**Late Cretaceous palynoflora from the central part of the Adriatic Carbonate Platform
(Islands of Hvar and Šćedro), southern Croatia**

Karmen Fio Firi^{a,*}, Antoine Bercovici^b, Olena Shevchuk^c, Jasenka Sremac^a

^a University of Zagreb, Faculty of Science, Department of Geology, Horvatovac 102a, HR-10000 Zagreb, Croatia; karmen.fio@geol.pmf.hr, jsremac@geol.pmf.hr

^b Department of Paleobiology MRC121, National Museum of Natural History, Smithsonian Institution, 10th Street and Constitution Ave. NW, Washington DC 20560-0121, USA; bercovicia@si.edu

^c Institute of Geological Sciences of NAS of Ukraine, O. Gonchara Str. 55-b, 01054 Kiev, Ukraine; hshevchuk@ukr.net

*Corresponding author: Karmen Fio Firi, Tel: +3851 4606112, Fax: +3851 4606081

Abstract: This paper provides the first palynological data from four Upper Cretaceous localities from the Islands of Hvar and Šćedro (southern Croatia), in the central part of the Adriatic Carbonate Platform. Studied material represents palynomorphs produced by coastal vegetation and transported to the shallow marine platform areas. Determined vegetation includes diverse hygrophilous, understory vegetation, range of evergreen needle trees attributable to Pinaceae and Podocarpaceae, as well as Araucarian conifers; ginkgo, cycads and/or bennettites. Flowering plants were likely represented by herbaceous forms. The palynoflora is generally indicative of a temperate, warm and humid climate.

The occurrence of the Normapolles group with the presence of *Plicapollis* sp. and *Pseudoculopollis* sp. point to Turonian or probable Turonian–Coniacian age, and represent the southernmost record of occurrence within the Normapolles palynological province.

Dominance of angiosperms and low abundance of ferns suggests an early-Late Cretaceous age. These findings are supported by the micropaleontological analyses and previously determined age of the sauropod dinosaur footprints described on the Island of Hvar. Based on the paleobotanical and palynological data, the dinosaur's diet probably included araucarian conifers, ginkgo and angiosperms, and ferns to a lesser extent.

Keywords: palynology, flora, Late Cretaceous, Island of Hvar, Island of Šćedro, Croatia

1. Introduction

The Island of Hvar and Island of Šćedro belong to the Dalmatian part of the Adriatic Carbonate Platform (AdCP; Vlahović et al., 2005). Both islands are mainly composed of Upper Cretaceous deposits (Fig. 1a; Marinčić and Majcen, 1968). Lower Cretaceous deposits can be found in the central part and Paleogene within a narrow area in the southern part of the Island of Hvar (Fig. 1a; Marinčić and Majcen, 1968). Sedimentology, stratigraphy and fossil assemblages of the Island of Hvar were studied by Marinčić and Majcen (1968), Herak et al. (1976), Jerinić et al. (1994); Marinčić (1997), Mezga et al. (2006) and Diedrich et al. (2011).

Plant macrofossil association from the Island of Hvar, collected by local people and forwarded to the Geologische Reichsanstalt at Vienna, was described by Kerner (1896). Original plants determinations include Pteridophyta: *Sphenopteris lesinensis* Kerner; Cycadaceae: *Pachypteris dalmatica* Kerner, *P. dimorpha* Kerner, *P. dalmatica* var. *dentata*, *P. ovata* Brongniart, *Thinnfeldia incisa* Saporta, *Dioonites* cf. *saxonicus* Reich sp.; Coniferae: Walchiaceae *Pachyphyllum* (*Pagiophyllum*) *rigidum* Saporta, *P. (P.) araucarinum* Saporta; Araucariaceae *Cunninghamia elegans* Corda; Taxodiaceae *Sphenolepidium kurrianum* (Schenk) Heer and *Ramus* incertae sedis. Findings of Dicotyledones include: Thymelinae:

Thymelaeaceae *Daphnites geopperti* Ettingshausen, *Proteoides* cf. *daphnogenoides* Heer, *P.* cf. *greviliaeformis* Heer; Leguminosae: Papilionaceae *Phaseolites formus* Lesquereux and *Folium* incertae sedis. Questionable determinations include *Trichopitys* sp. and *Vaccinium* sp. Unfortunately, the precise location where these floral remains were found is not indicated, since Kerner (1896) referred only to 'Lesina' (the Italian name for the Island of Hvar).

Plant remains from the Island of Hvar were also mentioned by Herak et al. (1976), from sporadic thin-bedded limestone intercalations within Cenomanian–Turonian dolomites, but they determined only calcareous green algae *Thaumatoporella parvovesiculifera* (Raineri). Plant remains in the Upper Cretaceous thin-bedded limestones of the Island of Hvar were also mentioned by Schubert (1909), Pantić (1962) and Diedrich et al. (2011).

Other significant fossil findings on the island of Hvar include diverse fish (mostly of Cenomanian–Turonian age; e.g., Gorjanović-Kramberger, 1892; Radovčić, 1973; Herak et al., 1976) and reptile remains (Gorjanović-Kramberger, 1892; Dutchak and Caldwell, 2006), together with the first report of dinosaur footprints in the Dalmatian part of the AdCP (Late Turonian–Early Coniacian; Mezga et al., 2006).

The aim of our study is to describe the fossil flora localities on the Island of Hvar, which are so far only known through personal communication with local people and museums from the Island of Hvar (city of Hvar and Stari Grad) and the Croatian Natural History Museum in Zagreb. Unfortunately, our investigation of the historical localities was not successful in finding fossil plants, and we therefore sampled shallow-marine limestones at three coastal localities of the Island of Hvar and one at the Island of Šćedro to determine if these deposits are palynomorph bearing. Based on the palynological associations, our aim is to estimate the diversity of the Late Cretaceous flora, which will be done for the first time in the area of the central part of the AdCP. We will compare the palynoflora with the previously reported macrofloral assemblages. These findings can extend our knowledge of the Late

Cretaceous fossil floras in the Dalmatian part of the AdCP, and determine possible food source for the herbivorous dinosaurs which were present in this part of the platform at that time, and studied in one of the analyzed sections (Mezga et al., 2006).

2. Study area and stratigraphic range of the deposits

The Island of Hvar is structured as a complex and slightly disturbed antiform, consisting mainly of Cretaceous and Paleogene carbonate deposits, with local occurrences of Paleogene flysch and Quaternary clastics (Fig. 1a; Marinčić and Majcen, 1968; Herak et al., 1976; Borović et al., 1977). The Island of Šćedro is situated south of the Island of Hvar, and, according to Marinčić and Majcen (1968), built of Upper Cretaceous (“Senonian”) well-bedded rudist limestones (Fig. 1a).

The studied deposits were previously determined as well-bedded and massive “Senonian” limestones with common rudist bivalves (Marinčić and Majcen, 1968; Herak et al., 1976), or Turonian to Santonian platform carbonates (Marinčić, 1997), which belong to the Gornji Humac formation (Gušić and Jelaska, 1990; Fig. 1b) of the AdCP.

During the Late Cretaceous, the AdCP was located within the central-western Tethys Sea, which separated Laurasiatic/Eurasiatic Continent from the Afro-Arabian Continent (Dalla Vecchia, 2003). Based on the previously determined flora (Kerner, 1896) and sauropod dinosaur footprints (Mezga et al., 2006), it can be concluded that the platform in the Late Cretaceous must have had emergent parts or islands hosting a terrestrial vegetation even in its central part, while in the NW part, area of Istria, emerged parts have been evidenced to exist since the Early Cretaceous (e.g. Matičec et al., 1996).

Studied shallow marine carbonates are exposed in four localities: (1) Žukova cove, situated in the northern part of the Island of Hvar, (2) Zavala, in the southern part of the Island

of Hvar, (3) NE part of the Island of Šćedro and (4) Vira cove in the western part of the Island of Hvar (Fig. 1a). The Žukova cove is known for the largest dinosaur footprints found on the AdCP (Fig. 2; Mezga et al., 2006). Detailed geological section of the Žukova cove locality with marked position of the layer with the dinosaur footprints can be found in Mezga et al. (2006). Microfacies analysis and biostratigraphy done by Mezga et al. (2006) indicate a Late Turonian–Early Coniacian age of the track-bearing layer (Fig. 2a) and dinoturbated layer below (Fig. 2b), positioning them as the geologically youngest footprints recorded on the AdCP. Studied layers are part of the shallowing-upward sequence and were deposited in the intertidal environment. Due to the morphology and size of the footprints, sauropod origin was postulated for these tracks, which were assigned by Mezga et al. (2006) to the *Brontopodus* ichnogenus sensu Lockley et al. (1994).

The Late Cretaceous (mostly “Senonian”) flora from the surrounding area, which belonged to the Tethyan realm, include mostly gymnosperms and rare angiosperms (Dalla Vecchia, 2003, and references therein), a composition that may be further confirmed by palynological analysis.

3. Material and Methods

On the trail of the formerly described fossil flora, for which exact position of localities within the island is not known (Kerner, 1896), samples were taken at four localities, three on the Island of Hvar and one on the Island of Šćedro (Fig. 1). Since plant fossils were not found during our field research, collected samples from the Upper Cretaceous shallow-marine carbonate rocks were mainly investigated to characterize palynofacies.

Altogether, 14 samples of fine-grained carbonate rocks were collected at four localities of the islands of Hvar and Šćedro (Fig. 1a) and prepared as thin-sections for

micropaleontological analyses (Fig. 3) at the Department of Geology of the Faculty of Science, University of Zagreb.

Palynological analysis were conducted on five samples: from Žukova cove in the northern part of the Island of Hvar (samples CRO-01 and CRO-02), Zavala area in southern part of Hvar (CRO-03), NE part of the Šćedro Island (CRO-04) and Vira cove in the western part of the Island of Hvar (CRO-05). Palynomorphs were identified in four out of five samples. Samples were processed using the standard palynological procedure at Global GeoLab Ltd., Canada. Approximately 20 grams of bulk rock was treated with dilute hydrochloric acid (HCl) to remove calcium carbonate, macerated in 75% hydrofluoric acid (HF), and cleaned of fluorosilicate byproducts in hot HCl. Organic residue was sieved at 10 µm and mounted un-dyed in polyester resin on one or two microscope slides depending on recovery. A representative selection of palynomorphs was photographed on the differential interference contrast Nikon Eclipse 80i microscope of the NMNH Paleobiology Department at the Smithsonian and post-processed using extended depth of field reconstruction (Bercovici et al., 2009). Palynofacies characterization was done by counting the relative abundance of organic particles (palynomacerals) based on 500 counts. Classification of palynodebris for the palynofacies analysis is based on the different groups established by Batten (1996) that are relevant to this study, namely: (I) Palynomorphs – including the sub-categories; pollen and spores (II) Structured Organic Matter (SOM) – including the sub-categories; black wood, brown wood, charcoal, cuticles and phytoclasts, and (III) Unstructured Organic Matter (USTOM) (Table 1). Each sample was plotted on the ternary diagram (Fig. 4) proposed by Tyson (1995), classifying different marine depositional environments as a function of palynofacies composition. Relative abundance counts for palynological taxa are provided in Table 2, and illustrated on Fig. 5. Only samples CRO-01 and CRO-02 were counted, as other samples are devoid of identifiable palynomorphs. Because of the low recovery of pollen and

spores, which is typical for shallow marine carbonate facies, it was not possible to reach the statistically significant number of ≥ 200 count, thus the palynological relative abundance data should be treated as a general indication only. Modern contaminants (a significant number of Betulaceae (triporates), Juglandaceae (stephanoporates), and Asteraceae (echinates) pollen grains) were identified but were excluded from the data set.

4. Results

4.1 Stratigraphy and microfacies

Studied carbonates are generally poor in sedimentary organic matter and were previously determined only as “Senonian” limestones (Marinčić and Majcen, 1968; Herak et al., 1976), Turonian to Santonian platform carbonates (Marinčić, 1997), or “Early Senonian” shallow-marine platform carbonates (Jerinić et al., 1994; Mezga et al., 2006).

Three microfacies types were recognized in the studied samples. Microfacies 1 (Fig. 3a) are mudstones to wackestones with pelloids, fragments of algae *Thaumatoporella parvovesiculifera* (Raineri) and rare ostracods. Microfacies 2 (Fig. 3b) consist of thin bedded laminae with rare *Thaumatoporella* fragments. Microfacies 3 (Fig. 3c) are wackestones to packstones with common *T. parvovesiculifera* (Fig. 3d, e) and miliolid foraminifera (Fig. 3c). These microfacies types, showing a vertical succession of mostly thin-bedded platform limestones, are characteristic of a shallow marine intertidal environment.

4.2 Palynofacies analysis

Five samples were prepared for palynological analyses, out of which four produced organic residue, while CRO-05 (Vira cove) was virtually barren.

Samples from the Žukova cove (CRO-01 and CRO-02) show a very similar composition and are largely dominated by dispersed plant cuticles (80.0% and 77.4% respectively, Table 1). The cuticles are thin and transparent, and are not showing any epidermal cells. Cuticles fragments are polygonal, square to elongated, with an average size around ~50 µm. Other palynomacerals include other phytoclasts (7.4% and 4.0% respectively, Table 1) and amorphous organic matter (10.4% and 7.8% respectively, Table 1). The recovery of miospores (pollen and spores) is relatively low, 9.6% in CRO-02 and 1.8% in CRO-01.

The sample from Zavala (CRO-03; Table 1) has a low recovery of organic matter and is dominated by black wood fragments (44.4%) and phytoclasts (33.2%). Unlike for the Žukova cove, cuticles are almost absent.

The sample from the Island of Šćedro (CRO-04; Table 1) shows palynofacies composition similar to that of the Žukova cove, dominated by cuticles (56.6%) and phytoclasts (24.8%).

Palynofacies composition of the studied samples indicates deposition in marginal dysoxic to anoxic intertidal shallow-marine environment (Fig. 4).

4.3 Palynological analysis

From five studied samples, only CRO-01 and CRO-02 from the Žukova cove yielded identifiable palynomorphs sufficient for taxonomical study. A total of 17 pollen and spore taxa were identified, including two bryophytes, two ferns, six gymnosperms, and seven angiosperms (Table 2).

Spores are chiefly represented by trilete forms, comprising *Densoisporites* sp., which is attributed to the family Selaginellaceae (spikemoss, Weyland and Krieger 1953), and *Aequitriradites spinulosus* (Cookson and Dettmann 1958) Cookson and Dettmann 1961, a Marchantiopsid (liverwort). Ferns are also represented by the small and round laevigate spore *Todisporites* sp., which is attributed to the family Osmundaceae (Singh, 1964).

Gymnosperm pollen taxa include *Cycadopites* sp., a morphotaxon including monosulcate pollen grains produced by cycads, ginkgo and bennettites. Several specimens of *Araucariacites* sp. are also present and represent the pollen of Araucariaceae (Reyre 1973). A diversity of several bisaccate pollen taxa including *Cedripites* sp., *Abiespollenites* sp., *Pityosporites* sp. (Pinaceae) and *Podocarpites* sp. (Podocarpaceae) indicate the presence of various conifers.

Angiosperms are dominant in the palynological assemblage. One monocot species is present, *Palmaepollenites minusculus* (Hedlund 1966), belonging to the family Arecaceae. Other angiosperms are represented by several dicot species of *Clavatipollenites*, including *Clavatipollenites* sp., *C. rotundus* Kemp 1968, *C. hughesii* (Couper 1958). *Clavatipollenites* was attributed to the family Chloranthaceae from shared characters with modern chloranthaceous pollen (Dettmann, 1986; Pedersen et al., 1991; Archangelsky and Taylor, 1993) and ultrastructural studies showing similarities between *Clavatipollenites* and *Ascarina* (Chloranthaceae, Chlonova and Surova, 1988; Friis et al., 2015). Two genera of Normapolles are also present, *Plicapollis* sp. and *Pseudoculopollis* sp. Additional angiosperms recorded include *Retitricolpites* sp., *Bacutricolpites constrictus* Pierce 1961 and *Ericaceoipollenites* sp.

One non-pollen palynomorph, a zygospore (Zygnemataceae, fresh water green algae), was also identified.

5. Discussion

5.1 Biostratigraphy and lithostratigraphy

Studied deposits are classified as mudstones to wackestones (Microfacies 1) and wackestones to packstones (Microfacies 3) with common occurrence of green algae *Thaumatoporella parvovesiculifera* (Raineri) and rare ostracods and miliolid foraminifera (Fig. 3). Laminites (Microfacies 2) also occur, with fragments of *Thaumatoporella*, and this microfacies is similar to the microfacies “b” determined in the area of the Žukova cove by Mezga et al. (2006). Mentioned microfacies types are typical for the intertidal environment which is characteristic for the Late Turonian–Santonian Gornji Humac formation of the AdCP (Fig. 1b; Gušić and Jelaska, 1990). Similar shallow-water successions, typical for the Upper Cretaceous deposits can be found in the carbonate platforms of the peri-Mediterranean region (Apulian, Apenninic, Adriatic, and other smaller carbonate platforms (e.g., Gušić and Jelaska, 1990; Carannante et al., 2000; Tišljär et al., 2002; Diedrich et al., 2011; Schlagintweit et al., 2015, and references therein).

Thaumatoporella parvovesiculifera was previously determined in the area of the AdCP and in the wider Mediterranean area within the Middle Jurassic to Upper Cretaceous deposits, with Late Cretaceous considered as a period of its maximal expansion (Radoičić, 1960). Due to the findings of *Thaumatoporella parvovesiculifera*, and according to micropaleontological determinations done by Mezga et al. (2006), Turonian or probable Turonian–Coniacian age can be proposed for the studied deposits, especially Žukova cove locality. Further biostratigraphic constraints in this study are provided by the angiosperm-rich palynological assemblages.

5.2 Paleoenvironmental reconstruction and interpretation based on palynology

Palynological samples were collected from shallow platform carbonates, and it is evident that the pollen and spore association recovered represent transported material produced from the coastal vegetation. As such, the low taxonomic diversity and low recovery of organic matter directly reflect taphonomic biases due to local depositional environment, classified as marginal dysoxic to anoxic part of the basin (Fig. 4; Tyson, 1995), rather than a true reflection of a low richness flora.

The parent plants of the spores *Densoisporites* sp., *Aequitriradites spinulosus* and *Todisporites* sp. represent a glimpse of a likely more diverse hygrophilous, understory vegetation. The canopy vegetation was represented by a range of evergreen needle trees producing bisaccate pollen grains attributable to Pinaceae and Podocarpaceae, as well as Araucarian conifers represented by *Araucariapollenites*. Ginkgo, cycads and/or bennettites were also part of a minor sub-canopy as represented by the occurrence of monosulcate pollen *Cycadopites* sp. Flowering plants were likely represented by herbaceous forms as indicated by *Clavatipollenites* (Chloranthaceae) and the Normapolles which relates to Juglandaceae. Altogether, the palynoflora is indicative of a temperate, warm and humid climate.

The sauropod dinosaurs that left the tracks on the Island of Hvar were likely foraging on araucarian conifers, ginkgo and angiosperms, and ferns to a lesser extent (cf. Hummel et al., 2008; Gee, 2011), the needle-leaved conifers and cycads being unlikely candidates.

The presence of the listed palynomorphs can indicate a presence of the wider subaerially exposed platform area or even an island in the early-Late Cretaceous of the AdCP (as proposed by Dalla Vecchia (2003) for the NW part of the AdCP). Based on our palynological determinations, previously determined flora (Kerner, 1896) and sauropod dinosaur footprints (Mezga et al., 2006), we can propose that during the Late Cretaceous the central part of the platform must have had emergent parts or islands, where fresh water was

provided, and plants as food supply existed in sufficient amount for supporting sauropod fauna. Since the dinosaur footprints from the Island of Hvar represent largest recorded forms in the Dalmatian part of the AdCP (Mezga et al., 2006), it can be presumed that the island where determined plants were growing was quite wide, or connected with the mainland (cf. Dalla Vecchia, 2003, and references therein).

5.3 Biostratigraphic significance of the palynoflora

Among the biostratigraphically significant taxa, occurrence of the Normapolles *Plicapollis* sp. and *Pseudoculopollis* sp. is the most remarkable. The Normapolles group appeared during the Cenomanian and diversified during the rest of the Cretaceous (Batten, 1981; Zaklinskaya 1981) specifically in a paleobiogeographic province restricted to Europe, eastern North America and western Siberia, which the AdCP was part of (Herngreen et al., 1996; Vajda and Bercovici, 2014). *Plicapollis* sp. and *Pseudoculopollis* sp. are most common within Turonian to Santonian palynological assemblages, and range up to the Maastrichtian. *Clavatipollenites* has been reported as early as the Lower Cretaceous (Barremian–Cenomanian) in European, North American and African localities. Within Europe, the AdCP represents the southernmost known occurrence for *Plicapollis* sp. and *Pseudoculopollis* sp.

Clavatipollenites usually represent a common component of many early angiosperm assemblages (Heimhofer et al., 2007) and is represented within the Žukova cove assemblage as the dominant angiosperm taxa.

Altogether, the dominance of angiosperms and the low abundance of ferns, as well as the absence of typical Early Cretaceous elements like *Classopollis*, is in accordance with an early-Late Cretaceous age.

Other palynological assemblages of similar taxonomic composition, but without the Normapolles *Plicapollis* sp. and *Pseudoculopollis* sp., have been described from the Middle Cenomanian of France (Azéma et al., 1972), including *Araucariacites australis*, *Bacutricolpites constrictus*, *Cedripites canadensis*, *Clavatipollenites rotundus*, *C. hughesii*, *Cycadopites* sp., *Palmaepollenites minusculus*, *Podocarpidites dettmannii*, and several species of *Retitricolpites*. Solé de Porta (1978) described Cenomanian assemblage of Oviedo, Spain, containing *Araucariacites australis*, *Clavatipollenites hughesii*, *Retitricolpites* sp. and *Todisporites* sp., and Médus and Berthou (1980) reported *Densoisporites* sp., *Araucariacites australis*, *Clavatipollenites rotundus*, *Palmaepollenites minusculus* and *Retitricolpites* sp. from the Albian of Portugal. Brattseva and Novodvorskaya (1979) also described an Albian assemblage from the Mongolian Khuduk region that include *Araucariacites* sp., *Aequitriradites spinulosus*, *Bacutricolpites constrictus*, *Cedripites* sp., *Densoisporites* sp., *Podocarpites* sp., *Retitricolpites* sp. and *Todisporites* sp., and Ravn and Witzke (1995) reported *Aequitriradites spinulosus*, *Clavatipollenites rotundus*, *Pityosporites constrictus*, *Palmaepollenites minusculus* from the Late Albian–Cenomanian Dakota Formation in Iowa and Nebraska. *Palmaepollenites minusculus* has also been reported from the Cenomanian of Oklahoma (Hedlund, 1966) and Utah (May and Traverse, 1973), and has also been identified in the younger Maastrichtian Esna Shale Formation in Egypt (Mohsen, 1987).

5.4 Problems with macroflora remains in the area of the Island of Hvar

Kerner (1896) described macroflora remains from the Island of Hvar as fern-like leaves, Cycadopsida, Ginkgopsida, Pinopsida and Magnoliopsida.

Sphenopteris-type leaves, represented worldwide with a large number of morphospecies, can be associated with ferns, or seed-producing plants. A new morphospecies

from the Island of Hvar, *Sphenopteris lesinensis* was affiliated to ferns, according to Kerner (1896). Another fern-like genus recorded by Kerner (1896), *Pachypteris* is a "seed fern" commonly associated with order Peltaspermales, and sometimes also considered as a synonym of the genus *Thinnfeldia*. Kerner originally described specimens from Hvar as Cykadeaceae: *Pachypteris dalmatica* Kerner, *P. dalmatica* var. *dentata*, *Pachypteris dimorpha* Kerner, *Pachypteris ovata* Brongniart and *Thinnfeldia incisa* Saporta.

Species from Kerner's list, determined as *Dioonites* cf. *saxonicus* (Reichenbach) Schimper, belongs to a doubtful extinct genus from the order Cycadales.

Kerner (1896) described several leaves from Hvar as *Pachyphyllum* (*Pagiophyllum*) *rigidum* Saporta and *Pachyphyllum* (*Pagiophyllum*) *araucarinum* Saporta. His determinations were discussed by Berry (1916), who suggested them to be redefined as *Araucaria toucasi* Saporta and *Araucaria bladenensis* Berry, species known from North America and France. Conifers from the Island of Hvar additionally comprise the cosmopolite taxa *Cunninghamites elegans* (Corda) Endlicher (in original: *Cunninghamia elegans*) and *Sphenolepidium kurrianum* (Dunker) Heer.

Findings of Dicotyledones include Malvales representative *Daphnites geoperti* Ettingshausen, also known from Sachsen, Germany. Leaves described by Kerner (1896) as *Proteoides* cf. *daphnogenoides* Heer and *Proteoides* cf. *greviliaeformis* Heer could be redefined as genus *Ficus* (e.g. Berry, 1916).

According to Kerner (1896) Leguminosae from the Island of Hvar are represented with genus *Phaseolites formus* Lesquereux and some undeterminable leaves. Nevertheless, Berry (1916) finds the determination of *Phaseolites* doubtful, but suggests Kerner's *Vaccinium* sp. possibly equal to "*Leguminosites*" *coronilloides* Heer, a leguminose found in North America.

Determination of Ginkgophyta, genus *Trichopitys* sp. also seems to be questionable (Berry, 1916).

Berry (1916) considered the description of Hvar fossil flora by Kerner (1896) generally problematic, indicating that plant remains are either misidentified, or collected from different horizons. Nevertheless, he points to some similarities with some Saxonian and Bohemian Cenomanian floras (Berry, 1916: 303–304).

During this research, we were not been able to find any plant macrofossils during field prospection. As Kerner's collection is not stored in Croatian museums, we do not have enough elements for critical review of this collection from our point of view. We can accept some of Berry's corrections only by comparing macrofossils to the determined palynoflora. Similarities can be noticed in the presence of araucariaceans, ginkgoales and cycadales/bennettiales, in both associations.

6. Conclusions

(1) This paper provides the first palynological data from the Upper Cretaceous deposits of the Islands of Hvar and Šćedro, southern Croatia, in the central part of the Adriatic Carbonate Platform.

(2) Microfacies determinations point to shallow marine, intertidal environment, with occurrence of the green algae *Thaumatoporella parvovesiculifera* (Raineri), miliolids and small ostracods.

(3) Studied material represent pollen and spores produced by coastal vegetation and transported to shallow platform areas.

(4) The miospore assemblage is attributed to a hygrophilous, understory vegetation of bryophytes and ferns, a range of evergreen needle trees attributable to Pinaceae and Podocarpaceae, as well as Araucarian conifers; ginkgo, cycads and/or bennettites. Flowering plants were likely represented by herbaceous forms.

- (5) The occurrence of the Normapolles *Plicapollis* sp. and *Pseudoculopollis* sp. is very significant, since their presence was not previously reported from the area of the Adriatic Carbonate Platform, and represent the southernmost report of occurrence for the Normapolles palynological province.
- (6) Determined palynoflora is indicative of a temperate, warm and humid climate.
- (7) The dominance of angiosperms and the low abundance of ferns, as well as the absence of typical Early Cretaceous elements such as *Classopollis* confirms an early-Late Cretaceous age determined by previous studies. Previously determined macroflora from the Island of Hvar, show similarities with the dominant palynomorph groups indicating similar conditions on the AdCP during the Late Cretaceous.
- (8) During Turonian–Coniacian time, the sauropod dinosaurs inhabiting the area of investigation were likely foraging on araucarian conifers, ginkgo and angiosperms, but ferns to a lesser extent. Due to the given determinations of the Late Cretaceous palynomorphs from the central part of the AdCP, our results are in accordance with the hypothesis of the connection with the nearby land, where dinosaurs could have been passing from and to.

Acknowledgments

This study was supported by the Croatian Ministry of Science, Education and Sports, project number 119-1951293-1162, and University of Zagreb, financial supports 20281002 and 20281004. We would like to thank student Bruno Polak (Faculty of Science) for help in field-work. We are grateful to R. Koščál from the Faculty of Science, University of Zagreb for preparation of graphics. Antoine Bercovici is currently supported by a Deep Time Peter Buck Postdoctoral Fellowship from the NMNH Smithsonian Institution. Russ Harms, Global

Geolab Ltd. is thanked for palynological processing for this project. We would like to thank two reviewers for constructive comments which significantly improved the manuscript.

References

- Archangelsky, S., Taylor, T.N., 1993. The ultrastructure of in situ *Clavatipollenites* pollen from the Early Cretaceous of Patagonia. *American Journal of Botany* 80, 879–885.
- Azéma, C., Durand, S., Médus, J., 1972. Some miospores from the Middle Cenomanian. *Paléobiologie Continentale* 3, 1–54.
- Batten, D.J., 1981. Stratigraphic, paleogeographic and evolutionary significance of Late Cretaceous and Early Tertiary normapollens pollen. *Review of Paleobotany and Palynology* 35, 125–137.
- Batten, D.J., 1996. Palynofacies and palaeoenvironmental interpretation, Chapter 26A. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications* 3. American Association of Stratigraphic Palynologists Foundation, Dallas, 1011–1164.
- Bercovici, A., Hadley, A., Villanueva-Amadoz, U., 2009. Improving depth of field resolution for palynological photomicrography. *Paleontologia Electronica*, PE Article Number: 12.2.5T, pp. 12.
- Berry, E.W., 1916. The Upper Cretaceous floras of the world. Maryland Geol. Survey. Upper Cretaceous, 183–311.
- Borović, I., Marinčić, S., Majcen, Ž., Magaš, N., 1977. Basic Geological Map of SFRY 1:100,000. Geology of the Vis, Jelsa, Biševo, Svetac and Jabuka sheets). Institut za geološka istraživanja, Zagreb (1972). Savezni geološki zavod, Beograd, 66 p. (in Croatian).

- Brattseva, G.M., Novodvorskaya, I.M., 1979. Palynological characteristics of the Lower Cretaceous deposits of the find-localities of Buylyasutuin-Khuduk and Anda-Khuduk, Bayan-Hongor Province, Mongolia. *Paleontologicheskaya Ekspeditsiya* 8, 98–99.
- Carannante, G., Ruberti, D., Sirna, M., 2000. Upper Cretaceous ramp limestones from the Sorrento Peninsula (southern Apennines, Italy): micro- and macrofossil associations and their significance in the depositional sequences. *Sedimentary Geology* 132, 89–123.
- Chlonova, A.F., Surova, T.D., 1988. Pollen wall ultrastructure of *Clavatipollenites incisus* Chlonova and two modern species of *Ascarina* (Chlorantaceae). *Pollen et Spores* 30, 29–44.
- Cookson, I.C., Dettmann, M.E., 1958. Some trilete spores from Upper Mesozoic deposits in the Eastern Australian region. *Proceedings of the Royal Society of Victoria* 70, 95–128.
- Cookson, I.C., Dettmann, M.E., 1961. Reappraisal of the Mesozoic microspore genus *Aequitriradites*. *Palaeontology* 4, 425–427.
- Couper, R.A., 1958. British Mesozoic microspores and pollen grains: a systematic and stratigraphic study. *Palaeontographica Abteilung B* 103, 75–179.
- Dalla Vecchia, F.M., 2003. Observations on the presence of plant-eating dinosaurs in an oceanic carbonate platform. *Natura Nascosta* 27, 14–27.
- Dettmann, M.E., 1986. Early Cretaceous palynoflora of subsurface strata correlative with the Koonwarra Fossil Bed, Victoria. *Mem. Association of Australasian Palaeontologists* 3, 79–110.
- Diedrich, C., Caldwell, M.W., Gingras, M., 2011. High-resolution stratigraphy and palaeoenvironments of the intertidal flats to lagoons of the Cenomanian (Upper Cretaceous) of Hvar Island, Croatia, on the Adriatic Carbonate Platform. *Carbonates Evaporites* 26, 381–399. DOI 10.1007/s13146-011-0073-2

- Dutchak, A.R., Caldwell, M.W., 2006. Redescription of *Aigialosaurus dalmaticus* Kramberger, 1892: a Cenomanian mosasauroid lizard from Hvar Island, Croatia. Canadian Journal of Earth Sciences 43(12), 1821–1834.
- Friis, E.M., Grimm, G.W., Mendes, M.M., Pedersen, K.R., 2015. *Canrightiopsis*, a new Early Cretaceous fossil with *Clavatipollenites*-type pollen bridge the gap between extinct *Canrightia* and extant Chloranthaceae. Grana 54, 184–212. DOI:10.1080/00173134.2015.1060750
- Gee, C.T., 2011. Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective. In: Klein, N., Remes, K., Gee, C.T., Sander, P.M. (Eds.), Biology of the Sauropod Dinosaurs: Understanding the Life of Giants. Indiana University Press, Bloomington, 34–56.
- Gorjanović-Kramberger, D., 1892. *Aigialosaurus*, novi gušter iz krednih škriljeva otoka Hvara s obzirom na opisane jur lacertide Komana i Hvara. Rad Jugoslavenske Akademije Znanosti i Umjetnosti 109, 96–123. (in Croatian)
- Gušić, I., Jelaska, V., 1990. Stratigrafija gornjokrednih naslaga otoka Brača u okviru geodinamske evolucije Jadranske karbonatne platforme (Upper Cretaceous stratigraphy of the island of Brač within the geodynamic evolution of the Adriatic-Dinaric carbonate platform). Djela Jugoslavenske Akademije Znanosti i Umjetnosti 69, 160 p.
- Hedlund, R.W., 1966. Palynology of the Red Branch Member of the Woodbine Formation (Cenomanian), Bryan County, Oklahoma. Bulletin of the Oklahoma Geological Survey 112, 1–69.
- Heimhofer, U., Hochuli, P.A., Burla, S., Weissert, H., 2007. New records of Early Cretaceous angiosperm pollen from Portuguese coastal deposits: Implications for the timing of the early angiosperm radiation. Review of Palaeobotany and Palynology 144, 39–76.

- Herak, M., Marinčić, S., Polšak, A., 1976. Geology of the Island of Hvar. *Acta Geologica, Prirodoslovna istraživanja*, 42, 5–14. (in Croatian, with English summary)
- Herngreen, G.F.W., Kedves, M., Rovnina, L.V., Smirnova, S.B., 1996. Cretaceous palynofloral provinces: a review. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications* volume 3. American Association of Stratigraphic Palynologists Foundation, Salt Lake City, 1157–1188.
- Hummel, J., Gee, C.T., Südekum, K.-H., Sander, M.P., Nogge, G., Clauss, M., 2008. *In vitro* digestibility of fern and gymnosperm foliage: implication for sauropod feeding ecology and diet selection. *Proceedings of the Royal Society B* 275, 1015–1021. doi:10.1098/rspb.2007.1728
- Jerinić, G., Jelaska, V., Alajbeg, A., 1994. Upper Cretaceous organic-rich laminated limestones of the Adriatic Carbonate Platform, Island of Hvar, Croatia. *AAPG Bulletin* 78/8, 1313–1321.
- Kemp, E.M., 1968. Probable angiosperm pollen from the British Barremian to Albian strata. *Palaeontology* 11, 421–434.
- Kerner, F., 1896. Kreidepflanzen von Lesina. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 45, 37–58.
- Lockley, M.G., Hunt, A.P., Meyer, C.A., 1994. Vertebrate tracks and the ichnofacies concept: implication for paleoecology and palichnostratigraphy. In: Donovan, S.J. (Ed.), *The Paleobiology of Trace Fossils*. Wiley and Sons, New York, pp. 241–268.
- Marinčić, S., 1997. Tectonic structure of the Island of Hvar, Southern Croatia. *Geologia Croatica* 50/1, 57–77.
- Marinčić, S., Majcen, Ž., 1968. Osnovna geološka karta SFRJ, list Jelsa, 1:100 000, K33-34 (Basic Geological map of SFRY: Sheet Jelsa K33-34). Institute of Geology/Head Geological Department, Zagreb/Beograd.

- Matičec, D., Vlahović, I., Velić, I., Tišljar, J. 1996. Eocene limestones overlying Lower Cretaceous deposits of western Istria (Croatia): did some parts of present Istria form land during the Cretaceous? *Geologia Croatica* 49, 117–127.
- May, F.E., Traverse, A., 1973. Palynology of the Dakota Sandstone (Middle Cretaceous) near Bryce Canyon National Park, southern Utah. *Geoscience and Man* 7, 57–64.
- Médus, J., Berthou, P.Y., 1980. Palynofloras from an Albian cutting, Foz do Folcao, (Portugal). *Geobios* 13, 263–269.
- Mezga, A., Meyer, C.A., Cvetko Tešović, B., Bajraktarević, Z., Gušić, I. 2006. The first record of dinosaurs in the Dalmatian part (Croatia) of the Adriatic-Dinaric carbonate platform (ADCP). *Cretaceous Research* 27, 735–742. doi:10.1016/j.cretres.2006.01.001
- Mohsen, S.A., 1987. Palynological studies of the Lower Esna Shale Formation (Cretaceous) in the Tushka Basin, Southern Egypt. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 6, 357–370.
- Pantić, N., 1962. Fosilni ostaci kopnenih biljaka u Jugoslaviji i njihova stratigrafska vrijednost. Referati 5. savjetovanja geologa FNRJ, 107–115, Beograd. (in Croatian)
- Pedersen, K.R., Crane, P.R., Drinnan, A.N., Friis, E.M., 1991. Fruits from the mid-Cretaceous of North America with pollen grains of the *Clavatipollenites* type. *Grant* 30, 577–590.
- Pierce, R.L., 1961. Lower Upper Cretaceous plant microfossils from Minnesota. *Minnesota Geological Survey Bulletin* 42, 1–86.
- Radoičić, R., 1960. On little known species *Thaumatoporella parvovesiculifera* (Rain.). *Vesnik, Geologija* A18, 133–139. (In Croatian, with English summary)
- Radovčić, J., 1973. O starosti i nalazima fosilnih riba u kredi Jadranskog pojasa. *Geološki Vjesnik* 25, 321–326. (in Croatian, with English abstract)

- Ravn, R.L., Witzke, B.J., 1995. The palynology of the Dakota Formation, (?Late Albian-Cenomanian) in its type area, northwestern Iowa and northeastern Nebraska, USA. *Palaeontographica Abteilung B* 234, 93–171.
- Reyre, Y., 1973. Palynologie du Mésozoïque saharien. *Mémoires du Muséum National d'Histoire Naturelle, nouvelle série, Série C, Sciences de la terre* 27, 284 p.
- Schlagintweit, F., Kołodziej, B., Qorri, A., 2015. Foraminiferan-calcimicrobial benthic communities from Upper Cretaceous shallow-water carbonates of Albania (Kruja Zone). *Cretaceous Research*, 56, 432–446.
<http://dx.doi.org/10.1016/j.cretres.2015.04.009>
- Schubert, R.J., 1909. *Geologija Dalmacije*. Matica Dalmatinska, Zadar, 181 p. (in Croatian)
- Singh, C., 1964. Microflora of the Lower Cretaceous Mannville Group, east-central Alberta. *Research Council of Alberta Bulletin* 15, 1–239.
- Solé de Porta, N., 1978. Palynology of two Cenomanian sections near Oviedo, Spain. *Palinologia, Núm. Extraord.* 1, 435–441.
- Tišljar, J., Vlahović, I., Velić, I., Sokač, B., 2002. Carbonate platform megafacies of the Jurassic and Cretaceous deposits of the Karst Dinarides. *Geologia Croatica* 55, 139–170.
- Tyson, R.V., 1995. *Sedimentary Organic Matter. Organic facies and palynofacies*. Chapman and Hall, London, 615 p.
- Vajda, V., Bercovici, A., 2014. The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: A template for other extinction events. *Global and Planetary Change* 122, 29–49. doi:10.1016/j.gloplacha.2014.07.014
- Vlahović, I., Tišljar, J., Velić, I., Matičec, D., 2005. Evolution of the Adriatic Carbonate Platform: palaeogeography, main events and depositional dynamics. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 333–360. doi:10.1016/j.palaeo.2005.01.011

Weyland, H., Krieger, W., 1953. Die Sporen und Pollen der Aachener Kreide und ihre Bedeutung für die charakterisierung des Mittleren Senons. *Palaeontographica Abteilung B* 95, 6–29.

Zaklinskaya, E.D., 1981. Phylogeny and classification of the Normapolles. *Review of Paleobotany and Palynology* 35, 139–147.

Figure captions

Fig. 1 A Geographic position and simplified geological map of the western part of the Island of Hvar and Island of Šćedro (modified after Marinčić and Majcen, 1968), with asterisk marking positions of the four studied localities: 1. Žukova cove in the northern part of the Island of Hvar (pollen samples CRO-01 and CRO-02), 2. Zavala area in southern part of Hvar (pollen sample CRO-03) 3. NE part of the Šćedro Island (pollen sample CRO-04), and 4. Vira cove in the western part of the Island of Hvar (pollen sample CRO-05). **B** Schematic lithostratigraphic column of the Upper Cretaceous deposits of the Adriatic Carbonate Platform, with box marking the approximate stratigraphic position of the studied deposits (modified after Jerinić et al., 1994) and lithostratigraphic units (thickness of entire shown sequence ~1000 m) by Gušić and Jelaska (1990).

Fig. 2 The locality Žukova cove, Island of Hvar, with the (A) track-bearing layer (from which the CRO-01 sample was studied), and (B) dinoturbated layer below (CRO-02 sample).

Fig. 3 Photomicrographs of the microfacies types and fossil assemblages: A. Microfacies 1: mudstones to wackestones with pelloids, fragments of green algae *Thaumatoporella parvovesiculifera* and rare ostracods; B. Microfacies 2: thin bedded laminae with rare *Thaumatoporella* fragments; C. Microfacies 3: wackestones to packstones with common

Thaumatoporella parvovesiculifera and miliolid foraminifera; D, E *Thaumatoporella parvovesiculifera* (Raineri).

Fig. 4 Ternary plot for palynofacies composition and corresponding paleoenvironmental interpretation (after Tyson, 1995) with position of the studied samples CRO-01, CRO-02, CRO-03 and CRO-04.

Fig. 5 Extended depth of field light micrographs of a selection of representative palynomorphs. Numbers in brackets corresponds to samples and England Finder position on slide. Scale bar = 20 µm. 1: *Densoisporites* sp. [CRO-01a_O26-4]; 2: *Aequitriradites spinulosus* (Cookson & Dettmann 1958) Cookson & Dettmann 1961 [CRO-01a_R31-1]; 3: *Todisporites* sp. [CRO-02_G39-1]; 4: *Todisporites* sp. [CRO-02_U44-1]; 5: Trilete spore [CRO-01b_K13-3]; 6: *Cycadopites* sp. [CRO-02_X43-1]; 7: *Cedripites* sp. [CRO-01b_Q46-1]; 8: *Abiespollenites* sp. [CRO-02_H28-2]; 9: *Pityosporites* sp. [CRO-01a_G41-3]; 10: *Podocarpites* sp. [CRO-02_M17-2]; 11: *Araucariacites* sp. [CRO-01b_H18-3]; 12: *Araucariacites* sp. [CRO-02_W30-2]; 13: *Palmaepollenites minusculus* Hedlund 1966 [CRO-02_L21-1]; 14: *Clavatipollenites* sp. [CRO-02_L21-1]; 15: *Clavatipollenites* sp. [CRO-02_K32-2]; 16: *Clavatipollenites rotundus* Kemp 1968 [CRO-02_U31-1]; 17: *Clavatipollenites hughesii* Couper 1958 [CRO-02_P46-4]; 18: *Retitricolpites* sp. [CRO-02_L41-3]; 19: *Bacutricolpites constrictus* Pierce 1961 [CRO-02_E40-3]; 20: *Bacutricolpites constrictus* Pierce 1961 [CRO-02_N43-4]; 21: *Bacutricolpites constrictus* Pierce 1961 [CRO-02_M18-1]; 22: *Ericaceoipollenites* sp. [CRO-01a_P36-4]; 23: *Ericaceoipollenites* sp. [CRO-01a_Q29-4]; 24: *Plicapollis* sp. [CRO-02_K18-3]; 25: *Plicapollis* sp.; 26: *Pseudoculopollis* sp. [CRO-02_H18-2]; 27: Zygosporangium of Zygnemataceae (fresh water green algae) [CRO-02_J32-4].

Table 1. Relative abundance counts for palynofacies composition of the palynological samples (raw count number in bold, percentage in parenthesis). Palynomaceral categories are defined after Batten (1996).

Table 2. Palynomorph relative abundance counts (raw count number in bold, percentage in parenthesis). A total of two entire slides were scanned for sample CRO-01 and one entire slide for sample CRO-02.

A

massive limestones

pelagic limestones

laminated micritic limestones

platy limestones

laminites

RUDISTS

RUDIST FRAGMENTS

FISH

FORAMINIFERA

CALCISPHERES

B

- I, Highly proximal shelf or basin
- II, Marginal dysoxic-anoxic basin
- III, Heterolithic oxic shelf (proximal shelf)
- IVa and b, Shelf to basin transition
- V, Mud dominated oxic shelf (distal shelf)
- VI, Proximal suboxic-anoxic shelf
- VII, Distal dysoxic-anoxic shelf
- VIII, Distal dysoxic-oxic shelf
- IX, Proximal suboxic-anoxic basin

Palynomaceral	CRO-01 Hvar Žukova	CRO-02 Hvar Žukova	CRO-03 Hvar Zavala	CRO-04 Šćedro	CRO-05 Hvar Vira
I: Palynomorphs					
All	9 (1.8%)	48 (9.6%)	9 (1.8%)	17 (3.4%)	-
II: SOM					
Black wood	1 (0.2%)	3 (0.6%)	222 (44.4%)	5 (1.0%)	-
Brown wood	1 (0.2%)	3 (0.6%)	5 (1.0%)	2 (0.4%)	-
Charcoal	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	-
Cuticles	400 (80.0%)	387 (77.4%)	9 (1.8%)	283 (56.6%)	-
Phytoclasts	37 (7.4%)	20 (4.0%)	166 (33.2%)	124 (24.8%)	-
III: USTOM					
Amorphous	52 (10.4%)	39 (7.8%)	89 (17.8%)	69 (13.8%)	-
Total:	500	500	500	500	Barren

Taxa	CRO-01 (2 slides)	CRO-02 (1 slide)
Bryophytes		
<i>Aequitriradites spinulosus</i>	1 (2.2%)	0 (0.0%)
<i>Densosporites</i> sp.	1 (2.2%)	0 (0.0%)
Ferns		
<i>Todisporites</i> sp.	0 (0.0%)	11 (6.5%)
Trilete spore	1 (2.2%)	1 (0.6%)
Gymnosperms		
<i>Abiespollenites</i> sp.	2 (4.3%)	5 (3.0%)
<i>Araucariacites</i> sp.	1 (2.2%)	2 (4.1%)
<i>Cedripites</i> sp.	1 (2.2%)	7 (4.1%)
<i>Cycadopites</i> sp.	0 (0.0%)	1 (0.6%)
<i>Pityosporites</i> sp.	8 (17.4%)	67 (39.6%)
<i>Podocarpites</i> sp.	0 (0.0%)	2 (1.2%)
Angiosperms		
<i>Bacutricolpites constrictus</i>	12 (26.1%)	32 (18.9%)
<i>Clavatipollenites</i> sp.	5 (10.9%)	18 (10.7%)
<i>Ericaceoipollenites</i> sp.	2 (4.3%)	2 (1.2%)
<i>Palmaepollenites minusculus</i>	3 (6.5%)	1 (0.6%)
<i>Plicapollis</i> sp.	7 (15.2%)	15 (8.9%)
<i>Pseudoculopollis</i> sp.	0 (0.0%)	1 (0.6%)
<i>Retitricolpites</i> sp.	1 (2.2%)	2 (1.2%)
Others		
Algae	0 (0.0%)	1 (0.6%)
Fungal spore	1 (2.2%)	1 (0.6%)
Total:	46	169