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New Cenomanian florule and a leaf mine from southeastern Morocco: Palaeoecological and climatological inferences

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ABSTRACT

The recently found Gara Sbaa florule of southeastern Morocco comes from distinctive carbonate lamellites with abundant fish fauna above the terrestrial/paralic Kem Kem sequence and correlated with the basal horizon of the open shelf carbonate Akrabou Formation. It is a "mixed" assemblage of ferns and gymnosperms of "Wealden aspect" associated with relatively advanced angiosperms, suggesting floristic exchanges between the insular land masses of northern Africa and southern Europe. The climatic conditions are inferred to have been similar to the mildly dry subtropical climate of the western Canary Islands. New taxa of aquatic angiosperms *Garasbahia fexuosa* Krassilov et Bacchia gen. et sp nov. and a leaf mine *Troponoma constricta* Krassilov, sp. nov. are described.

1. Introduction

This paper reports on fossil plants from the Gara Sbaa locality of the Kem Kem region, southeastern Morocco, recently described as a new "Plattenkalk Konservat Lagerstätte" mainly owing to preservation of soft tissues in fish remains impressed on the dolomitic limestone lamellae (Martill et al., 2011). In these paralic deposits, plant remains constitute a minor part of the fossil material, but they characterize the source of terrestrial material and are important for understanding of both sedimentary environment and taphonomic processes.

The mid-Cretaceous floras of northern Africa and Middle East are diverse plant assemblages documenting successive stages of floristic evolution, but with large gaps in the sequence and uncertainties in stratigraphic correlation. A new plant assemblage from the Gara Sbaa Konservat Lagerstätte may seem too poor for definite palaeofloristic and palaeoecological conclusions, yet it presents some points of interest regarding the age of fossiliferous strata, phytogeography, climate and advancement of the early angiosperms.

Although it is currently taken for granted that the African landmass was situated much to the south of its present day position, steadily drifting to the east relative to a fixed Europe, while climate was tropical through the mid-Cretaceous (e.g., Cuvin et al., 2010), these are in fact assumptions that are drastically in need of verification (or falsification), and no piece of evidence should be neglected.

2. Material and methods

The material was collected by Flavio Bacchia at Gara Sbaa (transliterated also as Gara Sba or Gara Sbah), a flat-topped hill (mesa) on the northern side of the Kem Kem Plateau about 25 km northeast of the village of Tafraoute in southeastern Morocco (Fig. 1). Finely laminated fossiliferous limestones about 5 m thick crop out at the top of the hill (30° 30′ 28.40″ N, 4° 50′ 33.94″W). The fossils, mostly fish, but also plants, crustaceans and rare reptiles and birds, are restricted to a few lamellae that are intensively dug out by professional collectors and local people. In comparison with contemporaneous localities elsewhere in southern Morocco reviewed in Cuvin et al. (2010), the floristic remains are scanty and small, the largest dimension rarely being more than 5 cm.

We have at our disposal 17 slabs with plant fossils. These are presently located in the palaeobotanical collection of the Institute of Evolution, University of Haifa, nos. NTA 1–17. Several specimens, including a shoot with *Pseudotorellia* foliage, were donated to Professor Giacomo Tripodi, Palermo University, who courteously provided us with photographs of the material. The plant fossils are complete or more often fragmentary leaves and occasional leafy shoots sparsely scattered over the limestone lamellae and never

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Fig. 1. The Gara Sbaa Hill locality, southeastern Morocco (30° 30′28,40″ N, 4° 50′33.94″W).

forming mat-like accumulations. They are preserved as yellowish brown ferruginous impressions spotted with black manganese, which precludes the use of dissecting or scanning microscopy. Morphological details were studied under the stereomicroscope and the photographs were taken with a Leica 300 camera.

3. Stratigraphic correlation

In the North Sahara region, the mid-Cretaceous sequence is divided into the Ifezouane, Aoufous, and Akrabou formations, comprising predominantly terrestrial red beds, a paralic sequence of variegate mudstones and marls, and open shelf carbonates, respectively (Ettachfini and Andreu, 2004). On the northern slope of the Kem Kem Plateau, the Ifezouane and Aoufous deposits are poorly differentiated, constituting the continuous Kem Kem sequence (Sereno et al., 1996). In the absence of standard biostratigraphic markers, age assignments are based on faunistic comparisons involving fish and terrestrial vertebrate faunas. As reviewed in Cuvin et al. (2010), the Kem Kem vertebrate assemblages are most similar to, and probably coeval with, the Early Cenomanian Bahariya assemblage of southwestern Egypt (stratigraphic documentation reviewed in Catuneanu et al., 2006), but older than the late Middle Cenomanian Nammoura assemblage of northern Lebanon.

The open shelf carbonates of the Akrabou Formation are at several places conformable on the paralic upper Kem Kem deposits, whereas their stratigraphic equivalent in Egypt, the Ein Heiz Formation, is described as unconformable on the Bahariya Formation. The patchily distributed marginal marine deposits of intermediate Kem Kem/Akrabou aspect containing highly endemic vertebrate assemblages are described as the OT1, Daoura, Agoult, and Gara Sbaa beds (Cuvin et al., 2010) of uncertain position in the regional chronostratigraphic scale. Critical for stratigraphic correlation of these deposits is the so-called "*Neolobites* bioevent" marking the onset of widespread Late Cenomanian–Turonian transgression. *Neolobites vibrayeanus* has been reported recently from below the Gara Sbaa beds (Cuvin et al., 2010), giving weight to their correlation with the basal Akrabou Formation. Their supposed lateral equivalents in the Goulmima region are marine carbonates with Late Cenomanian foraminifera, which enabled Martill et al. (2011) to infer an influence of the Cenomanian/Turonian anoxic event on deposition of the Gara Sbaa lamellites.

4. Floristic assemblage

The Gara Sbaa assemblage consists of eight species representing pteridophytes, gymnosperms and angiosperms. All species are morphologically well defined and belong to different genera, yet most of them are the single specimen records, which make species level assignments problematic.

4.1. Pteridophytes

Four specimens of detached pinnae in our collection and a bipinnate fragment depicted in Martill et al. (2011) are readily recognizable as *Coniopteris*-type sterile foliage, which is ubiquitous in Jurassic and Early Cretaceous deposits of Eurasia. It is far less common in the Late Cretaceous. The Moroccan species has linear pinnae with catadromous, shallowly incised, proximal pinnules and entire distal pinnules (Fig. 2A), resembling the Late Cretaceous

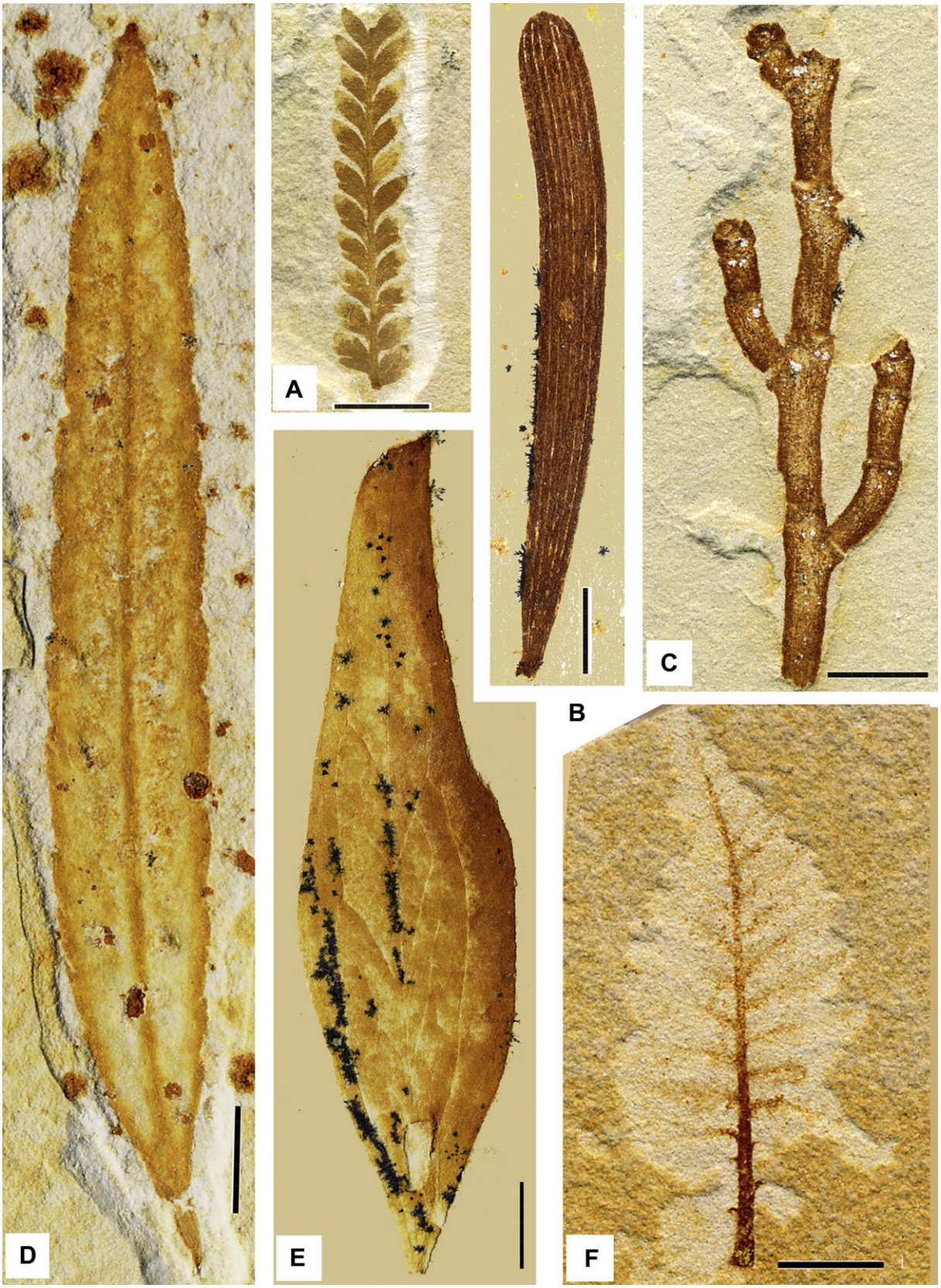

Fig. 2. The Gara Sbaa fossil plant assemblage. A, *Coniopteris* cf. *Dicksonia mamiyai* Kryshtofovich. B, *Pseudotorellia* cf ensiformis (Heer) Florin. C. *Frenelopsis* cf. *teixeirae* Alvin et Pace. D, *Dryophyllum* cf. *subcretaceum* Debey ex Saporta. E, *Cocculophyllum* cf. *furcinerve* Krassilov. F, *Barykovia* cf. *tschukotica* (Abramova) Moiseeva. Scale bars represent 5 mm.

Dicksonia (*Coniopteris*) *mamiyai* Kryshtofovich. The sterile leaf morphology is similar to *Cibotium* and *Culcita*, as well as *Davallia* having anadromous asymmetric pinnules that are broader and more deeply dissected acroscopically. However, the spore-bearing structures with bivalved indusia of the marginal sori indicate affinities with extant *Dicksonia* (Krassilov, 1978, 1979).

4.2. Gymnosperms

Of three gymnospermous genera, *Pseudotorellia* is numerically most prominent, being represented by a leafy shoot and detached leaves (Figs. 2B, 3A, B). The shoot axis is similar to *Sulcatocladus robustus* Watson et Harrison from the English Wealden (Watson et al., 2001), no doubt representing the same or closely allied species. The better preserved leaves are practically identical to *Pseudotorellia ensiformis* (Heer) Florin.

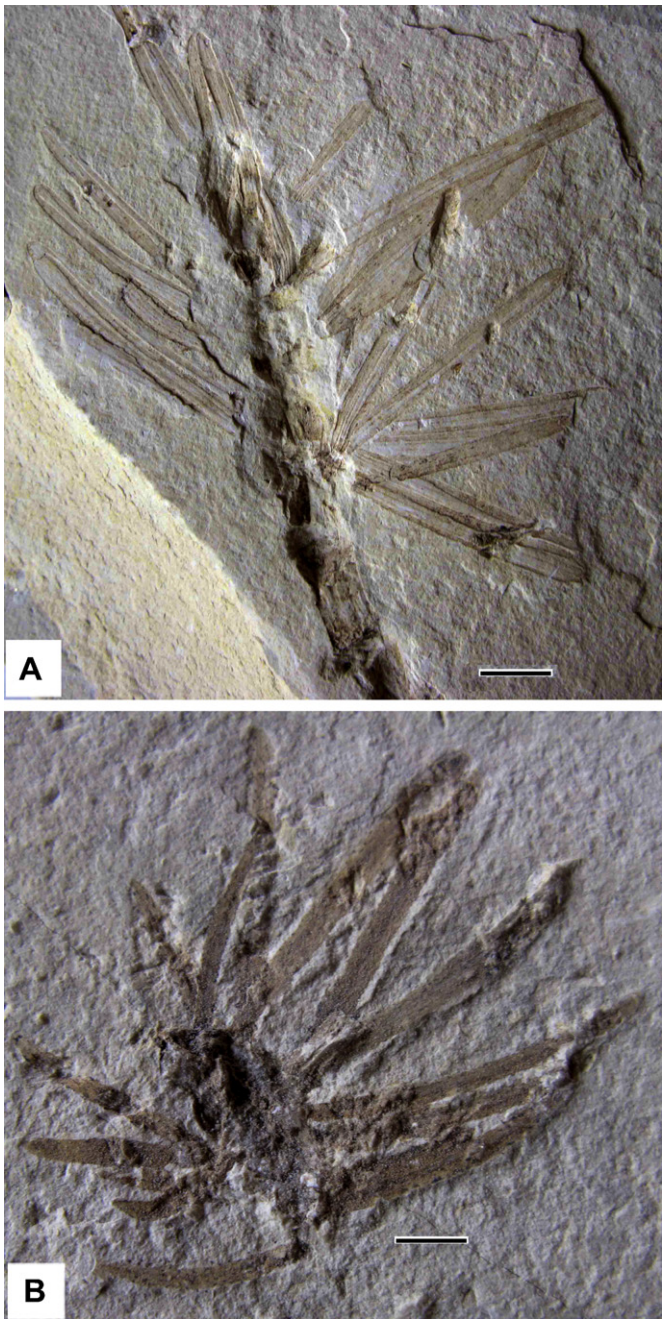

Fig. 3. The Gara Sbaa fossil plant assemblage. A, *Sulcatocladus* cf. *robustus* Watson et Harrison, bearing *Pseudotorellia*-type leaves. B, shoot fragment with spreading needle leaves of *Abietites* (*Tritaenia*) *linkii* type. Scale bars represent 5 mm in A, 2 mm in B.

Previously assigned to the Pseudotorelliaceae, an extinct family of ginkgoalean affinity (Krassilov, 1969), *Pseudotorellia* is presently controversial because of its arbitrary distinction from the leaf genera of the Miroviaceae, a morphological group of gymnosperms assigned to ginkgoaleans or conifers. A shoot fragment with radially spreading linear leaves (Fig. 3B) is comparable with *Tritaenia* (*Abietites*) *linkii* (Römer) Mägdefrau in Rudolf, a Wealden species related to this group (Mägdefrau in Rudolf, 1969; Wilde, 1991), but assigned to *Pseudotorellia* by Watson et al. (2001). The miroviaceous needle-leaf morphotypes are phyllodic or bilaterally compressed, as in *Sciatopityoides* and *Paracmopyle*, with the median groove corresponding to leaf margin rather than midrib. Without going deeper into the confused taxonomic problem of "miroviaceous conifers", which probably include foliar remains of mixed taxonomic affinities, we assert the presence of this hitherto unrecorded morphological group in the Cenomanian of Morocco.

Frenelopsis cf. *teixeirae* Alvin et Pais is a distinctive morphotype of articulated shoots with decurrent phyllodic leaves. The Gara Sbaa representative (Fig. 2C) has them in opposite pairs on two orders of branches as in *F. teixeirae* (Alvin and Pais, 1978), in which this character was recently found to be inconstant (Mendes et al. 2010), and probably in *F. silfoana* Watson from the Jebel Dirra, Eastern Darfur, Sudan (Watson, 1983), where it was said to be mixed with, and sometimes indistinguishable from, *Pseudofrenelopsis parceramosa*. *Frenelopsis alata* (Feistmantel) Knobloch from the Middle Cenomanian of Bohemia is similar in general aspect, although more typically having leaves in three-member whorls (Kvaček, 2000).

4.3. Angiosperms

In the Gara Sbaa assemblage, angiosperms are the most diverse, but numerically subordinate group, mostly represented by one-specimen records of complete or fragmentary leaves assigned to four morphological genera.

Cocculophyllum cf. *furcinerve* Krassilov designates two specimens of small, narrow, ovate, entire-margined leaves with acrodromous primary laterals that depart at slightly different levels and are joined by transverse laterals that are sparse and fork irregularly (Figs. 2E, 5A). *Cocculophyllum* from the Cenomanian and Senonian of Bohemia comprises larger leaves (Němejc and Kvaček, 1975) as well as a similar species from the Senonian of Sakhalin (Krassilov, 1979). It is comparable with climber leaves of not only *Cocculus* but also *Smilax*, which does not imply taxonomic affinities. A noteworthy feature of the Gara Sbba species is the composite appearance of the acrodromous laterals that are formed by coherence of the distally up-curved secondary laterals. This feature is also observed in *Acaciaephyllum* from the Albian of the Negev (Silantieva and Krassilov, 2006a), prompting a comparison with gnetaleans climbers that have scarcely been pursued so far.

Dryophyllum cf. *subcretaceum* Debey ex Saporta (Fig. 2D) is a small-leafed representative of a genus that first appeared in the Cenomanian and became a dominant element of subtropical European and North American floras through the Late Cretaceous and Paleogene. Its affinities are sought with the Fagaceae or Juglandaceae (Jones et al., 1988), although similar leaf morphotypes convergently occur in taxonomically unrelated Mediterranean genera.

Barykovia is another type of small lobed to crenulate, quercoid leaves with parallel craspedodromous secondaries running into the lobes (Fig. 2F), similar to *B.* ("*Quercus*") *tschukotica* (Abramova) Moiseeva and a precursor of the group that is dominant in

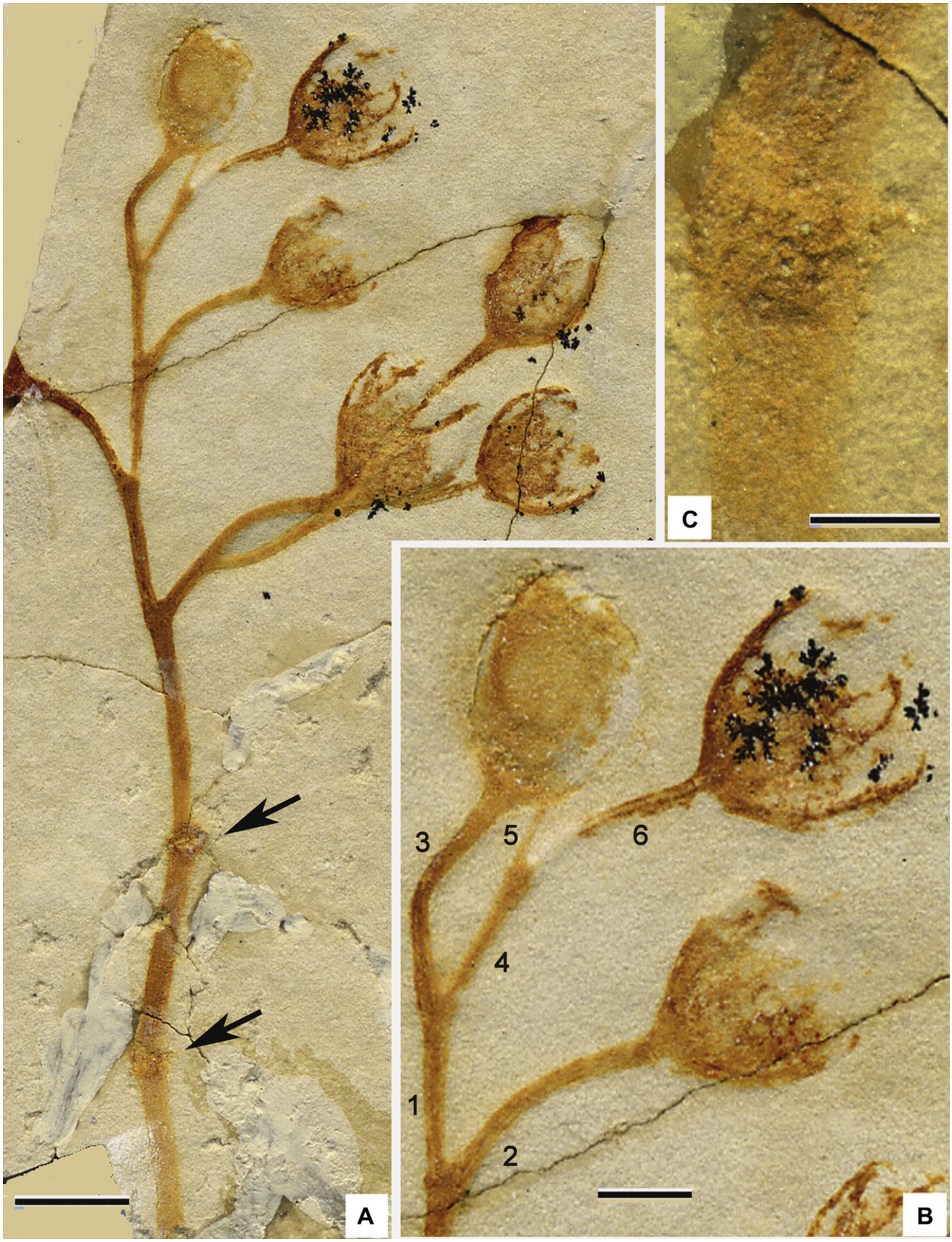

Fig. 4. The Gara Sbaa fossil plant assemblage: aquatic angiosperm *Garasbahia flexuosa* gen. et sp. nov. (Cabombaceae), holotype no. NAT-9, Paleobotanical Depository, Institute of Evolution, University of Haifa. A, branching shoot with peltate leaves; arrow indicates basal node with root scars. B, terminal sympodium; numbers indicate order of branching. C, basal node with root scars. Scale bars represent 5 mm in A, 2.5 mm in B, 1 mm in C.

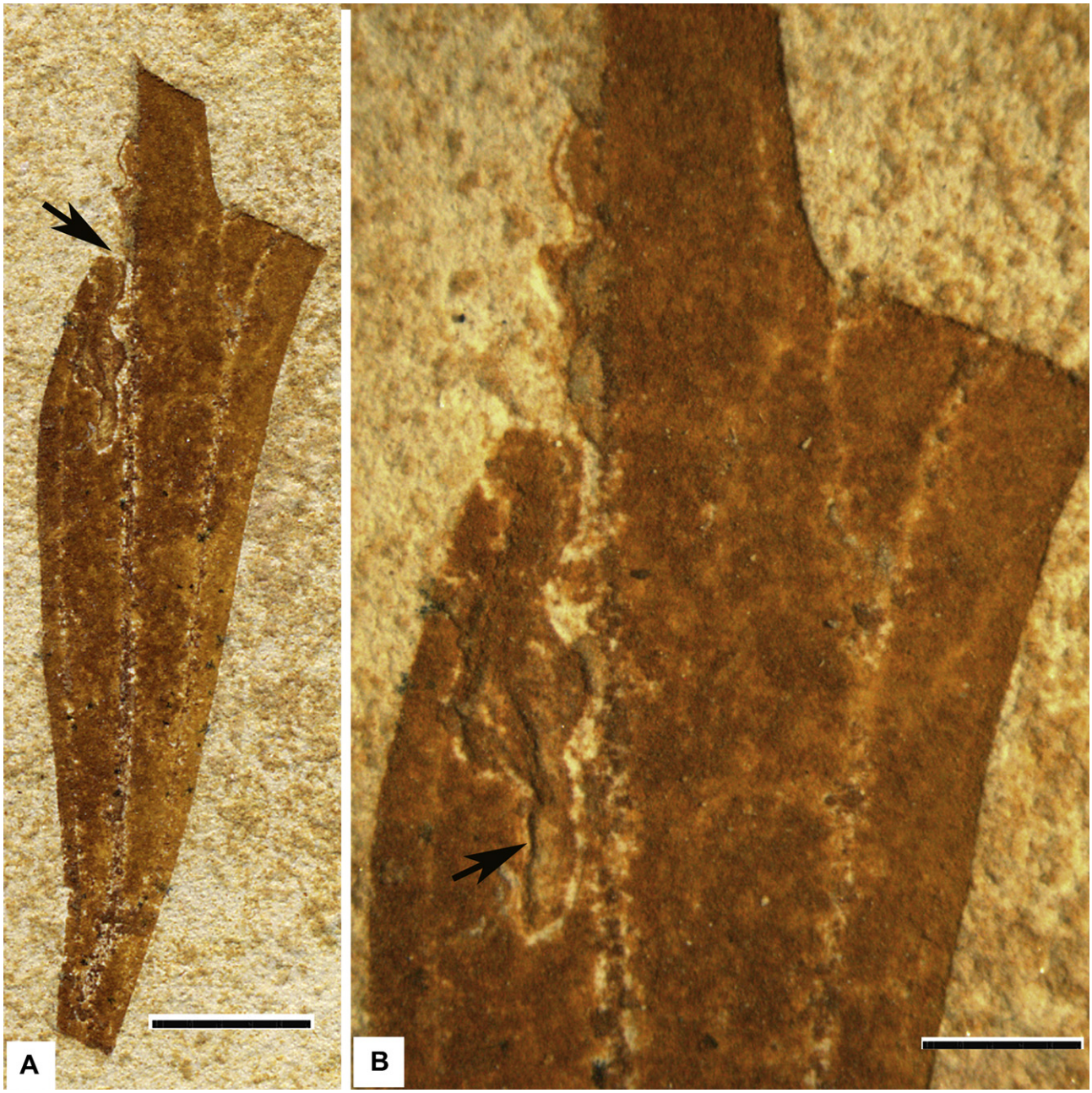

Fig. 5. *Troponoma constricta* sp. nov., insect mine from the Gara Sbaa fossil plant assemblage. A, position of the mine on *Cocculophyllum* leaf. B, mine track showing a continuous frass line and distinct frass pellets before the opening. Scale bars represent 5 mm in A, 2 mm in B.

northeastern Asia during the Campanian thermal maximum (Moiseeva, 2012).

Aquatic angiosperms occur in all the mid-Cretaceous floristic assemblages of northern Africa and Middle East and are fairly diverse, testifying to widespread eutrophic lacustrine habitats as well as to the high rate of evolution of macrophytes with floating leaves. The Gara Sbba representative is distinctive enough to be described as a new morphogenus.

5. Taxonomic description of a new angiosperm genus and species

Garasbahia Krassilov et Bacchia, gen. nov.

Derivation of name. After the locality Gara Sbah, a correct transliteration for "Gara Sbaa".

Type species. *Garasbahia flexuosa* Krassilov et Bacchia sp. nov.

Type locality and horizon. Gara Sbaa Hill, southeastern Morocco (30° 30′ 28.40″ N, 4° 50′ 33.94″W); Gara Sbaa beds, laminated limestones at the top of the Kem Kem sequence, Cenomanian.

Species content. Monotypic.

Diagnosis. Stem slender, elongate, proximally rhizomatous with adventitious roots clustered at the lower nodes, somewhat flexuous, changing direction at slightly expanded nodes. Branches distichous alternate or (distal) turned to one side, departing at upward-decreasing distances along the stem, flexuous. Branching system irregular sympodial, the distal arms appearing as leaf petioles or terete. One arm of an apical fork continuous with the stem. Leaf blades small, peltate, broadly elliptical to orbicular,

entire, with the central part thickened as a pad. Venation acrodromous with cross veins.

Garasbahia flexuosa Krassilov et Bacchia sp. nov.
Fig. 4A–C

Derivation of name. L, *flexuosa*, flexible.

Holotype. Paleobotanical Depository, Institute of Evolution, University of Haifa, No. NAT-9 (Fig. 4A–C) designated here.

Diagnosis. As for the genus.

Remarks. Interpretation of stem morphology in *Garasbachia* is somewhat ambiguous as is often the case in aquatic angiosperms. The leafy axis is not clearly delimited from the rhizome with minute root scars discernible at the nodes (Fig. 4C). The branching is sympodial, but irregular, the lower right-hand branch of three consecutive forking points producing three leaf-bearing arms (petioles) and one terete arm. The next two branches are simple on both sides, and the apical ramification is obviously sympodial of two branching points producing one leaf in the terminal position and another on the stronger arm of the right side branch (in Fig. 4A the arms are numbered according to their branching order).

The veins protrude beyond the leaf blade at places where the mesophyll had decayed, appearing as lobes of a floral cup, but this feature is preservational.

In aquatic plants with floating leaves, sympodial branching is characteristic of *Cabomba* (Williamson and Schneider, 1993), to which our new genus seems to be allied at family level. The Late Cretaceous leaf genus *Brasipelta* Krassilov from the Turonian of Israel (Krassilov et al., 2005) and a synonymous leaf genus *Brasinites* Wang et Dilcher from the Cenomanian of Dakota, USA (Wang and Dilcher, 2006) and Bohemia, Czech Republic (Herman and Kvaček, 2010) have orbicular leaves with a radial vein pattern. Peltate floating leaves of *Limnobium* (Hydracharitaceae) and *Limnocharis* (Limnocharitaceae) are similar, but stipulate, developing on unbranched stems (Krassilov, 1976; Kvaček, 1995; Cook, 1998).

Because leave production on branching shoots (rather than leaf shape) is critical for recognition of the Cabombaceae, this seems to be the earliest reliable record of this phylogenetically important nymphaealean family.

6. Taxonomic description of leaf mine

A looping mine on *Cocculophyllum* is evidence of endoparasitic insect life on Cenomanian Gara Sbaa angiosperm leaves. Previously a mine track of a simpler configuration was found on *Pseudotorellia* from the Nammoura assemblage (Krassilov and Bacchia, 2000).

A classification of mine tracks developed by Krassilov (in Krassilov and Rasnitsyn, 2008) for the Turonian plant–arthropod assemblage of Arava, southern Israel, refers to the diversity of mining habits (rather than taxonomy of the miners) and includes several types of linear mines (ophionomes), the most diverse of which are troponomes, looping mines that cross their own track.

The idea behind this classification is that formal descriptions would help in accumulating and systemizing fossil evidence of co-evolution in leaf parasitic systems through geological time. In particular, troponomes represent a near-extinct mining type that seems to have been much more widespread during the Cretaceous. Our material from Gara Sbaa is the earliest troponome that has been recorded so far.

Troponoma Krassilov

Type species. *Troponoma crucitracta* Krassilov and Rasnitsyn (2008), p. 101, pl. 34, fig. 3; Late Cretaceous (Middle Turonian), Arava, Israel.

Troponoma constricta Krassilov sp. nov.
Fig. 5A, B

Derivation of name. L, *constrictum*, compressed or constricted.

Holotype: Plant Depository of the Institute of Evolution, University of Haifa, Israel, No. NAT-2 (Fig. 5A, B) designated here.

Type locality and horizon. On *Cocculophyllum* cf. *furcinerve* Krassilov from Gara Sbaa, southeastern Morocco (30° 30′ 28.40″ N, 4° 50′ 33.94″W); Gara Sbaa beds, laminated limestones at the top of the Kem Kem Sequence, Cenomanian.

Diagnosis: Mine track with a sinuous segment tracing arches of minor veins on the outside of a primary acrodromous vein, forming a narrow loop between the primary and intramarginal veins and terminating in an opening (exit hole?) at intersection with the older part of the mine. Frass in continuous median line, divided into elongate pellets before the opening.

Comments: Resembles *Troponoma curvitracta* Krassilov on *Dewalquea gerofiitca* from the mid-Turonian of Arava, southern Israel, which differs in the orientation of the mine track across lateral veins.

7. Discussion

A series of well dated Aptian–Turonian floras in Israel and Lebanon (Krassilov and Bacchia, 2000; Krassilov et al., 2005; Silantieva and Krassilov, 2006a, b; Krassilov and Schrank, 2011) testifies to a high rate of regional floristic evolution and evolutionary advancement of angiosperms correlated with climate change. Rich Middle/Late Albian floras of the Negev Desert are confined to an interval of fluvial to paralic deposition between the *Knemiceras* beds marking a brief transgressive episode, and the open shelf carbonates with diverse marine fauna. The flora is dominated by ferns and gymnosperms. Angiosperm contribution is strongly affected by sedimentary facies, being rather modest in the *Weichselia* pre-mangrove assemblage, but increasing in the mesic, conifer-dominated assemblages (Krassilov and Schrank, 2011). In addition to remarkable conifer diversity, the broad-leafed platanoid angiosperms indicate a relatively humid phase of climatic evolution in the region.

The late Middle Cenomanian Nammoura flora of Lebanon, dated on the basis of a foraminiferal zonation (Dalla Vecchia et al., 2002), consists of ferns, *Pseudotorellia* and diverse terrestrial as well as aquatic angiosperms. The xeromorphism of angiosperm morphologies indicates a dry phase of mid-Cretaceous climatic evolution.

The mid-Turonian flora of Gerofit, Arava Rift Valley, southern Negev is a diverse angiosperm assemblage with a wide range of ecological provenance, from mangroves and freshwater macrophytes to broadleaf forests, testifying to the recovery of mesic subtropical vegetation after the xeric Cenomanian phase. The regional floristic changes through the mid-Cretaceous climatic cycle are interpreted as shifts of a latitudinal boundary between xeric and mesic subtropical vegetation zones that alternately expanded and contracted over the region.

The Early Cenomanian stage of floristic evolution is poorly known in the Negev, being much better represented by the Bahariya flora of western Egypt and stratigraphic equivalents that retained *Weichselia* as a wetland dominant, but it exceeded Albian floras in diversity and abundance of laurophyllous angiosperms (Lejal-Nicol and Dominik, 1990).

The Gara Sbaa florule of southeastern Morocco is closer to the Nammoura than the Bahariya assemblage in lacking *Weichselia* but

sharing *Pseudotorellia* as their most prominent gymnosperm component, The ecological aspect of small serrate angiosperm leaves or leaflets is compatible with that of Nammoura, although taxonomically different. The age difference scarcely exceeded one ammonite zone of the *Glycoceras jukesbrownei–Glycoceras querangeri* sequence over the Middle/Late Cenomanian boundary. Yet such "Wealden-type" elements of the Gara Sbaa assemblage as *Sulcatocladus* cf. *robustus* and *Frenelopsis* cf. *teixeirae*, lacking in Nammoura, may suggest a slightly older stage of floristic evolution (here and elsewhere in the paper, "Wealden" refers to the classical Wealden flora of southern England and immediately adjacent successions in northern Europe, e.g., Batten, 2011). There is no evidence in favour of a younger Cenomanian/Turonian age of the Gara Sbaa laminites as advocated by Martill et al. (2011).

Floristic exchanges with landmasses situated north of the Tethys have been inferred for the Nammoura assemblage (Krassilov and Bacchia, 2000), yet Gara Sbaa is peculiar among the coeval floras of northern Africa and the Middle East in the Eurasian affinities of virtually all of its taxonomic components apart from a solitary aquatic species probably representing an endemic element. It may be reasoned that this florule is not representative enough for broad phytogeographic comparisons, but it does not seem realistic that an enigmatic selection factor has promoted preservation of Eurasian species in preference of Gondwanan or endemic elements. This florule composition is not compatible with the idea of Africa being separated from Europe by vast seaways, but complies with insular land masses of northern Africa and southern Europe being close to each other, possibly forming mixed archipelagos, so that floristic exchanges between them or lack of such might have depended on intricacies of wind and sea currents providing close similarities in some cases, while enhancing endemism or Gondwanan influence in others.

Regarding an insignificant terrestrial input in the Gara Sbaa fossil-bearing limestones on the one hand and the fragmentation of plant remains on the other, a high-tide ebb or tsunami backwash can be inferred as the main source of terrestrial and freshwater plant material collected over the tidal flat and, in the case of a tsunami, as far as 1 km inland (Dawson and Shi, 2000).

In looking for a modern ecological equivalent of the Gara Sbaa vegetation, it is important to note that tree fern and needle-leaved gymnosperm prominence in association with serrated angiosperm microphylls is by no means trivial for present-day plant cover. It occurs in very few places, the closest of which are the Canary Islands, with *Culcita macrocarpa*, *Dracaena drago* and *Quercus canariensis* standing in, respectively, for the Gara Sbaa *Coniopteris*, *Sulcicaulis* and *Dryophyllum*. The subtropical, mildly seasonal climate of the islands with aridity markedly increasing to the east results from a unique combination of many factors, such as the Canary current, the proximity of Azores High and the direct influence of Trade winds, but this type climate might have been more widespread during the Cenomanian transgressions.

8. Conclusion

The Gara Sbaa florule of southeastern Morocco is a "mixed" assemblage of "Wealden-type" ferns and gymnosperms and relatively advanced angiosperms. Scattered over the limestone lamellae and size sorted, the plant debris might have been transported by a high-tide ebb or tsunami backwash from over the tidal flat and adjacent dry land.

The age range of the Gara Sbaa limestones is late Middle–early Late Cenomanian based on stratigraphic correlation. The florule is similar to the latest Middle Cenomanian Nammoura assemblage of northern Lebanon on account of *Pseudotorellia* and the xeromorphic aspect of small serrate angiosperm leaves or leaflets, but differs in the numerically more prominent fern–gymnosperm component, including *Coniopteris*, *Sulcatocladus robustus*, *Pseudotorellia* (*Tritaenia*) *linkii*, and *Frenelopsis* cf. *teixierae*, giving it a somewhat more archaic aspect.

Taxonomically, the Gara Sbaa assemblage is of Eurasian affinity, the only exception being a new taxon of aquatic angiosperms. Floristic exchanges responsible for such phytogeographic affinities indicate the proximity of insular land masses of northern Africa and southern Europe.

The nearest ecological equivalent of the Gara Sbaa plant assemblage with tree ferns, needle-leaved gymnosperms, and microphyllous angiosperms is vegetation of the western Canary Islands, suggesting similar climatic conditions.

The new taxa are *Garasbahia fexuosa* Krassilov et Bacchia, an early representative of a phylogenetically important family Cabombaceae, the Nymphaeales, and the mine track classified as a new species *Troponoma constricta* Krassilov of a form-genus prominent in the Turonian leaf mine assemblage.

References

Alvin, K.L., Pais, J.J.C., 1978. A *Frenelopsis* with opposite decussate leaves from the Lower Cretaceous of Portugal. Palaeontology 21, 873–879.

Batten, D.J. (Ed.), 2011. English Wealden Fossils. Field Guides to Fossils 14. Palaeontological Association, London, ix + 769 pp.

Catuneanu, O., Khalifa, M.A., Wanas, H.A., 2006. Sequence stratigraphy of the Lower Cenomanian Bahariya Formation, Bahariya Oasis, Western Desert, Egypt. Sedimentary Geology 190, 121–137.

Cook, C.D.K., 1998. Hydrocharitaceae. In: Kubitzki, K. (Ed.), The Families and Genera of Vascular Plants. Flowering Plants, Monocotyledons, vol. 4. Springer, Berlin, pp. 234–248.

Cuvin, L., Tong, H., Boudad, L., Meister, C., Piuz, A., Tabouelle, J., Aarab, M., Amiot, R., Buffetaut, E., Dyke, G., Hua, S., Le Loeuff, J., 2010. Vertebrate assemblages from the early Late Cretaceous of southeastern Morocco: an overview. Journal of African Earth Sciences 57, 391–412.

Dalla Vecchia, F., Venturini Eni-Agip, S., Tentor, M., 2002. The Cenomanian (Late Cretaceous) Konservat-Lagerstätte of en Nammoûra (Kesrouâne Province), northern Lebanon. Bollettino della Società Paleontologica Italiana 41 (1), 51–68.

Dawson, A.G., Shi, S., 2000. Tsunami Deposits. Pure and Applied Geophysics 157, 875–897.

Ettachfini, El M., Andreu, B., 2004. Le Cénomanien et le Turonien de la platforme Préafricaine du Maroc. Cretaceous Research 25, 277–302.

Herman, A.B., Kvaček, J., 2010. Late Cretaceous Grünbach flora of Austria. Naturhistorischen Museum Wien, Wien, 142 pp.

Jones, A.H., Manchester, S.R., Dilcher, D.L., 1988. *Dryophyllum* Debey ex Saporta, juglandaceous not fagaceous. Review of Palaeobotany and Palynology 56, 205–211.

Krassilov, V.A., 1969. Approach to classification of Mesozoic "Ginkgoalean" plants from Siberia. Palaeobotanist 18, 12–19.

Krassilov, V.A., 1976. Tsagayan flora of Amur Province. Nauka, Moscow, 92 pp. (in Russian).

Krassilov, V.A., 1978. Mesozoic lycopods and ferns from the Bureja Basin. Palaeontographica B 166, 16–29.

Krassilov, V.A., 1979. Cretaceous flora of Sakhalin. Nauka, Moscow, 182 pp. (in Russian).

Krassilov, V.A., Bacchia, F., 2000. Cenomanian florule of Nammoura, Lebanon. Cretaceous Research 21, 785–799.

Krassilov, V.A., Lewy, Z., Nevo, E., Silantieva, N., 2005. Turonian Flora of Southern Negev, Israel. Pensoft, Sophia, 252 pp.

Krassilov, V.A., Rasnitsyn, A.P., 2008. Plant–Arthropod Interactions in the Early Angiosperm History. Pensoft, Brill, Sophia, 229 pp.

Krassilov, V., Schrank, E., 2011. New Albian macro- and palynoflora from the Negev (Israel) with description of a new gymnosperm morphotaxon. Cretaceous Research 32, 13–29.

Kvaček, J., 2000. *Frenelopsis alata* and its microsporangiate and ovuliferous reproductive structures from the Cenomanian of Bohemia (Czech Republic, Central Europe). Review of Palaeobotany and Palynology 112, 51–78.

Kvaček, Z., 1995. *Limnobiophyllum* Krassilov – a fossil link between the Araceae and the Lemnaceae. Aquatic Botany 50, 49–61.

Lejal-Nicol, A., Dominik, W., 1990. Sur la paleoflore a Weichseliaceae et a angiosperms du Cenomanien de la region de Bahariya (Egypte du Sud-Oest). Berliner Geowissenschaften Abhandlungen A 120, 957–992.

Mägdefrau, K.S., Rudolf, H., 1969. Morphologie und Hystologie der Nadel der Conifere *Abietites linkii*. Neues Jahrbuch für Geologie und Palaeontologie Monatshefte 1969, 269–297.

Martill, D.M., Ibrahim, N., Brito, P.M., Baider, L., Zhouri, S., Loveridge, R., Naish, D., Hing, R., 2011. New Plattenkalk Konservat Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-eastern Morocco. Cretaceous Research 32, 433–446.

Mendes, M.M., Jorge, L., Gomez, D.B., Pais, J., 2010. Reassessment of the cheirolepidiaceous conifer *Frenelopsis teixeirae* Alvin et Pais from the Early

Cretaceous (Hauterivian) of Portugal and palaeoenvironmental considerations. Review of Palaeobotany and Palynology 161, 30–42.
Moiseeva, M., 2012. *Barykovia*, a new genus of angiosperms from the Campanian of northeastern Russia. Review of Palaeobotany and Palynology 178, 1–12.
Němejc, F., Kvaček, Z., 1975. Senonian Plant Macrofossils from the Region of Zliv and Hluboká (near České Budějovice) in South Bohemia. Universita Karlova, Praha, 182 pp.
Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J., Wilson, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. Science 272, 986–991.
Silantieva, N., Krassilov, V.A., 2006a. Evolution of early angiosperm ecosystems: Albian–Turonian of Negev, Israel. In: Barrett, P.M., Evans, S.E. (Eds.), Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Natural History Museum, London, pp. 118–122.
Silantieva, N., Krassilov, V.A., 2006b. *Weichselia* Stiehler from Lower Cretaceous of Makhtesh Ramon, Israel: new morphological interpretation and taxonomical affinities. Acta Palaeobotanica 46, 119–136.
Wang, H., Dilcher, D.L., 2006. Aquatic angiosperms from the Dakota Formation (Albian, Lower Cretaceous), Hoisington III Locality, Kansas. USA. International Journal of Plant Sciences 167, 385–401.
Watson, J., 1983. A new species of the conifer *Frenelopsis* from the Cretaceous of Sudan. Botanical Journal of Linnaean Society (London) 86, 161–167.
Watson, J., Lydon, S.J., Harrison, N.A., 2001. The revision of the Wealden Flora, III: Czekanowskiales, Ginkgoales and allied Coniferales. Bulletin of the Natural History Museum, Geological Series 57, 29–82.
Wilde, V., 1991. *Tritaenia* (al. *Abietites*) *linkii* (Roemer) Mägdefrau et Rudolf (Coniferae inc. sed.) und ihr Forcommen in der Wealden-Facies der unteren Kreide von Nordwestdeutschland. Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen 183, 363–374.
Williamson, P.S., Schneider, E.L., 1993. Cabombaceae. In: Kubitzki, K., Rohwer, J.G., Bittrich, V. (Eds.), The Families and Genera of Vascular Plants, vol. II. Springer, Berlin, pp. 157–160.

Appendix. Supplementary material

Supplementary data related to this article can be found online at http://dx.doi.org/10.1016/j.cretres.2012.07.005.