.

**Gloria H. Mouanga** & Martin R. Langer (2014). At the front of expanding ranges: Shifting community structures at amphisteginid species range margins in the Mediterranean Sea, In: Grzybowski Foundation Special Publication No. 20, Marchant, M. & Hromic, T. (eds). 2014 International Symposium on Foraminifera FORAMS 2014, Chile, 19-24. January 2014, Abstract Volume, p. 53.

**Gloria H. Mouanga** & Martin R. Langer (2015). Foraminiferal Range Expansions: The Mediterranean Sea as a natural laboratory for climate induced invasions. EGU General Assembly 2015. Geophysical Research Abstracts Vol. 17, EGU2015-737, 2015.

**Gloria H. Mouanga** & Martin R. Langer (2016). Invasion, Impact and range shifts in modern amphisteginid foraminifera: Insights from the Mediterranean Sea. 87 th Annual conference of the Paläontologische Gesellschaft e. V. Abstractband, pp, 111-112.

**Gloria H. Mouanga** & Martin R. Langer (2016). Range expansion and impact of amphisteginid foraminifera in the Mediterranean Sea. 87 th Annual conference of the Paläontologische Gesellschaft e. V. Abstractband, pp, 111-112.

# 7.10 Publications

**Gloria H. Mouanga** & Martin R. Langer (2013). Environmental-Driven Trends in shallow-water Foraminiferal Assemblages from Fetovaia Bay (Elba Island, Mediterranean Sea). Berichte, MARUM – Zentrum für Marine Umweltwissenschaften, Fachbereich Geowissenschaften, Universität Bremen, No. 292, 134 pages, Bremen 2013. ISSN 0931-0800, p. 36.

**Gloria H. Mouanga** & Martin R. Langer (2014). At the front of expanding ranges: Shifting community structures at amphisteginid species range margins in the Mediterranean Sea, Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 271 Band Heft 2 (2014). Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, p. 141-150.

Martin R. Langer & **Gloria H. Mouanga** (2016) Invasion of amphisteginid foraminifera in the Adriatic Sea. Biological Invasions 18(5): 1335-1349. doi: 10.1007/s10530-016-1070-0.

Martin R. Langer, **Gloria H. Mouanga** & Olugbenga T. Fajemila (2016). Shallow-water nearshore benthic foraminiferal assemblages from Gabon. Micropaleontology 62 (1): 69-80.

Asma Ben Hamad, Finn Andreas Viehberg, Afef Khadroui, Chahira Zaibi, Yasser Trabelsi, **Gloria H. Mouanga**, Martin R Langer, Habib Abida, Fekri Kamoun (2018). Water level and atmospheric humidity history of Lake Ichkeul (Northern Tunisia) during the last 3000 years. Arabian Journal of Geosciences (akzeptiert und in Begutachtung).

**Gloria H. Mouanga** & Martin R Langer (2018). Shallow-water benthic foraminiferal assemblages from the coast of Albania (Mediterranean Sea). Paleontographica (akzeptiert und in Begutachtung).