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Review paper

Contribution of Soft-shelled Monothalamous Taxa to Foraminiferal Assemblages in the Adriatic Sea

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Abstract. Monothalamous foraminifera with organic and agglutinated test walls ("allogromiids" *sensu lato*) deserve attention because of their importance in deep-sea and shallow-water soft-bottom communities and their crucial phylogenetic position at the base of the foraminiferal evolutionary tree. However, our knowledge of the biodiversity and ecology of monothalamous foraminifera is very incomplete and geographically patchy. Here, we present a short review based on the available data on monothalamous, soft-walled foraminiferal taxa from the Adriatic Sea in response to several environmental parameters (i.e. organic matter, oxygen, grain size, depth). The main results of the studies provide evidence of the importance of these foraminiferal taxa in this shallow, temperate latitude area; they represent a start for the identification of soft-shelled monothalamous morphotypes that could be potential bioindicators of environments influenced by inputs of fresh waters, increasing eutrophication and consequent fluctuations in bottom-water oxygenation. The contribution of this soft-shelled component to living benthic foraminiferal assemblages appears not negligible and excluding it from foraminiferal studies can potentially lead to a loss of ecological information. The study, therefore, provide an atlas of the Adriatic soft-shelled foraminiferal taxa in order to: 1) encourage the species-level description, if possible, or alternatively a basic morphotype characterization; 2) facilitate future comparisons of taxa from similar settings; 3) promote their potential use in future biomonitoring investigations together with the hard-shelled foraminifera.

Key words: Soft-shelled foraminifera, allogromiids, shallow water setting, Adriatic Sea, bioindicator.

INTRODUCTION

Benthic foraminifera are protists that constitute a significant component of marine ecosystems, from the intertidal to the deepest ocean trenches, from brackish to hyper-saline waters and from the tropics to the poles. Their quick reactions to environmental changes reflect their unicellular organisation and short life cycles and make them efficient environmental indicators. Most foraminifera build a calcium carbonate shell that persists through time and into the geological record. The fact that the chemical composition of the shell is influenced by natural and anthropogenically-induced features of the environment in which foraminifera live makes them particularly useful for the analysis of recent and current

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marine environments as well past habitats. Ecological studies of modern foraminifera (especially benthic taxa) started in the 1950s (Phleger 1960) and have increased over the past 60 years. Nevertheless, the main scientific interest in this group remains focused on the use of their excellent fossil record. Many of such studies, however, consider only the hard-shelled (calcareous and agglutinated), mainly polythalamous, foraminifera and disregard taxa with soft, flexible test walls composed of organic material (allogromiids in the traditional sense) or finely agglutinated material (saccamminids and psammosphaerids). These soft-walled, monothalamous foraminifera are an important, diverse but often overlooked component of marine benthic communities (see Table 2 in Gooday 2002 for the principal occurrence of some described allogromiids species; Habura *et al*. 2008). They have been reported at all depths in the oceans and are particularly common in the deep sea, Antarctic sites (Bowser *et al.* 1995, 2002; Pawlowski *et al.* 2002) and Arctic coastal sites influenced by turbid glacial meltwater, and in some estuaries (e.g. Dahlgren 1962; Nyholm 1974 and earlier papers; Cato *et al*. 1980; Gooday and Fernando 1992; Korsun 1999, 2002; Korsun and Hald 1998, 2000; Gooday 2002; Sabbatini *et al.* 2007). Relatively few species have been formally described and most of these are from nearshore and intertidal environments (e.g. Huxley 1910; Hadley 1967; Hadley *et al.* 1968; Golemansky 1999; Larkin and Gooday 2004; Sergeeva and Anikeeva 2006, 2008; Majewski *et al.* 2005, 2007; Pawlowski *et al.* 2008; Altin *et al.* 2009; Goldstein *et al.* 2010; Sergeeva *et al.* 2010).

The distribution of benthic hard-shelled foraminifera in the Adriatic Sea is relatively well known from the studies by Jorissen (1987, 1988), Jorissen *et al.* (1992, 1995), Barmawidjaja *et al.* (1995), Donnici and Serandrei Barbero (2002), Duijnstee *et al.* (2004), Albani *et al.* (2007) (see review by Sabbatini *et al.* 2014). These studies revealed that these organisms play an important role in this basin, which is characterized by increasing eutrophication and related fluctuations in bottom-water oxygenation. Here, we present a short review based on the available data on monothalamous, soft-walled taxa from the Adriatic Sea in relation to various environmental parameters (i.e. organic matter, oxygen, grain size, depth). Our aim is to show: 1) how soft-shelled monothalamous foraminifera can be important, in terms of total absolute and relative abundances, in comparison to hard-shelled taxa in shallow water Adriatic Sea locales and 2) to address the diversity of this delicate group that is represented by numerous morphotypes. At the same time 3) to provide a first taxonomical support that, even if still (and inevitably) presenting undescribed species, could be a tool to approach the complex taxonomy of these foraminiferal component in a more uniformed way and, thus, to help the comparison of data among authors and areas in the future. This step is fundamental to improve our understanding of the distribution and ecology of soft-shelled monothalamous foraminifera and, lately, to start to identify some potential bioindicator key-taxa.

MATERIALS AND METHODS

Data summarized in this review come from several shallow-water sites (< 50 m water depth) in the Adriatic Sea (see Table 1 in the Supplementary material and Appendix 1). The sediment samples were processed using the same laboratory protocol (Pucci 2006; Nardelli 2012; Sabbatini *et al.* 2010, 2012). The material was sieved through 63 and 150 μm mesh (in order to evaluate the size structure of foraminiferal assemblage and for comparison with other studies from the Adriatic Sea and shallow-water settings) and preserved in 10% formalin buffered with sodium borate to which had been added Rose Bengal (1 g l^{-1}). The residues were hand-sorted for stained benthic foraminifera in water in a Petri dish using a binocular microscope. Soft-shelled monothalamous specimens were placed in cavity slides in glycerol and photographed under a compound microscope (Nikon Eclipse E 600 POL). Data presented in this paper all refer to the size fraction > 63 μm (Table 1).

The identification of morphotypes is based on the test morphology (i.e. individual shape, apertural morphology, colour and density of the cytoplasm, presence/absence of stercomata and other organic (algae) and inorganic (mineral) matter) even if a distinction that may have taxonomic significance can be made on the basis of the presence of single terminal or more terminal apertures (Avnimelech 1952). These diagnostic criteria could be forced for this type of taxa that actually lacks clear morphological differences. For this reason we recognize three informal groups of soft-walled monothalamous foraminifera following the guidelines proposed by Gooday (1986, 2002). Allogromiids are monothalamous foraminifera with organic-walled tests and one or more terminal apertures. Saccamminids are monothalamous foraminifera with agglutinated tests and one or more apertures; the wall consists of an inner organic layer with an overlying deposit of agglutinated particles, which are sufficiently small and weakly cemented for the test to remain flexible. Psammosphaerids are monothalamous foraminifera with agglutinated, more or less spherical or oval tests devoid of apertures. It is noteworthy that these groups are artificial rather than being phylogenetically coherent entities as revealed by molecular evidence (Pawlowski *et al.* 2002). However, in the absence of molecular data, terms such as allogromiids, saccamminids and psammosphaerids, are convenient labels for categorizing these organisms sorted from samples under a stereomicroscope. In order to limit incongruences we decide to differentiate between organic-walled allogromiids, in which the organic composition of the wall is unambiguous and saccamminids and psammosphaerids that include agglutinated monothalamous morphotypes (Gooday 2002). Other monothalamous foraminifera having hard, or at least rigid, tests with either calcareous or agglutinated walls are not considered in this paper.

Regional distribution of soft-shelled monothalamous taxa in the Adriatic Sea

Despite the Adriatic Sea is one of the most studied areas for the ecology and the distribution of hard-shelled foraminifera, only a few studies of shallow-water Adriatic foraminifera have included soft-shelled monothalamous morphotypes. Pucci (2006), Nardelli (2012) and Sabbatini *et al.* (2010, 2012) studied this component in terms of abundance and morphotypes diversity and in relation to the environmental setting. Even if, using different approaches and in several areas of the Adriatic Sea, these studies highlight some common results; we retain important to observe them globally in order to summarise on some significant aspects of the ecology of the soft-shelled monothalamous component in these locales.

Pucci (2006) reports the biodiversity of benthic foraminifera along a shallow transects from the Po River outflow to the central Adriatic Sea. Data obtained in the period between May and June 2004 along the coast between Goro (near the mouth of the River Po) and Cattolica (see Supplementary material, Appendix 1) reveal three areas with different foraminiferal assemblages as well as different physical-chemical characteristics (chlorophyll-α, oxygen, temperature and turbidity) and specific grain sizes. Soft-shelled monothalamous taxa are present at all 14 studied transects along the Adriatic coast, and they are most abundant in the northern transects near the Po River outflow (Stations 1002, 121, 122 and 105) and at a site in the central Adriatic Sea (see Supplementary material, Table 1 and Appendix 1); conversely, they are generally not predominant, spanning from 1 to 30% of the total stained foraminiferal assemblage in the rest of studied samples. As mentioned above, at one station located near the coast, south of the Po River mouth, the relative abundance of soft-shelled monothalamous morphotypes reaches 83% of total living assemblage. Their higher presence in the Po area (Station 1002) is suggested to be associated to medium to high values of chlorophyll-α and relatively low oxygen concentrations. This area is typically affected by eutrophic conditions, high variability of environmental parameters (i.e. salinity, temperature and organic enrichment), and bottom-water anoxic and/or hypoxic events related to a combination of high downward organic flux and elevated microbial decay rates causing an important benthic oxygen demand. The high relative abundance of soft-shelled monothalamous foraminifera found there, thus, suggests their tolerance to the environmental stress caused by the river outflow, in particular to the induced conditions of low oxygen concentrations. Moreover, relatively high abundance of small, organic-walled specimens is reported by the author, that could reinforce the hypothesis of an opportunistic behaviour. These field observations would be consistent with the results of some experimental studies that highlighted the strong tolerance of some soft-shelled monothalamous foraminifera to oxygen depletion (e.g. Bernhard 1993, Moodley *et al.* 1997).

This positive response to environmental stress is also observed by Sabbatini *et al.* (2010). The authors investigate the foraminiferal faunas, including the soft-shelled monothalamous component, along a shallow bathymetric transect in the Gulf of Trieste (see Supplementary material, Appendix 1). The distribution of species is studied as a function of water depth, grain size, distance from fresh water sources and chemical-physical parameters (temperature, salinity, dissolved oxygen and organic matter). The soft-shelled monothalamous component in the transect stations contribute from 19 to 57% of the stained foraminiferal assemblage. The absolute and relative abundance of soft-shelled morphotypes decrease with distance from the coast and from the river input (the Isonzo River), once more suggesting their general preference for low-oxygen high-organic matter conditions. This is consistent with evidence that soft-walled monothalamous taxa are common in transitional environments where conditions may be considered extreme (Nyholm 1952, Duijnstee *et al.* 2004, Gooday *et al.* 2005). In particular, in the samples close to the river input, the morphotype Allogromiid sp. 1 (Table 1, Plate 1–8) is dominant (35%). The same morphotype, moreover, together with Saccamminid sp. 8 and Psammosphaerid sp. 4, shows a strong dominance at one station (Stn 120, Table 1) characterised by clayey inner-shelf sediments where the percentage of organic carbon was low and the C/N ratio, representing terrestrial organic matter input by the river, is high. This pattern, which is not reflected by the hard-shelled taxa (Sabbatini *et al.* 2010), suggests that these soft-walled monothalamous morphotypes flourish (57%) in stressed environments directly influenced by the proximity of the river. All the soft-shelled monothalamous taxa of this study are undescribed, in most cases, even at the genus level,

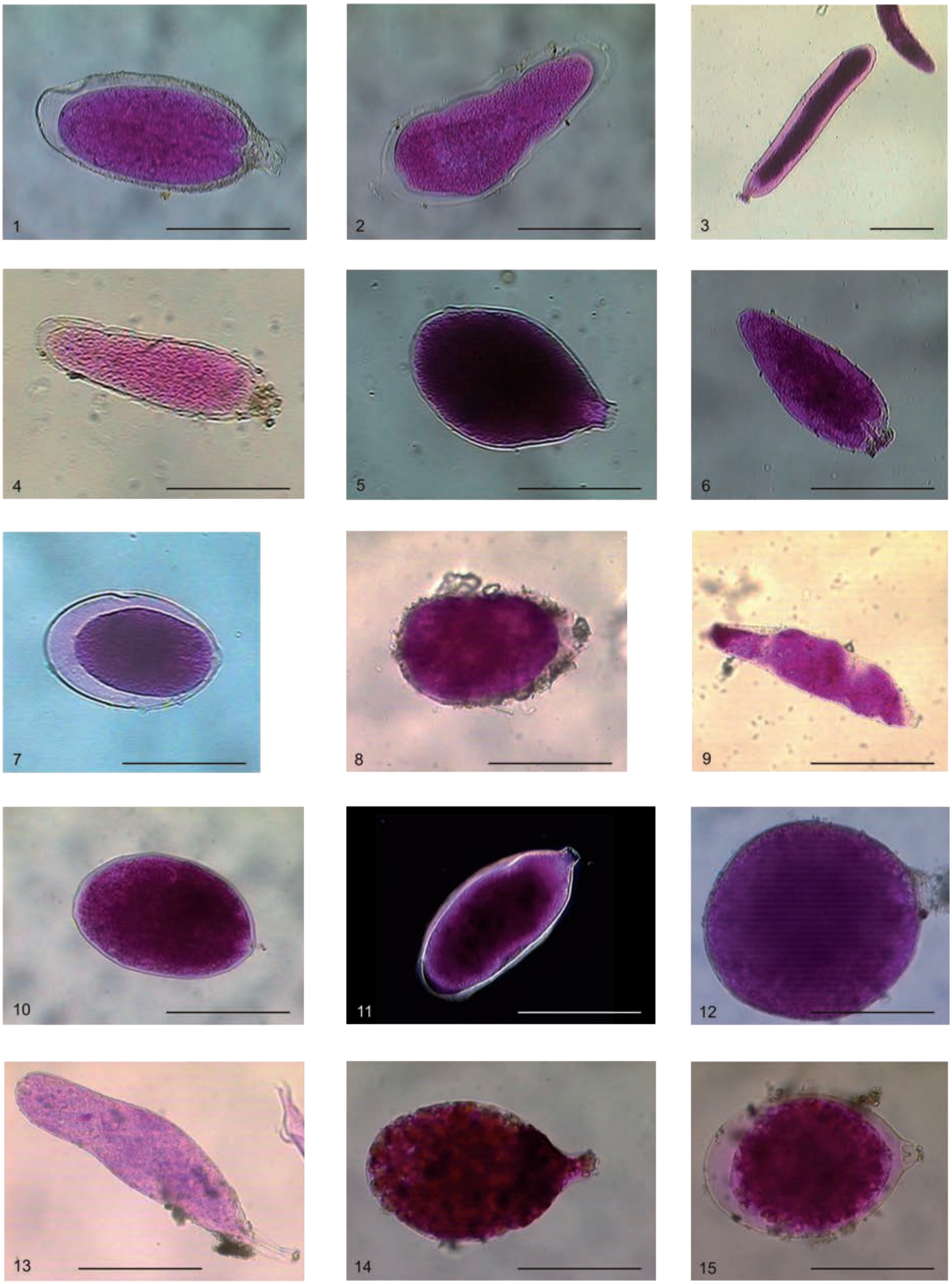

PLATE 1. Adriatic Rose Bengal stained allogromiids (organic-walled allogromiids in which the organic composition of the wall is unambiguous) photographed using transmitted light. **1** – Allogromiid sp. A; **2** – Allogromiid sp. B; **3** – Allogromiid sp. C; **4** – Allogromiid sp. D; **5** – Allogromiid sp. E; **6** – Allogromiid sp. F; **7** – Allogromiid sp. G; **8** – Allogromiid sp. 1; **9** – Allogromiid sp. 2; **10** – Allogromiid sp. 3; **11** – Allogromiid-like sp. 3; **12** – Allogromiid sp. 4; **13** – Allogromiid sp. 5; **14** – Allogromiid sp. 6; **15** – Allogromiid sp. 7. Allogromiid sp. H from the central Adriatic Sea (Civitanova sites) is not represented. Scale bar: 100 µm. See Supplementary material, Appendix 2 for locality details.

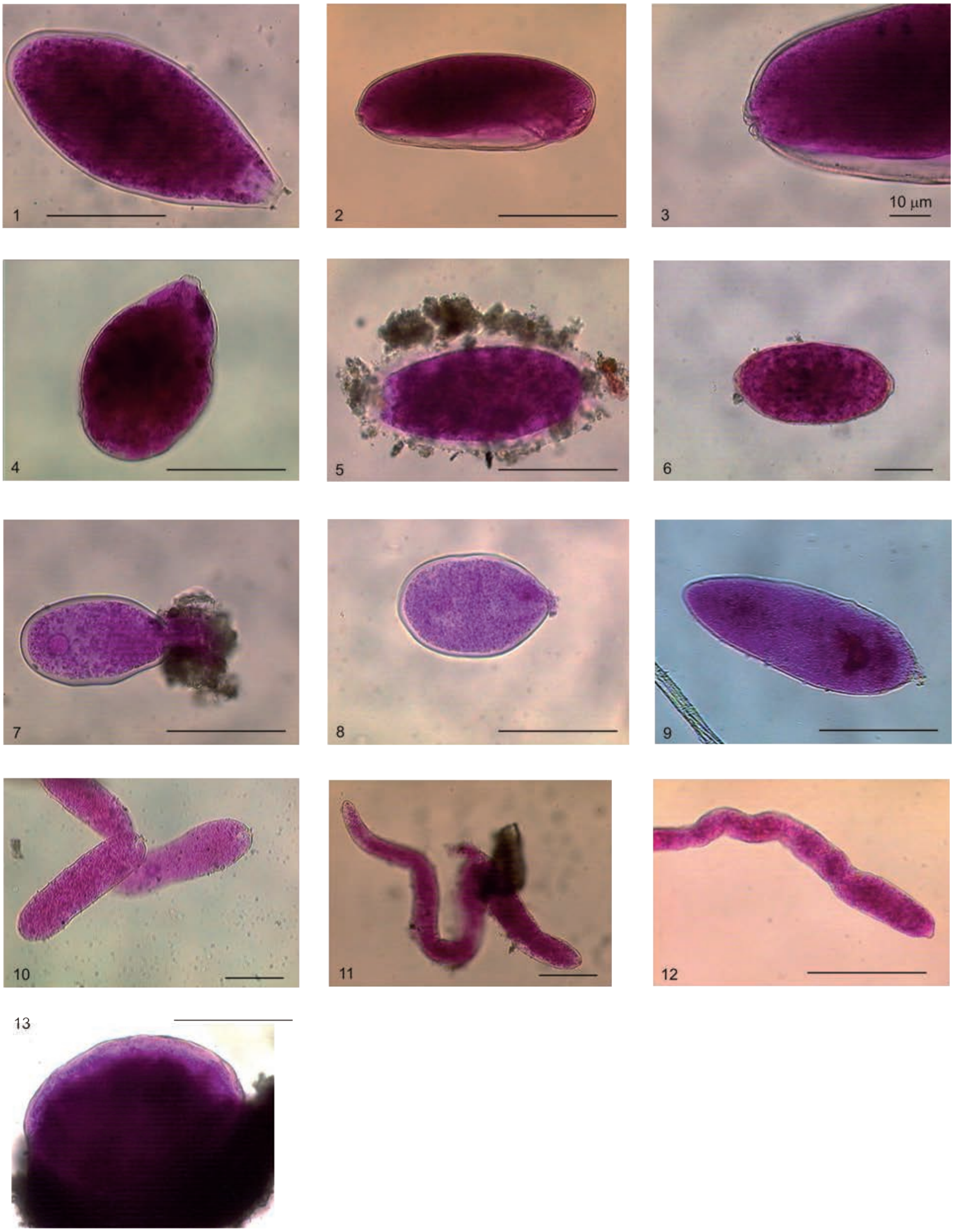

PLATE 2. Adriatic Rose Bengal stained allogromiids (organic-walled allogromiids in which the organic composition of the wall is unambiguous) photographed using transmitted light. **1** – Allogromiid sp. 8; **2** – Allogromiid sp. 9; **3** – Allogromiid sp. 9, detail of the aperture of the same individual in micrograph 2; **4** – Allogromiid-like sp. 9; **5** – Allogromiid sp. 10; **6** – Allogromiid sp. 11; **7–8** – Allogromiid sp. 13; **9–10** – Allogromiid sp. 35; **11–12** – elongate allogromiid; **13** – encased allogromiid. Allogromiids sp. **14**, **15** and **16** from the northern Adriatic Sea (Gulf of Trieste) are not represented. Scale bar: 100 µm, except where indicated if different. See Supplementary material, Appendix 2 for locality details.

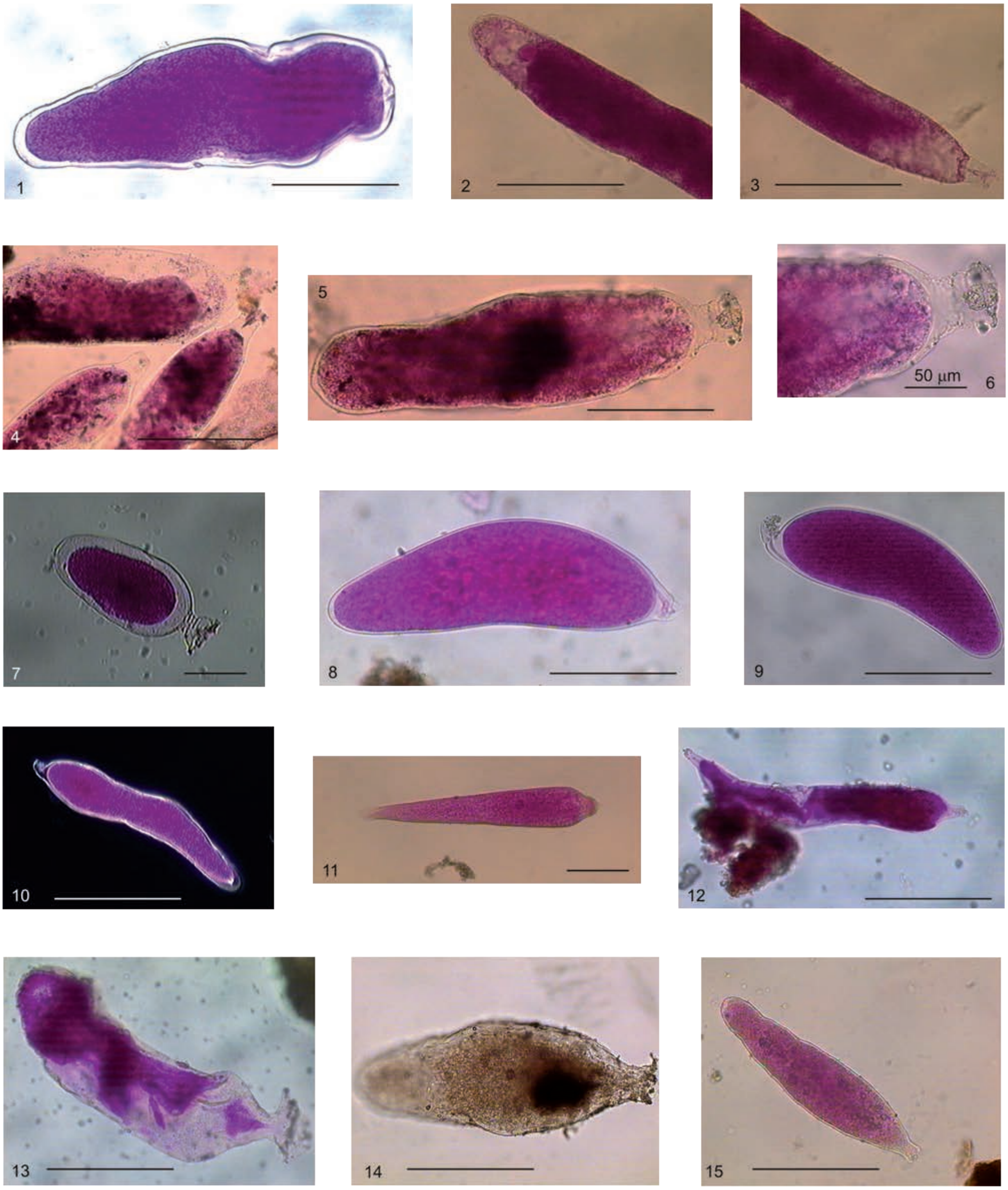

PLATE 3. Adriatic Rose Bengal stained allogromiids (organic-walled allogromiids in which the organic composition of the wall is unambiguous) photographed using transmitted light. **1** – *Bowseria*-like; **2–3** – *Cylindrogullmia* sp., aperture and part of the same individual; **4** – *Gloiogullmia* sp.; **5** – *Gloiogullmia* sp.; **6** – *Gloiogullmia* sp., detail of the aperture of the same individual in micrograph 5; **7** – *Gloiogullmia*-like; **8–10** – *Goodayia* sp.; **11** – *Micrometula* sp.; **12** – Tinogullmiid-like; **13** – *Vellaria*-like; **14** – *Vellaria* sp. 1; **15** – *Vellaria* sp. 2 photographed in sea water. Scale bar: 100 µm, except where indicated if different. See Supplementary material, Appendix 2 for locality details.

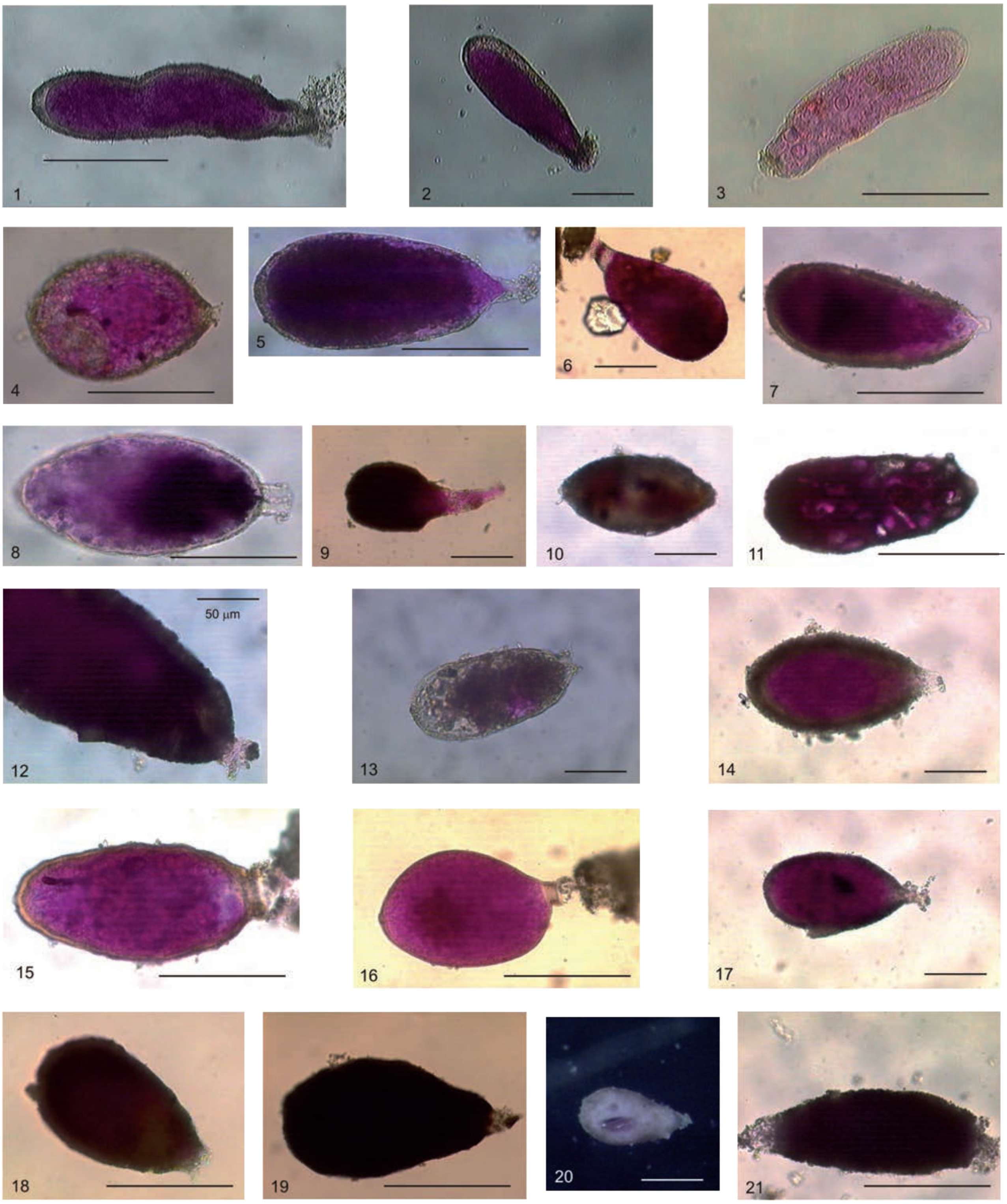

PLATE 4. Adriatic Rose Bengal stained saccamminids photographed using transmitted light. **1** – Saccamminid sp. A; **2** – Saccamminid sp. C; **3** – Saccamminid sp. D; **4** – Saccamminid sp. 1; **5** – Saccamminid sp. 2; **6** – Saccamminid sp. 3; **7** – Saccamminid sp. 4; **8** – Saccamminid sp. 5; **9** – Saccamminid sp. 6; **10** – Saccamminid sp. 7; **11** – Saccamminid sp. 8; **12** – Saccamminid sp. 8, particular of the aperture; **13** – Saccamminid sp. 9; **14** – Saccamminid sp. 10; **15** – Saccamminid sp. 11; **16** – Saccamminid sp. 12; **17** – Saccamminid sp. 13; **18** – Saccamminid sp. 14; **19** – Saccamminid sp. 15; **20** – Saccamminid sp. 15, stereomicroscope; **21** – Saccamminid sp. 16. Scale bar: 100 µm, except where indicated if different. See Supplementary material, Appendix 2 for locality details.

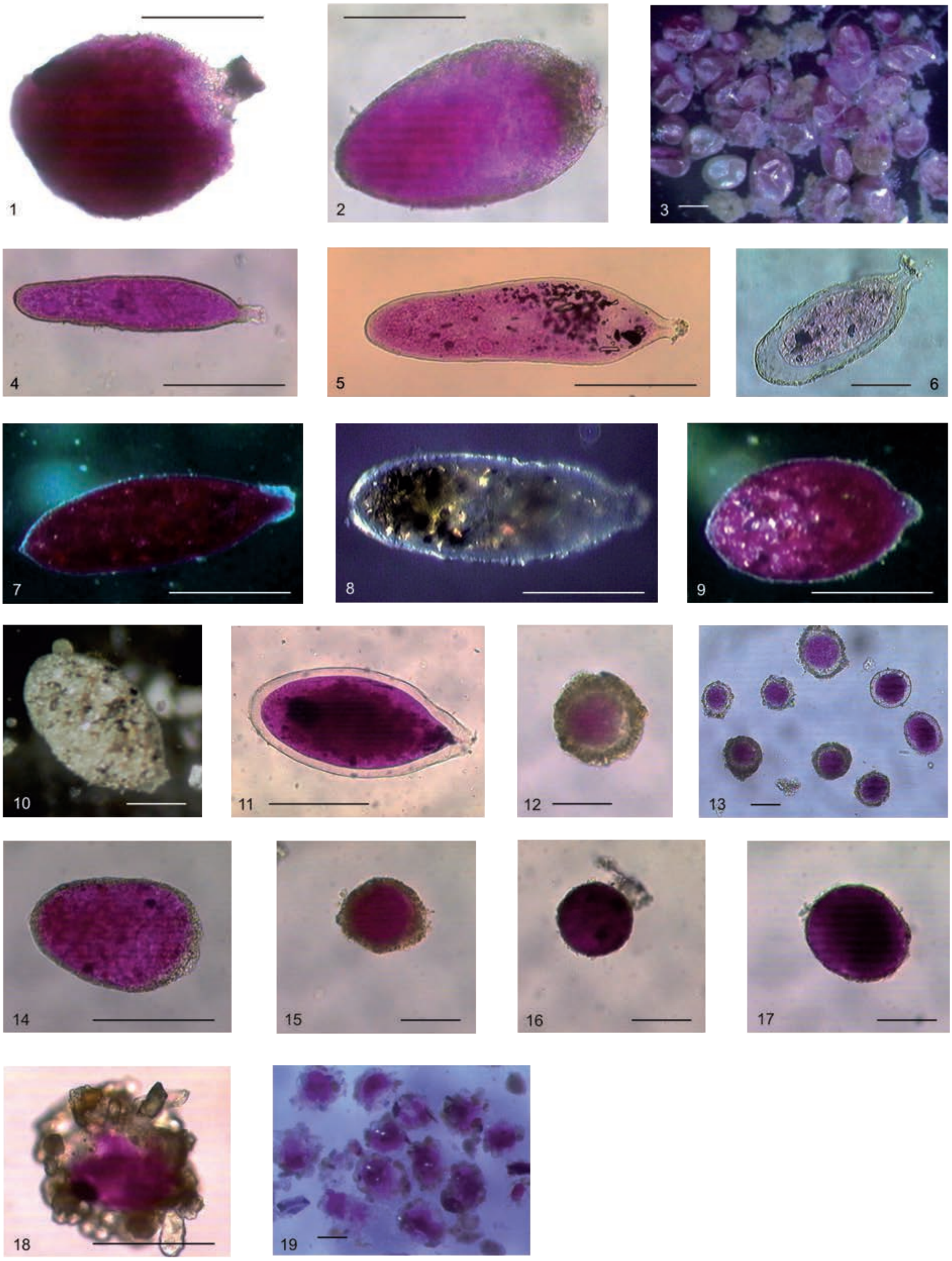

PLATE 5. Adriatic Rose Bengal stained saccamminids and psammosphaerids photographed using transmitted light. **1** – Saccamminid sp. 17; **2** – silver Saccamminid; **3** – silver Saccamminid, stereomicroscope; **4** – *Conqueria*-like; **5–6** – *Psammophaga* spp.; **7** – *Psammophaga* sp. 1, stereomicroscope; **8** – *Psammophaga* sp. 1, cross polarized light; **9** – *Psammophaga* sp. 2, stereomicroscope; **10** – *Psammophaga* sp. 2, stereomicroscope; **11** – *Psammophaga* cf. *crystallifera*; **12** – Psammosphaerid sp. 1; **13** – Psammosphaerid sp. 2; **14** – Psammosphaerid sp. 3; **15** – Psammosphaerid sp. 4; **16** – Psammosphaerid sp. 5; **17** – Psammosphaerid sp. 7; **18** – sphere; **19** – spheres, stereomicroscope. Scale bar: 100 µm. See Supplementary material, Appendix 2 for locality details.

therefore this study reports for the first time images that could help a future taxonomical formal description.

Then, a question arising after the evidences shown by Sabbatini *et al.* (2010) that only few morphotypes dominate in this kind of low-quality organic matter environments is: do all soft-shelled monothalamous foraminifera prefer low-quality organic matter?

To answer this question, the relationships between foraminiferal communities and trophic status in central Adriatic coastal sediments (see Supplementary material, Appendix 1) is further analysed by Sabbatini *et al.* (2012). The study shows that seasonal variability of available organic matter is responsible of the distribution of foraminiferal assemblages and that some soft-shelled monothalamous morphotypes positively respond to high-quality organic matter. In particular, a bloom of *Psammophaga* sp. 1 is associated to an increased quantity of nutritionally available organic matter on the sea floor, caused by a strong winter phytoplankton bloom. The opportunistic response of this saccamminid to an organic carbon pulse of high nutritional quality suggests its potential role as an indicator of benthic eutrophication in shallow waters. Moreover, this morphotype is apparently more sensitive to changes in the nutritional quality of sedimentary organic matter than hard shelled foraminifera (more rapid response). This is reflected by the fact that only the polythalamous agglutinated *Leptohalysis scottii* shows the same environmental signal as *Psammophaga* sp. 1 in our winter samples, and none of the other hard-shelled foraminifera of this geographical area, that are present in other seasons, show the same opportunistic behaviour. This strongly suggests the potential loss of ecological information due to the neglecting of soft-shelled monothalamous taxa.

The last study we report, goes beyond the relationship of soft-shelled monothalamous foraminifera with trophic status of the environments but it is the only one that investigate the response of these taxa to organic pollutants in the Adriatic sea. We retain, therefore, that it could be an important contribution to the knowledge of the sensitivity degree of these taxa to human-induced or, as in this case, natural coastal pollution.

Nardelli (2012) describes the occurrence of soft-shelled monothalamous foraminifera in a shallow water environment of the central Adriatic Sea where natural hydrocarbon seepage occurs (see Supplementary material, Appendix 1). The study shows that the soft-shelled monothalamous component of foraminiferal assemblages is always numerically important (20–80% relative abundance).

This component is particularly significant (80% of the entire stained assemblage) at one of the sampled stations (Station 13), which lie close to the hydrocarbon seep, and is influenced by particularly high concentrations of volatile aliphatic compounds (see Supplementary material, Table 1 and Appendix 1). In particular the morphotype Psammosphaerid sp. 1 represents approximately 50% of the assemblage, accompanied by lower abundances of *Psammophaga* spp. 1 and 2 and Saccamminid sp. 2. At the same station, hard-shelled foraminiferal taxa are few and the species composition similar to the one found at the near stations. These results show for the first time at least in the Adriatic Sea, that there are some target soft-shelled morphotype that could be taken into consideration as bioindicators of pollution. At the same time it underline how important can be to include soft-shelled monothalamous foraminifera in this kind of study to enhance our scarce knowledge on the topic for their potential use in biomonitoring.

Are soft-shelled monothalamous foraminifera useful in biomonitoring studies?

The recent FOBIMO (FOraminiferal Bio-Monitoring) initiative (Schoenfeld *et al.* 2012) establishes the guidelines for foraminiferal biomonitoring studies. One of the *Mandatory Recommendations* of the FOBIMO group is that: “Soft-shelled foraminifera should not be included in routine foraminiferal bio-monitoring studies.” The authors come to this conclusion because soft-shelled species: 1) are small and easily overlooked, 2) they lack diagnostic features and cannot be identified consistently on a morphological basis, and hence they are often undescribed, 3) their distribution and ecology is scarcely known and 4) sorting them is time-consuming. In addition, Bouchet *et al.* (2012), basing on a data set from high latitude coastal samples conclude that “excluding the organic-walled species did not lead to a significant loss of ecological information.”

The lack of a standardized protocol for hard-shelled foraminifera is addressed by Schönfeld (2012) who reviews the development of field and laboratory methods, their constraints and consequences for faunal and data analyses, concluding that much work remains to be done. The studies presented in this review suggest that soft-shelled monothalamous foraminifera should not be ignored, at least in the temperate latitude coastal environments, in order to achieve a comprehensive taxonomic and ecological overview of foraminiferal assemblages. As shown in the previous section, their study can add information of qualitative importance in biomonitoring studies, particularly in shallow-water ecosystems where soft-shelled taxa can account for > 80% of living foraminifera. Moreover, further ecological studies of some key "allogromiid" taxa in coastal environments could lead to the recognition of sensitive or opportunistic species with the potential to be used as bioindicators in the same way as hard-shelled foraminifera.

We conclude from this brief review that these delicate foraminifera have some potential utility in biomonitoring studies, even if they cannot provide information on past ecosystems because they do not fossilize.

Atlas of the soft-shelled monothalamous taxa in the Adriatic Sea

Few studies on taxonomic "allogromiids" identification are available either in the shallow (e.g. *Marenda nematodes* Nyholm 1951, Gulf of Lyon) or deep sea sites of the Mediterranean Sea (the only survey that included soft-shelled monothalamous foraminifera is Pancotti 2011). Other faunal density data of soft-shelled monothalamous taxa are reported from sediment samples off Corsica (Soetaert *et al.* 1991) and from sediment samples in the NW Adriatic (Moodley *et al.* 1997). However, these important, even if strongly patchy data, are produced using different methodologies (collection and sediment depth, different sieve fractions and treatment with Rose Bengal or Ludox or ethanol maintaining) and rarely contain the key to understand the variety of morphotypes. In order to provide a starting point to compare data among researchers, we present the atlas of the soft-shelled taxa described in the Adriatic Sea.

We expect that the atlas of soft-shelled taxa from the Adriatic Sea will encourage the recognition and description of many new species, and their analyses together with the well-known hard-shelled foraminiferal taxa.

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TABLE 1. Relative abundance of soft-shelled taxa and morphotypes diversity compared with the total assemblage of stained benthic foraminifera and their potential use as bioindicators in the reference sites of the Adriatic Sea.

Appendix 1. Summary of sampling stations in the Adriatic Sea.

Appendix 2. Taxonomic list and plates reference.