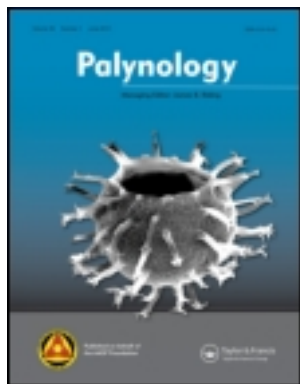


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Environmental significance of abundant and diverse hornwort spores in a potential submerged Paleolithic site in the Gulf of Mexico

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A palynological analysis of sediments sampled from core HI-178, offshore High Island, Texas, provided a diverse and well-preserved palynoflora. The main objective was to analyze the environmental conditions at time of deposition. A secondary objective was to evaluate whether or not this site might have been occupied by Native Americans by looking for signs of human-driven changes in vegetation. Here we focus on the abundance of hornwort spores recovered from these samples, review their diversity, compare the fossil spores to modern analogues and discuss the paleoenvironmental implications of hornwort abundance. Although no direct evidence of human occupation was found, the pollen and spore assemblage recovered, marked by high abundance and diversity in spores of hornworts belonging to the families Anthocerotaceae and Notothyladaceae, indicate that this site was most likely not submerged at the time of deposition; human occupation was therefore possible. This site represents a coastal low-lying area with ponds or slow-moving waters that provided the humid environment needed for hornworts to reproduce and thrive under warm climatic conditions.

Keywords: palynology; Gulf of Mexico; Holocene; *Anthoceros*; *Phaeoceros*; hornwort

1. Introduction

Hornworts (Anthocerotophyta) are a group of spore-producing plants that are usually not very abundant in Cenozoic palynological assemblages; they tend to be overshadowed by abundant pollen produced by gymnosperm and angiosperm plants that dominate most environments since the Paleocene. Hornworts are one of the three groups of bryophytes. When recovered, the trilete spores they produced are often grouped with spores from spore-producing pteridophytes and bryophytes such as the more common ferns and mosses. Few palynological studies have been published on hornwort spores alone; only a few authors (Dettmann 1963; Krutzsch 1963, 1967; Nagy 1968; Jarzen 1979; Hassel de Menendez 1989) have described or illustrated fossil spores comparable or belonging to the Anthocerotophyta.

In our recent archeological study of a landscape sampled off the Texas coast (Figure 1), abundant spores of the Anthocerotophyta were recovered. Because of their abundance at the site, a better understanding of the environmental significance of this group of land plants was needed to constrain the type of environment that existed at High Island at the time of deposition. Hence, this paper reviews

the morphological differences observed in two dominant fossil genera found in offshore Texas, *Anthoceros* and *Phaeoceros*, and discusses the environmental implications of this group of land plants as they occur at the High Island site.

2. Background data on fossil site selection

High Island 178 (HI-178) is located approximately 34 km off the shore of Texas, near Galveston Island (Figure 1). The site is currently located at a depth of about 16 m below modern sea level (Figure 2). Based on various studies of sea-level fluctuation reconstructions in the Gulf Coast region, it is possible that the general area was barely inundated or a few meters (up to 8 m) above sea floor between 7,000 and 9,200 BP, depending on the sea-level curve used (Curry 1960; Shepard 1964; Frazier 1974; Morton et al. 2000; Tornqvist et al. 2006; Blum et al. 2008; Milliken et al. 2008) and rates of subsidence (Milliken et al. 2008; figure 3). A geophysical survey was conducted in June 2008 using a chirp sub-bottom profiler to acquire acoustic data at 25 m intervals across the study site. A navigation system was used to follow a predesigned survey grid and the tow-fish was kept at a constant

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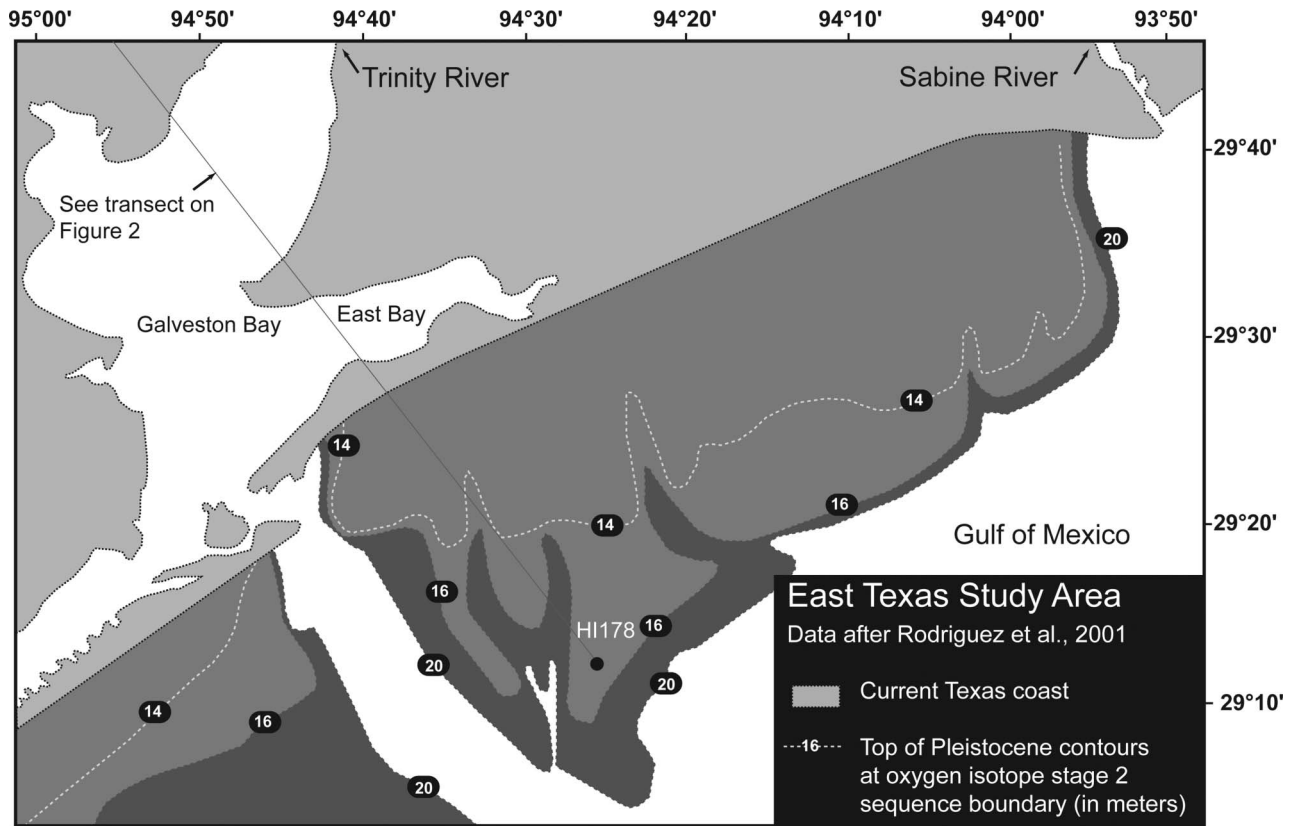


Figure 1. Location map showing the present-day offshore position of the High Island 178 (HI178) site. Structure map of the top of the Pleistocene surface (contours with numbers) are after Rodriguez et al. (2001). They delineate the Trinity/Sabine incised valley during oxygen isotope stage 2 sequence boundary.

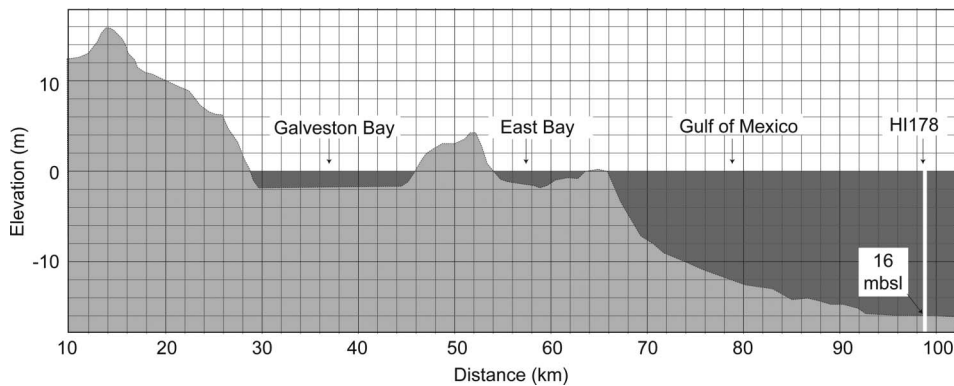


Figure 2. Transect showing depth of the High Island 178 (HI178) site at present, generated using GeoMapApp. mbsl: meters below sea level.

setback, which was applied during post-processing. An average speed of sound in saltwater of $1,500 \text{ m s}^{-1}$ (two-way time travel) was used to calculate depth. All sub-bottom data were interpreted digitally, with plan view maps and three dimensional (3D) contours created to illustrate the relict channel and associated landforms observed within the survey grid. Age estimates of interpreted features and existing datasets, including grey literature reports and proprietary

studies, were correlated with the geophysical data (Wille 2005). Absolute ages were established by carbon dating of samples collected from cores acquired in June and July 2009. Radiocarbon dating of charcoal units recovered yielded a range of 9,550–9,460 calibrated years BP.

Due to the variability of anticipated surficial and subsurface sediments, a pneumatic vibracore rig was used to acquire cores for this study. The coring rig was

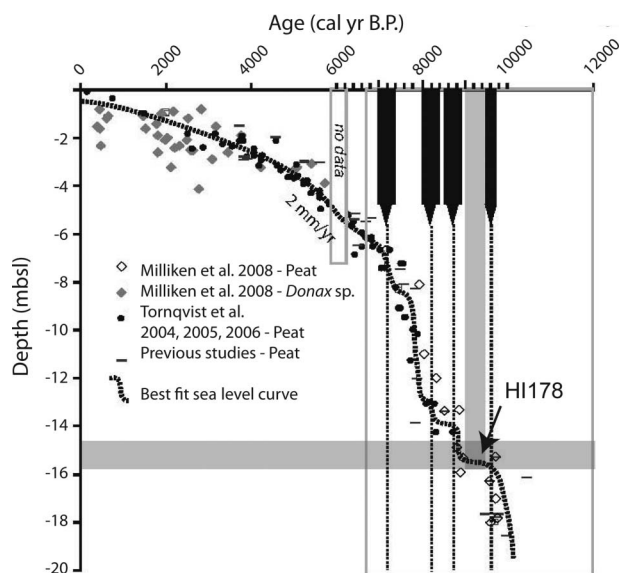


Figure 3. Relation between sea-level changes in the Gulf of Mexico during the past 18,000 years and age of the HI 178 core studied (sea-level graphic from Milliken et al. 2008).

equipped with 6.096 m long, 0.1016 m diameter core sleeves, and was positioned from the stern of the vessel. A penetrometer was attached to the rig and recorded core progress as both depth per second and time per foot. A penetrometer is an engineering tool typically used to measure sediment strength. In this case, it was used to calculate the amount of time the coring rig took to penetrate 0.3048 m of sediment. This precaution was taken because, in the Gulf of Mexico, some sediments are difficult to core through. For example, the Beaumont clay has a typical shear strength of 95,760 Pa. Coring crews usually deploy the rig at a given location until either the maximum core depth is achieved (in our case ~ 6 m) or the depth at which the rig hits refusal. For our purposes, refusal was defined as when the rig took more than 2 minutes to core 0.3048 m of depth. Trying to core past refusal can damage the rig and/or the compressor. To avoid potential problems, plots of the penetrometer data graphically depicting depth versus time and depth versus time per foot were monitored continuously during drilling operation. Core sleeves were extruded from the barrel, sectioned, capped and labeled on the boat before being transported back to Louisiana State University for processing and sampling in the H. Jesse Walker Geomorphology Laboratory.

This site is of particular interest to archaeologists because it was likely located above water at a time when Paleoindian civilizations lived in Texas. Indeed, according to Ricklis (2004), southeastern Texas has

been divided into three cultural chronological periods: the Paleoindian (11,500 – 8,000 BP); the Inland Archaic (8,000 – 1,500 BP); and the Coastal Archaic (5,000 – 2,200 BP). The designation ‘Coastal’ refers to sites located in the modern coastal zone and not the coastal zone at the time of occupation. The radiocarbon dates place the site between 9,550 and 9,460 calibrated years BP, suggesting these samples fall within the timeframe of Paleoindian occupation. Because the HI-178 site was possibly above sea level at the time when Paleoindian groups lived in Texas, this site is a prime target for archaeological investigations as it represents a coastal geographic area for which there is no previously defined cultural affiliation. In order to look for evidence of possible human presence 18 core samples were selected from core sediments, including the layers containing the charcoal inclusions.

3. Palynological techniques for collection of fossil and modern spores

The fossil palynomorphs were extracted by standard palynological techniques as outlined in Traverse (2007). Specimens for scanning electron microscopy (SEM) were cleaned in distilled water and a drop of residue was placed on a SEM stub overnight for drying. The dried residue was then coated with a thin gold layer (200 Å) applied by a glow plasma discharge for 2 minutes, using a Hummer IITM gold sputter coater. Photomicrographs of the results of SEM of fossil *Phaeoceros* and *Anthoceros* spores are presented in Plates 1–3.

To compare the fossil spores to modern spores of *Anthoceros* and *Phaeoceros*, spores of extant species were obtained via a loan from the Paleobiology Division of the Canadian Museum of Nature (CMN), Ottawa, Canada. SEM photomicrographs of these specimen are illustrated in Plates 4–9. The general locations where these specimens were collected are summarized in Figure 4. The spores illustrated herein were collected from vouchered herbarium sheets as described by Jarzen and Jarzen (2006) and processed using the techniques outlined in Jarzen (1979).

4. Results

The HI-178 fossil samples include up to 8% of various forms of Anthocerotophyta (Plates 1–3). Several of the different variations in spine length and overall morphology observed are probably derived from a single species. Jarzen (1979) compared some of the fossil species of *Phaeoceros* to modern specimens of the living genera and concluded that several fossil species and genera, as recorded from the Cretaceous of North

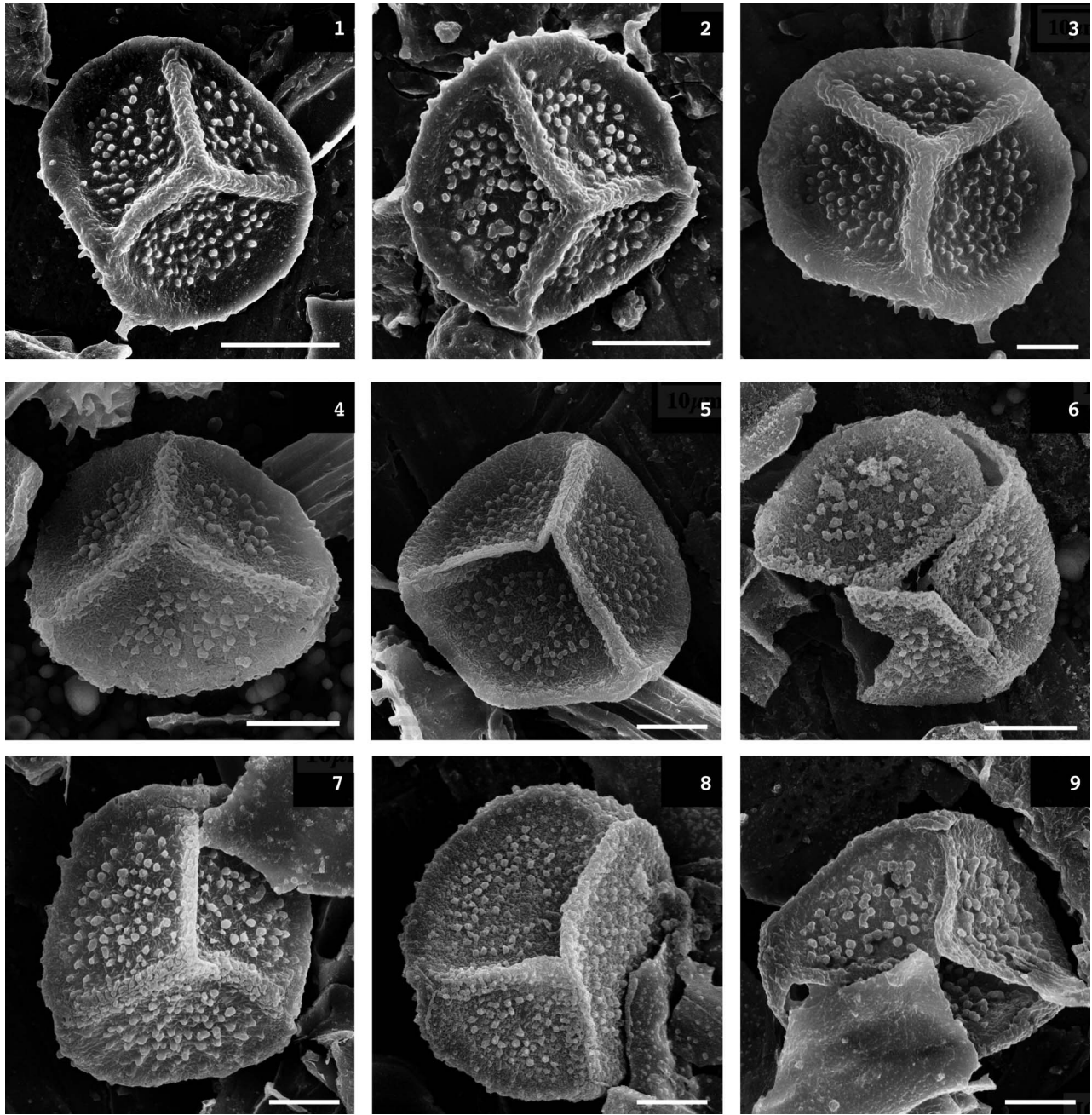


Plate 1. Scanning electron microscope (SEM) photographs of key specimens of fossils of Anthocerotaceae from the High Island drill hole HI-178, sample 32C, offshore Texas, US (see location 1 on Figure 4). Figures 1–9 show various surface sculpture found in the fossil specimens of *Phaeoceros laevis* type, with the granules dispersed in between the branches of the laesurae. The scale bar represents 10 microns.

America, are actually morphological variations within a single taxon. By using a cautious approach as highlighted in Jarzen (1979) and comparing the fossil spores (Plates 1–3) to the modern spores (Plates 4–9) obtained from the herbarium, we obtained information which helps in the accurate comparison of the fossils to extant taxa. Based on this evaluation, we concluded

that at least two species are abundant at our site; these are *Phaeoceros laevis* (L.) Prosk. and *Anthoceros multifidus* Lindb. The remaining forms recovered were grouped as *Anthoceros* spp. as they could be morphological variations within *Anthoceros*.

All spores show polar differences with a distinctive trilete mark on the proximal surface and with a

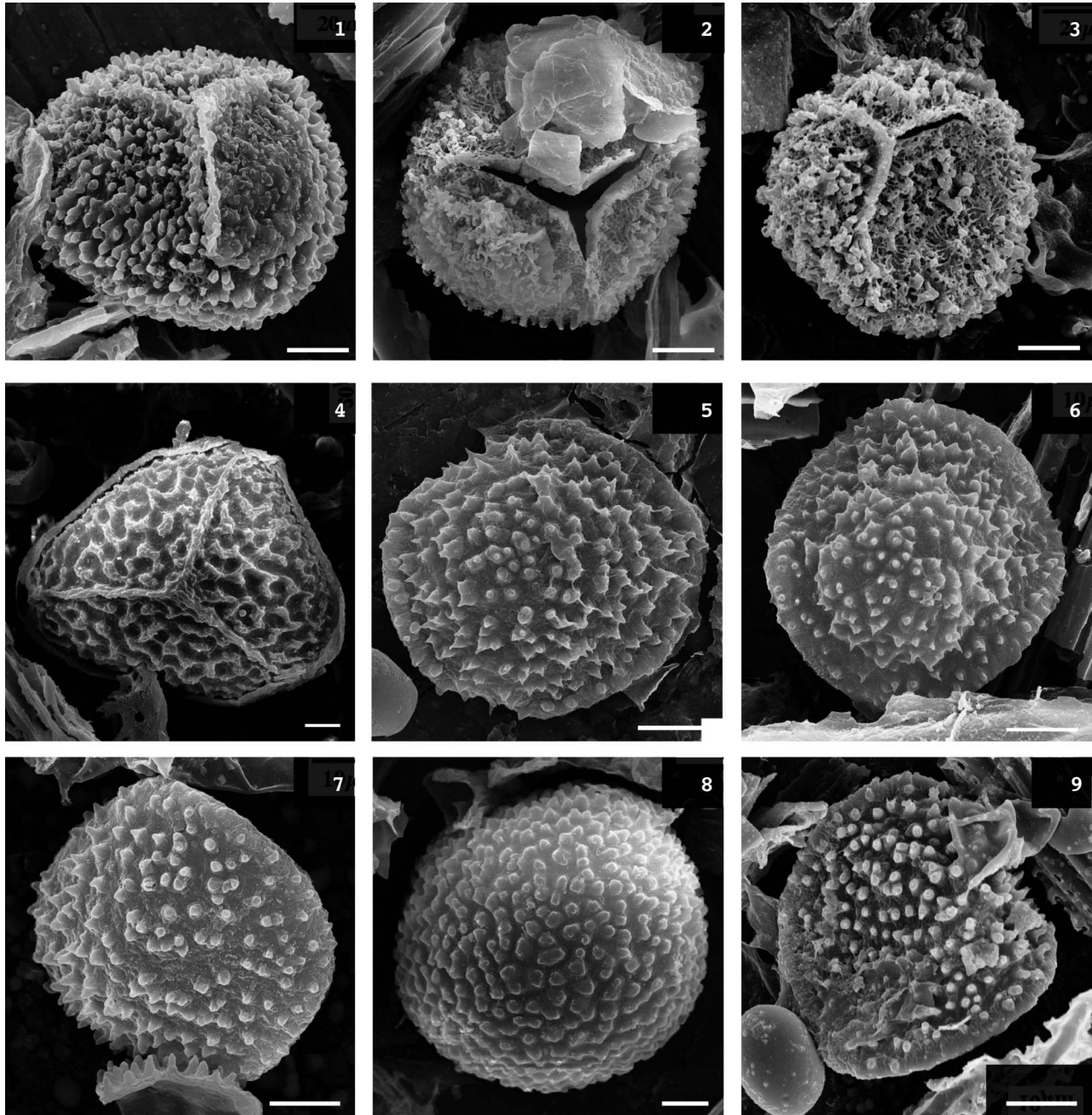


Plate 2. SEM photographs of key specimens of fossils of Anthocerotaceae from the High Island drill hole HI-178, sample 32C, offshore Texas, US (see location 1 on Figure 4). Figures 1–9 show various surface sculpture found in the fossil specimens of *Phaeoceros* spp. type, with more pronounced wall structures. Figures 1–4. Proximal views showing the trilete mark. Figures 5–9. Distal views. The scale bar represents 10 microns. Note the fluctuation in amb from oval to rounded triangular.

variation of ornamentation (variable density in spines between species and within the surface of a single spore, often stubby with broad-based and rounded edges) on the distal surface.

The fossil spores of *Phaeoceros laevis* recovered off the Texas coast resemble very closely those produced today by hornworts growing in warm environments, and are characterized by an amb that varies from a

circular to nearly square shape. An important diagnostic feature is the absence of heavy ornamentation on the laesurae (even less so on the fossil species), and the consistency of the thickening of the laesurae walls. The surface sculpturing is essentially restricted to the area between the arms of the laesurae. The ornamentation is composed of spine-like processes that are generally broader at the base. Their height tends to

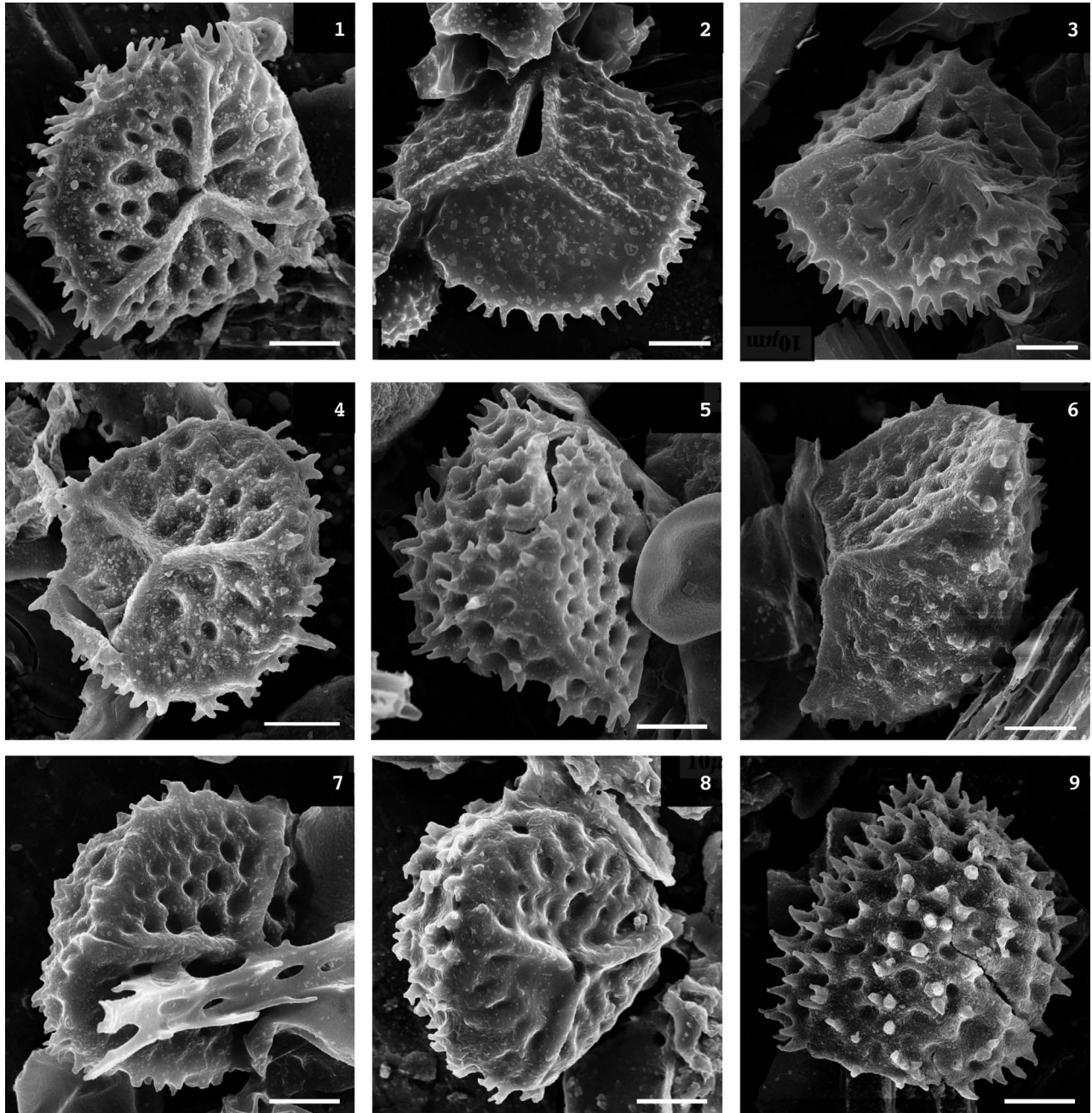


Plate 3. SEM photographs of key specimens of fossils of Anthocerotaceae from the High Island drill hole HI-178, sample 32C, offshore Texas, US (see location 1 on Figure 4). Figures 1–9 show various surface sculpture found in the fossil specimens of *Anthoceros multifidus* type with the spine-like processes and large lacunae. Figures 1–8. Proximal views with the trilete mark clearly marked by a smoother ridge. Figure 9. Distal side of the spore. The scale bar represents 10 microns.

be somewhat less in the fossil genus, although variation in this feature has been observed among specimens of extant species.

The other fossil form found at High Island is comparable to *Anthoceros multifidus*. Both fossil and modern spores are characterized by triangular to circular amb. The most striking feature is the network of thick spine-like processes on the distal side of the

spore which is also visible in equatorial view. The bases of these processes are connected to form a reticulate pattern separated by wide lumina or depressions, somewhat larger than the base of the processes themselves. The proximal side of the spore is covered in fine to thick granulations, but lacks spines. The entire proximal surface is characterized by about 20 large depressions in each of the three areas that are

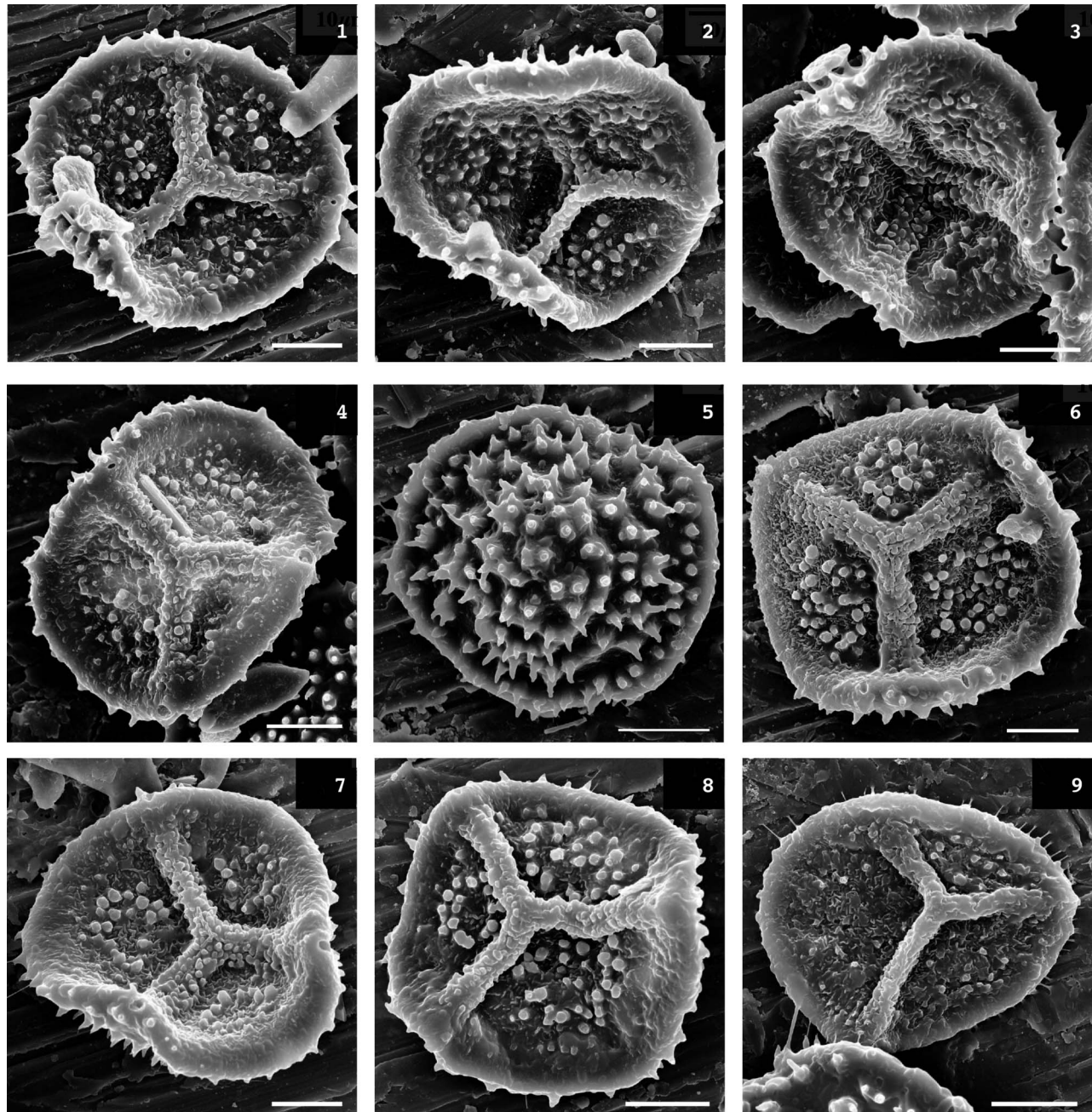


Plate 4. SEM photographs of key specimens of modern species of Anthocerotaceae from Turkey (see location 2 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Phaeoceros laevis*.

divided by the trilete mark. The trilete mark is expressed by the laesurae that is found broadly opened in several specimens.

5. Update on the phylogeny and taxonomy of the living Anthocerotophyta

Before looking into the environmental significance of the two genera recovered, it is important to understand

their position in the plant kingdom. It is well accepted that the bryophytes comprise three phyla (hornworts, liverworts and mosses) that are of particular interest to geologists and biologists as these are most likely the first extant lineages in the land-plant tree of life (Shaw and Renzaglia 2004). It is intriguing to think that the hornworts were among the first plants to colonize land in geological history (Villarreal et al. 2010b), with ancestral traits such as algal-like chloroplast (Vaughn

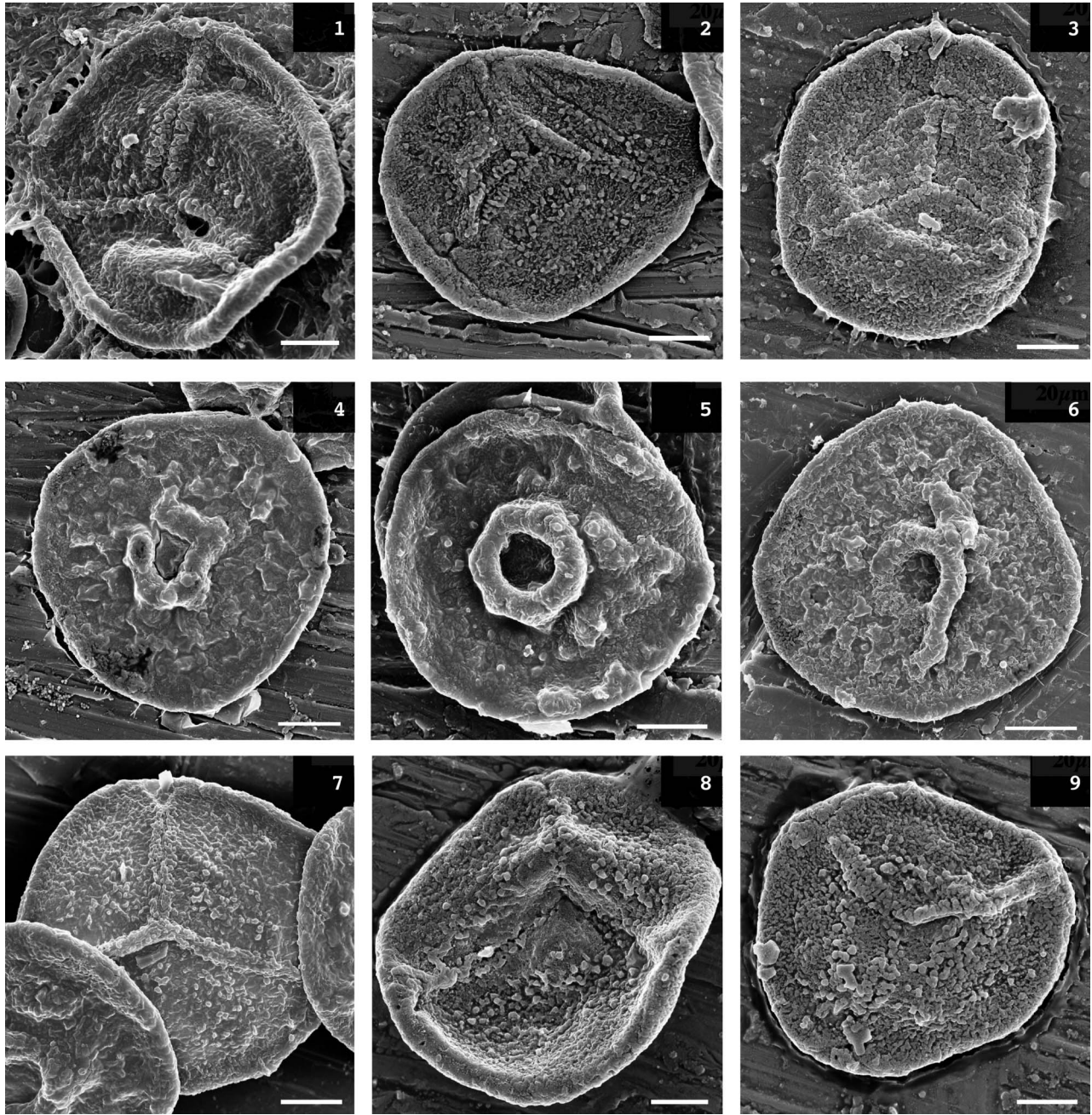


Plate 5. SEM photographs of key specimens of modern species of Anthocerotaceae from Chile (see location 3 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Phaeoceros skottsbergii*, emended *Phaeomegaceros skottsbergii* (Duff et al. 2007).

et al. 1990) and association with nitrogen-fixing cyanobacteria (Villarreal and Renzaglia 2006). If the phylum is well established, it is however apparent when reading the literature that there is a lack of consensus on hornwort phylogeny. The plant division Anthocerotophyta (Stotler and Crandall-Stotler 1977) indeed contains only the group of vascular plants referred to as the hornworts, and they are separated from the

division Bryophyta that is restricted *sensu stricto* to mosses and from the Marchantiophyta that is restricted to the liverworts.

Originally, the family Anthocerotaceae as described by Proskauer (1951) only included four genera: *Anthoceros*, *Phaeoceros*, *Dendroceros*, and *Megaceros*. Much work has been done on the hornworts since Proskauer (1951), separating out various generic

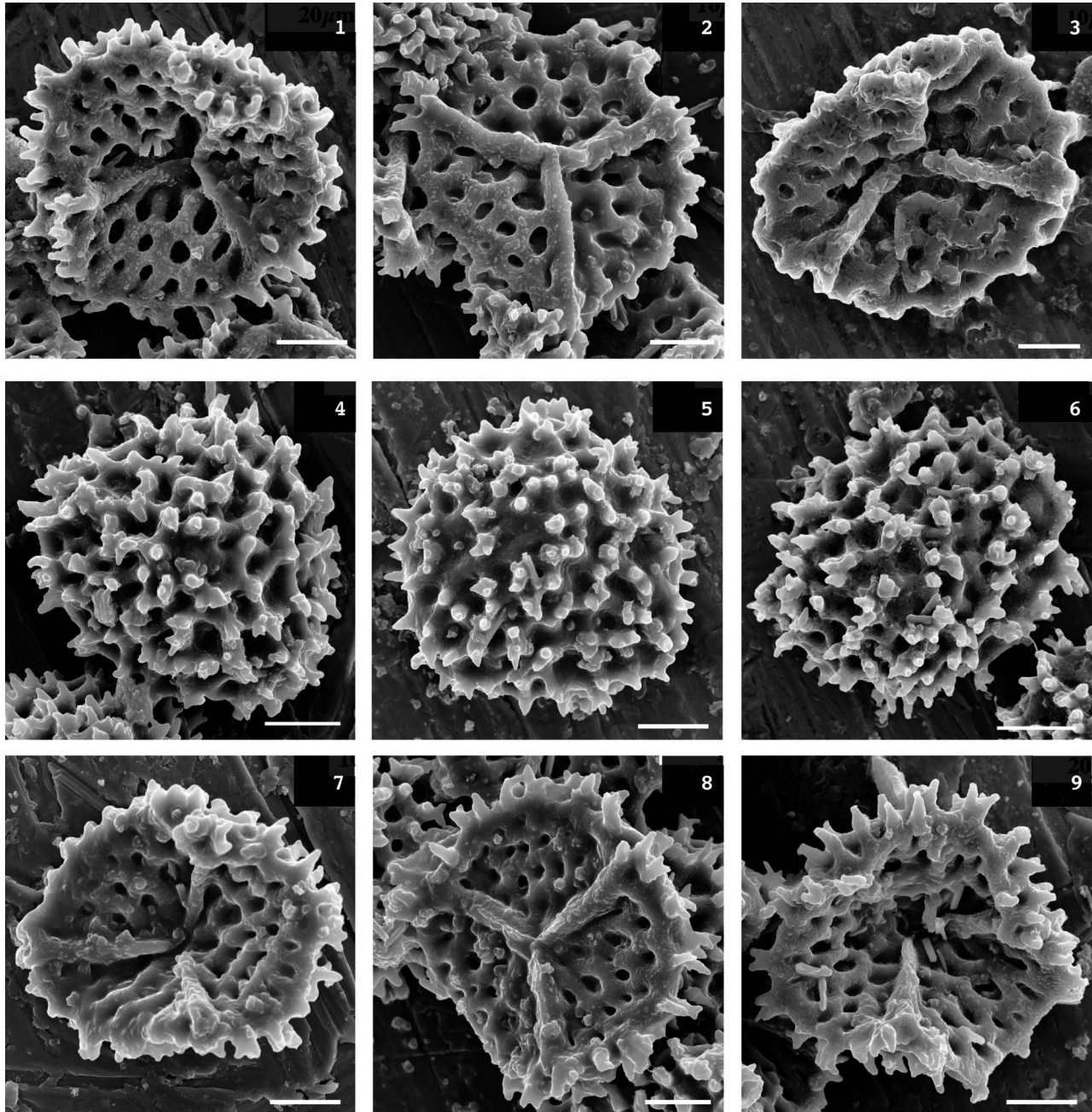


Plate 6. SEM photographs of key specimens of modern species of Anthocerotaceae from Russia (see location 4 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Anthoceros punctatus*.

groups into several families and subfamilies (Hyvönen and Piippo 1993; Stotler and Crandall-Stotler 2005; Duff et al. 2007). A new generally accepted classification includes two classes of hornworts (Figure 5a): the Anthocerotopsida and a new class, the Leiosporocerotopsida (only including *Leiosporoceros*). The classification of Anthocerotopsida (all other hornworts) based on Stotler and Crandall-Stotler (2005) recognizes three genera (*Anthoceros*, *Folioceros*, and

Sphaerosporoceros) in the order of Anthocerotales and seven genera (*Dendroceros*, *Hattorloceros*, *Megaceros*, *Mesoceros*, *Nothoceros*, *Notothylas*, and *Phaeoceros*) in the order of Notothyladales (Figure 5a). Stotler and Crandall-Stotler's classification was recently modified by Duff et al. (2007) who proposed a more complex classification based on molecular phylogenetic analyses (Figure 5b). Renzaglia et al. (2007, 2008), however, caution that more work is

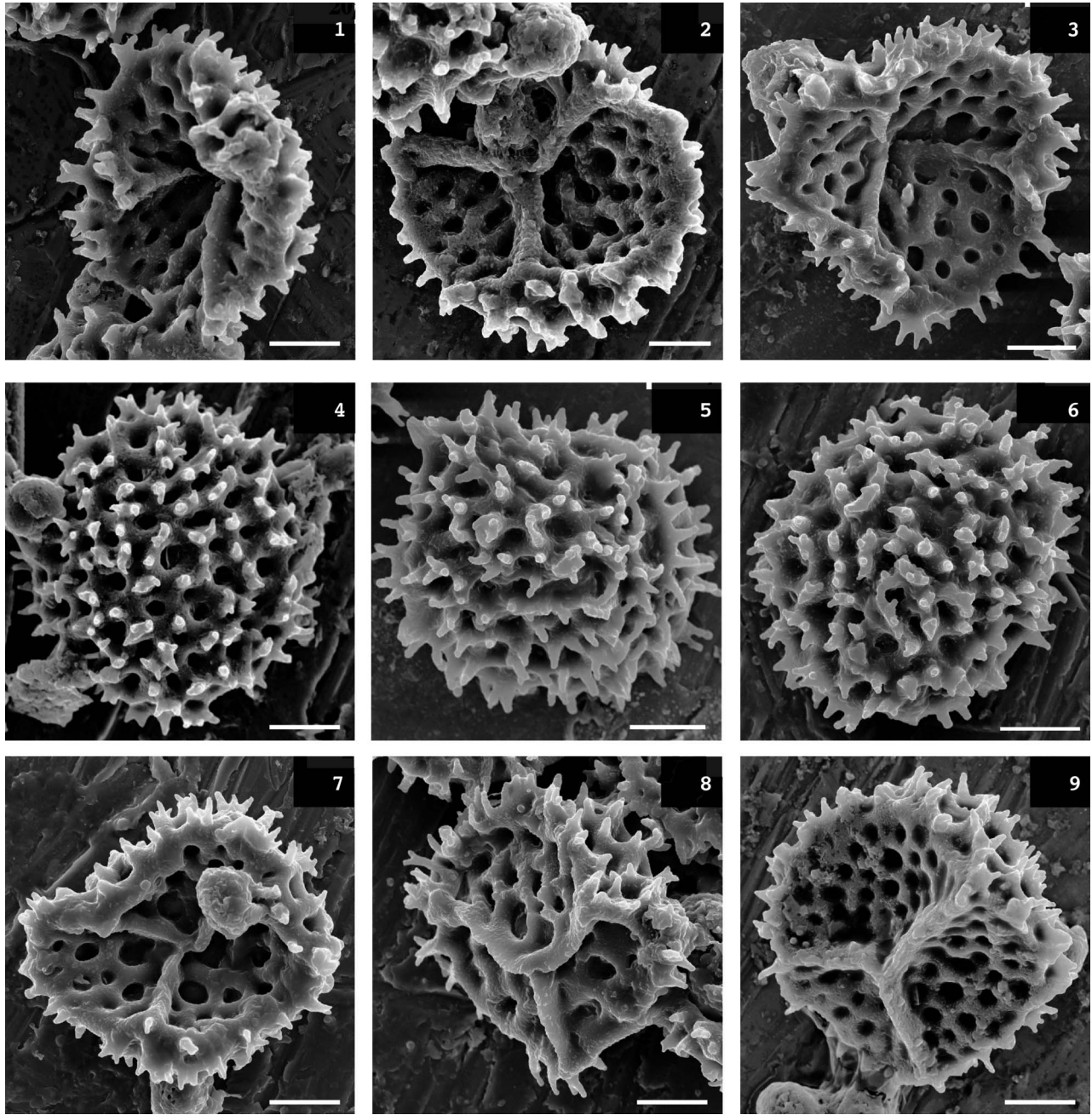


Plate 7. SEM photographs of key specimens of modern species of Anthocerotaceae from Sueca, Spain (see location 5 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Anthoceros multifidus*.

needed using sequencing and multigene analyses before a full comprehensive phylogeny of hornworts can be fully defined and accepted.

The two genera of interest in our study (*Anthoceros* and *Phaeoceros*) have a similar phylogenetic position in both the Duff et al. (2007) and Stotler and Crandall-Stotler (2005) classifications (Figure 4). This said, one of the modern herbarium species discussed here – *Phaeoceros skottsbergii* collected in Chile (CANM

#4305, Plate 5) – shows some distinct difference in its spore morphology. These differences are very uncharacteristic of spores of the *Phaeoceros* genus: it has a pronounced central depression or fovea, surrounded by a circular ridge. This is a very similar structure to that of spores of a new species defined in 2010 by Villarreal et al. (2010a), *Phaeomegaceros squamuliger*. In their new classification, Duff et al. (2007) proposed a new genus, *Phaeomegaceros*, that better fit four

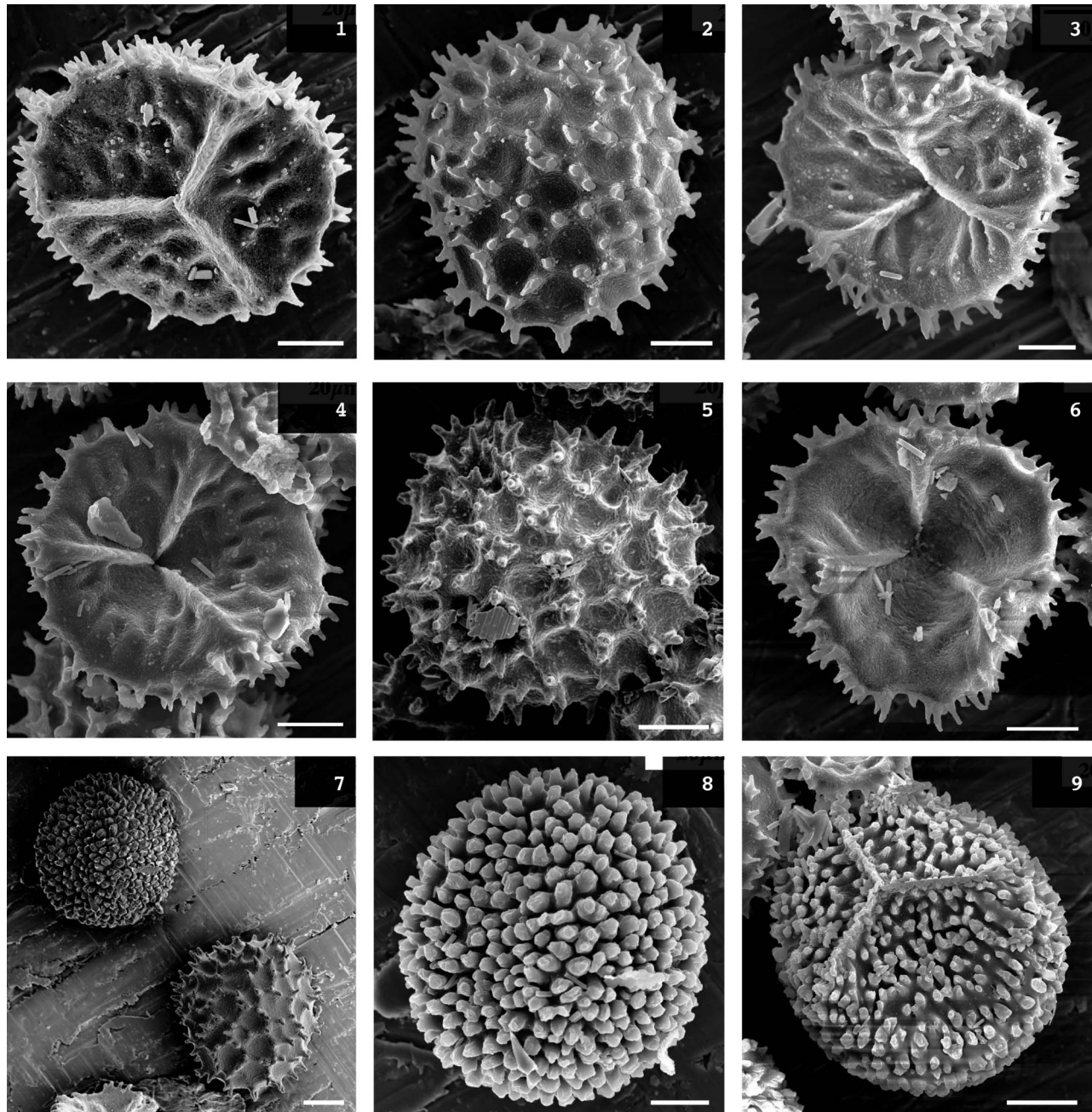


Plate 8. SEM photographs of key specimens of modern species of Anthocerotaceae from Japan (see location 6 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Anthoceros nagasakiensis*.

species previously included in the *Phaeoceros* genus; they include *Phaeoceros skottsbergii* as one of them. The spores of the new *Phaeomegaceros* genus seem to have in common a central circular depression surrounded by ridges on the distal surface. Hence, we follow the new classification of Duff et al. (2007) and accept that this species is now amended to *Phaeomegaceros skottsbergii*. New sequencing data presented by Villarreal et al. (2010a) also support this classification.

6. Spore, sporophytes and gametophyte of *Anthocerotophyta*

Palynologically, it is interesting to note that hornworts are named for their horn-shaped slender, upright sporophyte or spore capsule (Figure 6). One unique feature of hornworts is that the sporophyte, responsible for releasing spores, grows taller with age and is not dissociated from the gametophyte (Figure 7). Despite the importance of the sporophyte, hornwort spores are not often dealt with in palynological studies

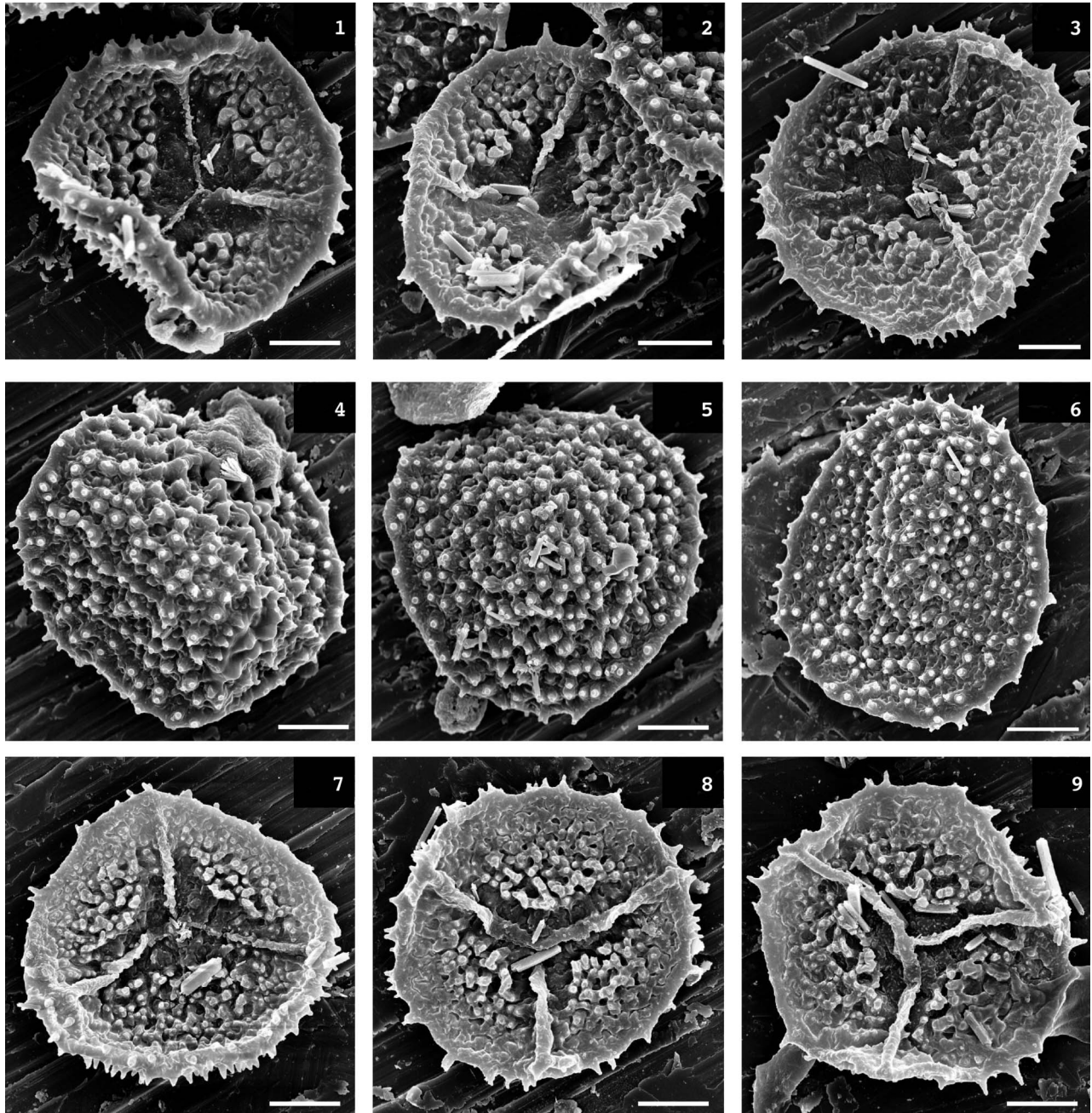


Plate 9. SEM photographs of key specimens of modern species of Anthocerotaceae from Canada (see location 7 on Figure 4). The scale bar represents 10 microns. Figures 1–9 are of specimens of *Anthoceros ravenellii*.

as they are usually not an abundant component of Cenozoic palynological assemblages. When found, they are often grouped with spores of land plants from other lineages of bryophytes, a fact that is not surprising as hornworts are the least species-rich lineage of bryophytes with only up to 250 species worldwide as opposed to ~1200 spp. for mosses and 8000 spp. for liverworts (Villarreal et al. 2010b). Hornworts mainly differ from liverworts in three main ways: (1) they have

only a few chloroplasts but these can store carbon dioxide (unlike liverwort chloroplasts); (2) hornworts do not have oil bodies in their cells; and (3) hornworts can produce spores for weeks as opposed to a few hours for the liverworts (Wassilieff 2009). Shaw and Renzaglia (2004) confirmed that latest point by stating that hornworts are the only plant group that have a constant production of spores, ensuring dispersal throughout the growing season.

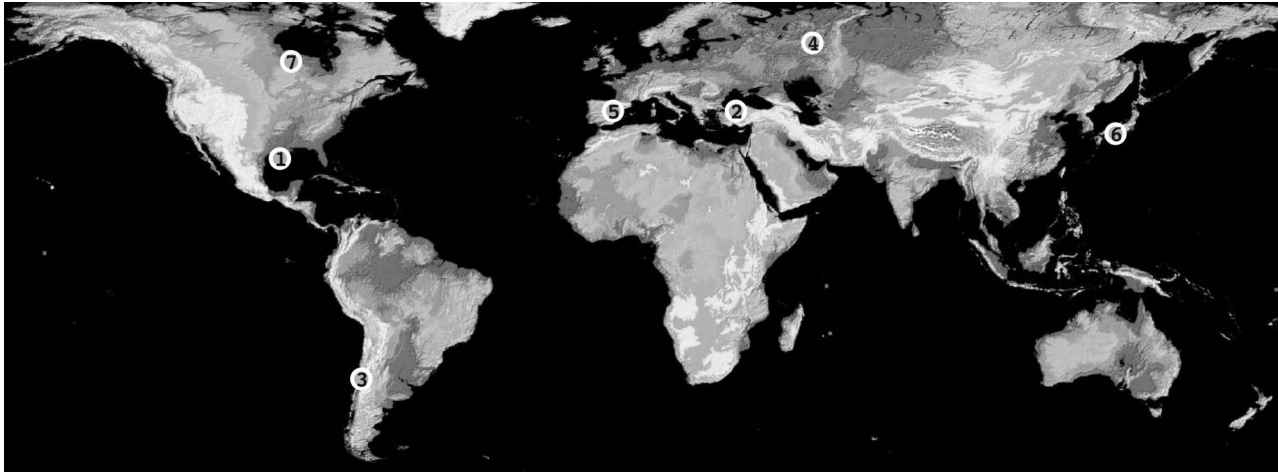


Figure 4. Geographic distribution of modern species collected at the Canadian Museum of Nature (CMN), Ottawa, Canada. Species collected includes two *Phaeoceros* and four *Anthoceros* species; a *Phaeoceros laevis* from Turkey (CANM #4292, Plate 4), a *Phaeoceros skottsbergii* from Chile (CANM #4305, Plate 5), an *Anthoceros punctatus* from Ukraine, USSR (CANM #4295, Plate 6), an *Anthoceros multifidus* from Sueca, Spain (CANM #4301, Plate 7), an *Anthoceros nagasakiensis* from Japan (CANM #4302, Plate 8), and an *Anthoceros ravenellii* from British Columbia, Canada (CANM #4306, Plate 9).

**Taxonomic classification by
Stotler and Crandall-Stotler 2005**

Class of Leiosporocertotopsida
Order Leiosporocerotales (1 genus)
Leiosporoceros

Class of Anthocerotopsida
Order Anthocerotales (3 genera)
Anthoceros
Folioceros
Sphaerosporoceros

Order Notothyladales (7 genera)
Notothylas
Phaeoceros
Hattorioceros
Mesoceros
Dendroceros
Nothoceros
Megaceros

**Taxonomic classification by
Duff et al. 2007**

Class of Leiosporocertotopsida
Order Leiosporocerotales (1 genus)
Leiosporoceros

Class of Anthocerotopsida
Order Anthocerotales (3 genera)
Anthoceros
Folioceros
Sphaerosporoceros

Order Notothyladales (4 genera)
Notothylas
Phaeoceros
Hattorioceros
Mesoceros

Order Phymatocerales (1 genus)
Phymatoceros

Order Dendrocerotales (4 genera)
Dendroceros
Nothoceros
Megaceros
Phaeomegaceros

Figure 5. Summary of latest hornwort phylogeny as proposed by (left) Stotler and Crandall-Stotler 2005 and (right) Duff et al. (2007). Gray-shaded box highlights the position of the two genera recovered at our site.

The presence of well-preserved, abundant and diverse hornwort spores at HI-178 indicates that the High Island site (or its proximity) was covered by these unusual-looking few-centimeter-tall narrow sporophytes embedded on the top of a gelatinous-looking, ground-cover of gametophyte plants (Figure 6). So, what does this imply for the type of environmental conditions that prevailed at the time of deposition?

7. Environmental significance of Anthocerotopsida

Because hornworts require a very specific environment in which to grow and reproduce, the spore abundance at the High Island site is interesting. The main goal of this project was to identify whether this site was, at least in part, above sea level during the Paleoindian period, and hence could have been occupied and/or utilized by humans as early as 9,460 years BP. Here we

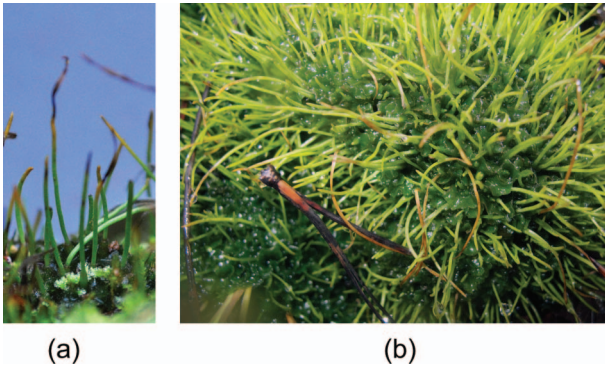


Figure 6. Photographs of a modern *Phaeoceros* plant, growing today in (a) Florida (David Jarzen) and (b) California (James Crame).

review the environmental data available on modern hornworts from the literature to summarize the type of environmental conditions needed for these primitive plants to grow.

7.1. Habitat preference

In general, hornworts are found mainly in damp places such as clay banks, along stream sides, ponds or swamps or settled on rocks, soil or even tree barks. *Anthoceros* species are often found on damp banks while other genera such as *Dendroceros* favor swampy ground (Wassilieff 2009). These plants, although small, can be found covering large areas of soil or trees. Breil (1970) conducted a detailed examination of hornworts and liverworts present at the same latitude as our study area, but about 170 miles east on the Alabama–Florida Gulf of Mexico coast. One of the most common hornworts found at these sites were species of *Anthoceros* and *Phaeoceros*, similar to what we found in High Island. In this study, Breil (1970) found that these two genera were strictly found in association with moist rotten stumps or logs, on moist soil, in moist quartzitic sand (but rarely on limestone), in ditches, along streams and riverbanks and commonly on wet floodplains and in freshwater swamps. While conducting a palynological analysis of non-pollen palynomorphs of Australia, Cook et al. (2011) noted that *Anthoceros* spores are generally found in moist shady environments during warm and wet time intervals conducive to swamp development.

7.2. Desiccation tolerance

In a review of desiccation-tolerance of hornworts, liverworts and mosses, Wood (2007) found that out of all bryophytes, the hornworts had a very low tolerance for reviving from the air-dried state, with only one

species of hornworts (*Dendroceros granulatus*) showing vegetative desiccation tolerance. Wood (2007) further noted that more experimental analyses are needed on other species of this group but that, so far, no other hornwort species have been documented as being desiccation tolerant. This inability to survive desiccation was confirmed by Schuette and Renzaglia (2010) who also stated that *Dendroceros* is the only desiccation-tolerant hornwort genus. This current state of knowledge indicates that finding so many spores of hornworts in the samples implies that the depositional environment was constantly moist, allowing these land plants to thrive and reproduce at the studied site. The importance of moisture for hornwort development is confirmed by Bisang et al. (2009) who found that hornwort occurrence at sites in Europe increases during time of high humidity level in the air. Bisang et al. (2009) added that high hornwort abundance is found during exceptionally wet growing seasons and concluded that humidity has a strong influence on hornwort population performance.

7.3. Submergence tolerance

If hornworts dry up and disintegrate very quickly when not kept moist, they will quickly rot if totally immersed. Working with closely allied species, Bates (2009) noted that bryophytes will not survive when permanently submerged. So, although hornworts require constant moist conditions, species of true hornworts (Anthocerotophyta) are likely to die in submerged conditions. Note that the true hornwort (Anthocerotophyta) discussed here are not related to the common aquatic ‘hornwort’ species *Ceratophyllum demersum* that is used in aquaria worldwide. This aquatic plant is actually a cosmopolitan flowering plant species belonging to the angiosperm family Ceratophyllaceae and is unfortunately commonly referred to as an aquatic hornwort, despite the lack of biological affinity with the Anthocerotophyta.

7.4. Saltwater tolerance

As our studied location is located today in the Gulf of Mexico, salinity must be considered as a controlling factor. Although some bryophyte species are found in marshes where the salinity is low but not zero, the need to identify the tolerance of hornworts for saline water is very important at our coastal site. Based on our review of the literature, it seems clear that hornworts are essentially found in association with freshwater habitats. Bates (2009) noted that very few bryophytes are halophytes and that they would not survive saltwater spray from the action of waves and tides. Tiedtje and Teer (1996) discussed hornwort abundance

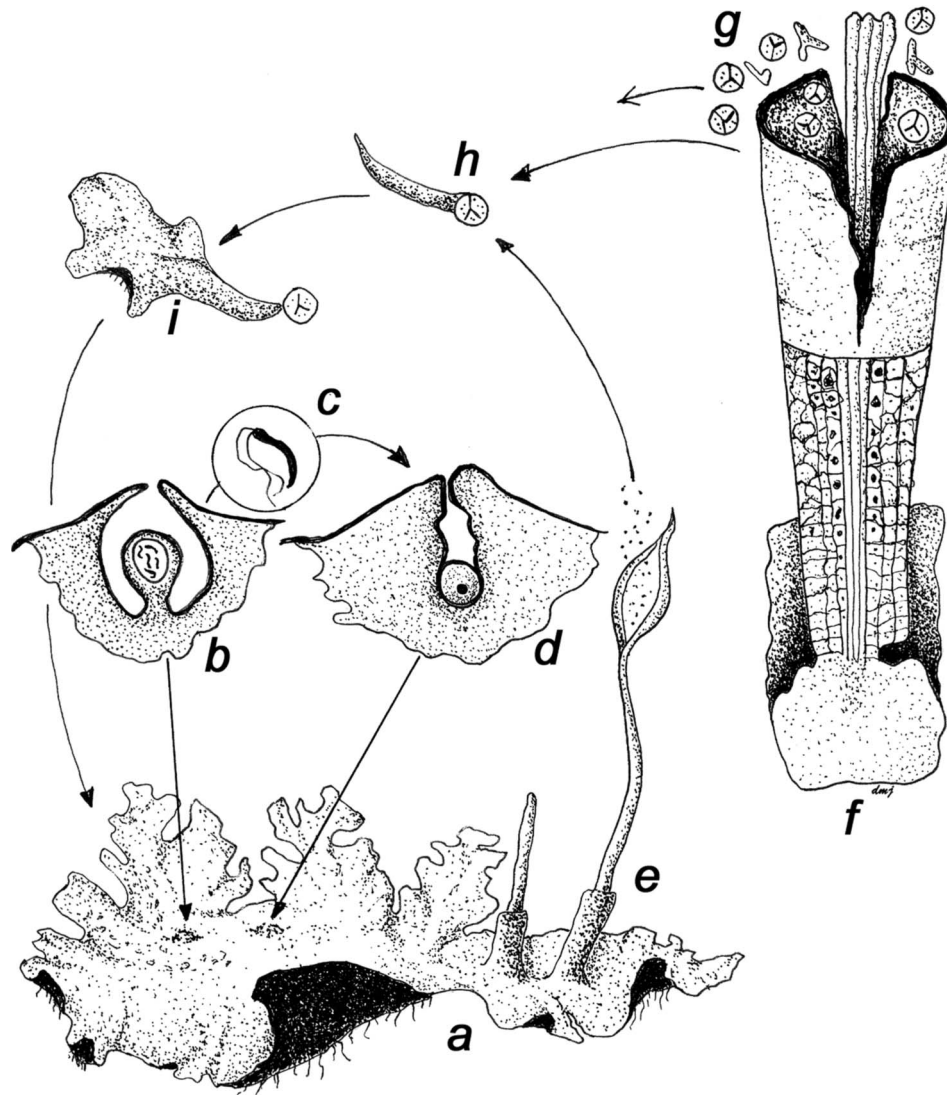


Figure 7. The life cycle (alternation of generations) of the hornworts. The (a) gametophyte generation with its thallus-like body and rhizoids on the under-surface bears the (b) male antheridium producing the (c) sperm which fertilize the egg within the (d) female archegonium, giving rise to the (e) sporophyte generation. The mature sporophyte generation – (f) enlarged cut-away view – develops the sporogeneous cells which upon maturity release the trilete spores and (g) pseudo-elaters, which grow into the (h) protonema, eventually developing into the (i) young gametophyte generation, completing the life-cycle. (Redrawn and modified from: <http://www.enotes.com/topic/Hornwort>.)

in freshwater wetlands while studying the feeding pattern of northern shovelers during overwintering in Texas. During year 4 of their study, Tiedtje and Teer (1996) found that the shovelers food source in freshwater wetlands included 37% of hornwort during middle winter (17 December–22 February) and 26% during late winter (23 February–6 May), indicating that these are an important component of these types of habitat. The fact that hornworts are essentially freshwater species and that they do not tolerate exposure to saltwater conditions is also of great interest to our paleoenvironmental reconstruction. Matheson et al.

(2007) reported that a species of hornwort (*Ceratophyllum demersum*) displays some degree of saltwater tolerance while judging the efficacy of saltwater solutions to kill freshwater species. As we discussed above however, this species should not be included into the true hornwort Antocerotophyta group. The only true exception we found regarding the Antocerotophyta is noted by J.C. Villarreal (pers. comm., 2011) who collected one species of true hornwort (*Notothylas dissecta*) near the sea where the specimens were splashed by the ocean waves, indicating that this species had some degree of salinity tolerance.

7.5. Temperature tolerance

When considering the known distribution of hornwort worldwide, data show that the genera *Anthoceros* and *Phaeoceros* include some of the most common and diverse species of hornworts found throughout the world (Figure 8). The proportions of species from these two genera in comparison to all hornworts species average between 47% on the Indian subcontinent (where diversity in hornworts is high) to up to 100% for Southern Africa and Russia (Renzaglia et al. 2007). The modern spores of species of *Anthoceros* and *Phaeoceros* presented in Plates 4–9 were extracted from specimens collected in six locations (Chile, Japan, Turkey, Canada, Spain, and Russia). Clearly, some of these species were collected in cold to temperate settings such as Russia or Canada. The literature however shows that hornwort sporophytes are not able to survive during winters in these cold regions (Bisang 1995), although he noted that only few precise population ecological studies of hornworts have been conducted to date. Specifically, the species collected in Russia (*Anthoceros punctatus*) is known to tolerate colder temperatures. Bisang et al. (2009) noted that this species is found in Switzerland, confined to a region south of the Alps.

Despite their broad distribution, studies so far indicate that both *Anthoceros* and *Phaeoceros* clearly favor warmer temperatures and that they are known to be particularly abundant in tropical regions (Villarreal et al. 2010b).

7.6. Response to fire

As noted earlier, several charcoal layers were found at and around depths where hornwort spores are abundant. This provides potential evidence that the area was in proximity to sites of wild or potentially controlled fires. As a twist, the charcoal evidence could explain the unusual dominance of hornworts. Bates (2009) noted that bryophytes, although usually readily destroyed in fires, are often a predominant plant element in the early recolonization of burned land.

8. Implications of environmental evaluation for our Paleindian landscape

The presence of hornwort spores has important implications for the type of environment that must have existed at the High Island site about 9,000 years BP. Based on the very specific requirements of hornworts, as discussed earlier, we postulate that the site was most likely a freshwater swamp or an area with constant moist soil, possibly close to streams, and that the site was above sea level during at least part of the Paleindian period. The climate of offshore Texas at that time was indeed likely warm and humid. The seismic survey data indicate that the site under investigation was located on natural levees and river terraces and that the flooding of the HI-178 location was likely delayed (Figure 2). Furthermore, subsidence must be considered. The current depth of the studied site is 16 m below sea level. The radiocarbon dates

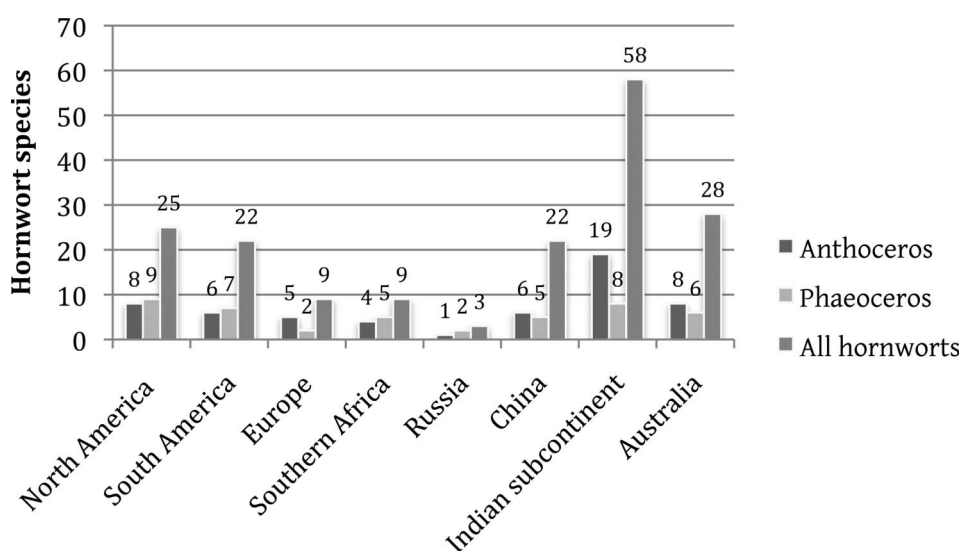


Figure 8. Relative distribution of *Anthoceros* and *Phaeoceros* species worldwide in comparison to all hornwort species. The data represented here are based on proportion of hornwort species in the different genera across regions of the world as summarized in Villarreal et al. (2010b).

Table 1. A range of estimates of subsidence and changes to the core-site elevation corrected with respect to modern sea level and the lower sea-level elevation existing at 9.5 ka BP. The first column provides the time elapsed since erosion of the Last Glacial Maximum (LGM) surface and the radiocarbon age of in situ material at the core site (see Figure 1 for LGM contour line). The last column is the inferred range of core-site elevations corrected for 8.5 ka of subsidence measured with respect to the lower sea level elevation (−15.5 mbsl) that existed at 9.5 ka BP.

Elapsed time between 18.0 and 9.5 ka BP (ka)	Average subsidence rate (mm a ⁻¹)	Total magnitude of subsidence between 18 and 9.5 ka (m)	Current-day elevation at core site (mbsl)	Core site elevation corrected for 8.5ka subsidence (mbsl)	Core-site elevation relative to sea-level at 9.5 ka BP (m)
8.5	1.0	8.5	16	7.5	8.0
8.5	0.8	7.6	16	9.2	6.3
8.5	0.6	5.7	16	10.9	4.6
8.5	0.4	3.8	16	12.6	2.9
8.5	0.2	1.9	16	14.3	1.2
8.5	0.1	0.95	16	15.15	0.35
8.5	0	0	16	16	−0.5 (mbsl)

indicate that the area was deposited about 9,500 years BP. Although this places the site just below or at sea level at that time using most sea-level rise estimates, this does not take into account subsidence in the region. A subsidence rate of 0 would place the site at 0.5 m below sea level, but conservative estimates indicate that the region subsided by at least 1 mm per year (Milliken et al. 2008) which would translate to a 8 m total subsidence since the deposition of the radiocarbon-dated charcoal (see Table 1 for details). This clearly supports our premise that the High Island site was indeed above water and was occupied by freshwater habitats.

Although no evidence of cultivated grains were found in our palynological assemblage, we cannot rule out that Paleoindian populations were present on this portion of the now-submerged continental shelf or that they manipulated their environment. A few recent studies have shown that agricultural practices such as land disturbance through tillage impact the distribution of hornworts (Bisang 1998; Bisang et al. 2009). Bisang (1998) and Bisang et al. (2009) specifically show that *Anthoceros* and *Phaeoceros* were found in abundance in abandoned stubblefields, but that these two genera were rare in stubblefields with maize, root-crops, and fodder-crops. Unfortunately, whether the abundance of hornworts at our site is a result of landscape manipulation by Paleoindians is a matter we cannot evaluate.

9. Conclusions

Two species of hornworts, *Phaeoceros laevis* (L.) Prosk. and *Anthoceros multifidus* Lindb., dominate the spore assemblage recovered from a potential Paleoindian landscape sampled offshore High Island, near Galveston, Texas. Because these plants do not

tolerate being submerged or being in contact with salt water, the presence of these two species of Anthocerotophyta growing in close proximity to the study area along with other evidence (e.g. charcoal) strongly suggests that this site was indeed not submerged at the time of deposition and that human occupation was therefore possible at or very near the site. In addition, since hornworts are commonly one of the first plants colonizing burnt sites (Bates 2009), a link between burning (either naturally occurring or human-induced) and high numbers of hornworts is established. The types of spore species present represent plants which are most commonly found today in countries with tropical climates where these hornworts thrive under moist but never submerged conditions. The warm, moist high land on the shelf of the northern Gulf of Mexico was therefore potentially hospitable to human occupation between 9,550 and 9,460 calibrated years BP.

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invoked to cause this abrupt climatic change need not be as dramatic as has traditionally been assumed.

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