Cenomanian florule of Nammoura, Lebanon

*Valentin Krassilov and †Flavio Bacchia

*Paleontological Institute, 1123 Profsoyusnaya St., Moscow 117641, Russia
†Stoneage S. R. L., Via Torino, 15, 34123 Trieste, Italy

Revised manuscript accepted 8 August 2000

The mid-Cenomanian fish beds of Nammoura, Mont-Liban district, Lebanon contain a diverse fauna of aquatic and terrestrial vertebrates, a few crustaceans and moderately well-preserved plant remains of which a single species, *Sapindopsis anhouryi*, was previously described by Dilcher & Basson (1990). We add 11 species of ferns, gymnosperms and angiosperms of which *Nammouria cretacea* gen. et sp. nov., *Nupharanthus cretacea* gen. et sp. nov., *Sapindopsis libanensis* sp. nov. and *Nammourophyllum altingioides* gen. et sp. nov. are new taxa. The florule differs markedly from both Early Cretaceous and Turonian plant assemblages of the Middle East, thereby representing a distinct stage of the regional floristic evolution. Its phytogeographic affinities are with contemporaneous floras of North America, Central Europe and the Crimea. A combination of such features as xeromorphism, the prevalence of compound leaves, and the presence of deciduous angiosperm components and gymnosperms may indicate climatic conditions similar to those of the present day Mediterranean.

KEY WORDS: aquatic ferns; early angiosperms; Middle East; Cretaceous; palaeoclimates.

1. Introduction

The material described in this paper comes from two quarries in the Al Gabour Valley near the village of Nammoura, Mont-Liban district, about 20 km northeast of Beirut and about 10 km south-southeast of Hjoula, a well-known Cenomanian fish locality. The quarries cut a sequence of Cretaceous platform carbonates with a fossiliferous horizon, the fish beds, near its base. The fish beds incorporate the same facies as those represented at Haqel and Hjoula (Hückel, 1970). They consist of alternating carbonaceous mudstones and wackestones followed up-section by greenish or bluish-grey, thinly laminated limestones with chert nodules, altogether 15–30 m thick. The fish beds are overlain by a rudist bank, the foraminiferal assemblage of which contains a characteristic Cenomanian species *Rhapydionina laurinensis* Saint-Marc.

In addition to the diverse medium-sized to large fish remains, including a large shark tooth, the fossiliferous horizon has yielded a few small crustaceans, coprolites and fecal pellets a few millimeters in diameter. There are also dismembered skeletons of aquatic and terrestrial reptiles, including a forelimb of a large theropod dinosaur and a few bird feathers. The holotype of the recently described dolichosaur *Aphanizocnemus libanensis* Dal Sasso & Pinna (1997) supposedly came from this locality. The faunal remains are housed in the Milan Museo Civico di Storia Naturale and in private collections.

The terrestrial plants are preserved as impressions with fragmentary compression films. Previously, a single plant species, *Sapindopsis anhouryi*, was described from Nammoura by Dilcher & Basson (1990). We add 11 forms of ferns, gymnosperms and angiosperms. Natalia P. Maslova (Palaeontological Institute, Moscow) contributed to the recognition and description of the new species *Sapindopsis lebanensis* and *Nammourophyllum altingioides*. The fossil plant collection is presently housed in the Paleontological Institute, Moscow, catalogue no. 4799.

2. Systematic palaeontology

Pteridophytes

*Pteris* sp.

Figure 1C–F

Description. Three fragments of pinnate leaves 50 mm long, with a thin, longitudinally striate, rachis distally forking at an acute angle. The pinnae are alternate, well spaced on the main rachis, more crowded on the distal arms, arising at about 60°–80°, lanceolate, up to 7 mm long, variably dissected, with a pair or two pairs
Figure 1. Cenomanian plants of Nammoura, Lebanon. A, B, *Pseudolarix* sp., conifer needle, no. 4799/4, × 1 and × 15. C–F, *Pteris* sp., fern leaf fragments, no. 4799/15, × 1; pinna enlarged to show marginal coensors, × 8; and cuticle with hair bases, SEM, × 400. G–I, *Pseudotorellia* sp., a ginkgophyte leaf, no. 4799/1, × 1 and enlarged, × 7, to show resin canals (dark slightly sinuous lines); note a transverse insect mine (arrows).
of proximal pinnules, the latter distally slightly incised or entire. The pinnules are anadromous or catadromous, elliptical to rounded, in the distal pinnae reduced to lobes. A typical condition of the distal pinnae is a short lanceolate blade with a single abaxial lobe and a shallow adaxial incision. The venation is pinnate, with 2–3 pairs of lateral branches in the entire part of the pinna, 1–2 branches in the basal pinnules. The fertile pinnules show linear marginal coenosori of proximal pinnules, the latter distally slightly incised or entire. The pinnules are anadromous or catadromous, elliptical to rounded, in the distal pinnae reduced to lobes. A typical condition of the distal pinnae is a short lanceolate blade with a single abaxial lobe and a shallow adaxial incision. The venation is pinnate, with 2–3 pairs of lateral branches in the entire part of the pinna, 1–2 branches in the basal pinnules. The fertile pinnules show linear marginal coenosori 0.3 mm wide. Our attempts at obtaining spores failed, but the pinnae yielded thin cuticle with rounded-polygonal cells (Figure 1F).

Remarks. The pinnule morphology and the position of coenosori are rather typical of the extant genus *Pteris* (Pteridaceae). Forking leaves occasionally occur in the closely related family Vittariaceae (Copeland, 1945). No comparable forms are currently known among Cretaceous ferns.

*Nammouria* Krassilov gen. nov.

Derivation of name. From the Nammoura locality.

Type species. *Nammouria gracilis* sp. nov.

Diagnosis. Leaf stalked, dichopodially divided, with the pinnae repeatedly forked. Sterile pinnules terminal on pinna rachis, broadly lanceolate, with flabellate venation. Elliptical to spindle-shaped hirsute bodies (sporocarps?) are born singly or in pairs at each branching node.

*Nammouria gracilis* Krassilov, sp. nov.

Figures 2C, D, 3, 4A–C

Holotype. Palaeontological Institute, Moscow, Catalogue no. 4799-10, Nammoura locality, Lebanon.

Diagnosis. As for the genus.

Description. The species is based on the part and counterpart of a stalked, dichopodially divided leaf (with the exterior segments overtopping the interior ones). The stalk is straight, 20 mm long, 1 mm thick, longitudinally striate, distally divided into three pinnae that spread in one plane, apparently arising from one point, but actually produced by two dichotomies rapidly following one another (Figure 2C, D). The median pinnma is relatively short, bearing a terminal sterile pinnule. The marginal pinnules diverge at about 60°. Their rachises are less than 0.5 mm thick, curved, with 2–3 longitudinal furrows, repeatedly forked at intervals 7, 4 and 2 mm in distally decreasing order, bearing thick, elliptical to spindle-shaped hirsute bodies (sporocarps?) at each branching node. Ultimate divisions of the marginal pinnae might also terminate in sterile pinnules, but these are either shed or poorly preserved.

The sterile pinnule is broadly lanceolate, 2 mm wide, with six diverging, sporadically anastomosing veins (Figure 4B). The hirsute bodies arise singly or in pairs at an acute angle to the rachis. They are sessile, slightly decurrent, elliptical to spindle-shaped, acuminate, the proximal ones relatively large, about 5 mm long, 2 mm wide, distally decreasing to 3 × 1 mm. Their surface is pitted, with long hairs leaving faint impressions along the margins (Figure 4A, B). Under an SEM, the ferruginous impressions show reticulate spherical structures about 90–100 μm in diameter that appear to be megaspores (Figure 4C), but their preservation is too poor for a definite interpretation.

Remarks. The leaf has a distinctive morphology that is not matched by any known Mesozoic plant. It is, therefore, deserving a status of a new morphological genus. In the lack of well-preserved structural details its taxonomic assignment is admittedly ambiguous. A comparison with aquatic ferns is based on the morphology of both the sterile pinnule and hirsute bodies that resemble, respectively, the floating leaf segments and sporocarpia of extant *Marsilea* and *Regnellidium*, as well as those of fossil *Rhodeites* and *Hydropteris* (Chitaley & Paradkar, 1972; Rothwell & Stockey, 1994). In these ferns sporocarpia typically attach at the branching nodes of the rhizome. Dichopodial branching occurs in submerged leaves of the Salviniales, but has not been recorded hitherto in the floating or emergent leaves. *Nammouria* might represent an extinct line of initial hydropterid radiation that took place in the Early to mid-Cretaceous (Krassilov & Golovneva, 1999).

Gymnosperms

*Pseudotorellia* sp.

Figure 1G–I

Description. A lanceolate leaf, 67 × 7 mm, bluntly pointed, with margins parallel for most of the length, gradually converging to the base which shows a thickened abscission scar (Figure 1I). The veins diverge from the base, subparallel above, seven in the middle part. Irregularly twisted resin ducts occur between the veins. The blade is traversed by a leaf mine of the type described by Labandeira et al. (1994, Figure 11–L) on *Densinervum* sp. from the Dakota Formation.
Figure 2. Cenomanian plants of Nammoura, Lebanon. A, B, *Phragmites* sp., monocot leaf, no. 4799/13, × 1 and detail of venation (B, orientated at 90° to A), SEM, × 50. C, D, *Nammouria gracilis* gen. et sp. nov., aquatic fern (?), holotype no. 4799/10a, dichopodially divided leaf bearing sterile pinule (arrow) and sporocarps (?), × 1 and × 3.5.
Remarks. Of the pseudotorellias with resin ducts, *P. linkii* (Römer) Watson is similar but considerably smaller (Watson & Harrison, 1998).

**Pseudolarix** sp.  
**Figure 1A, B**

*Description.* A linear-oblanceolate needle-leaf, 25 mm long, 2 mm wide. The leaf is widest below the apical constriction from where it gradually tapers towards the base, lacking a distinct petiole, but with the base constricted and twisted, showing a straight abscission line. The apex forms a short, blunt point. The leaf surface shows a median costal zone 1 mm wide, wedging out a little below the apex, and two slightly depressed submarginal stomatal zones, each 0.3 mm wide.

Remarks. This leaf might belong to a deciduous conifer with *Larix*-*Pseudolarix* affinities. It is similar to the extant *Pseudolarix kemferi* Gord., the Paleogene *P. nipponica* Kimura & Horiuchi (1978) and the Early Cretaceous *P. erensis* (Krassilov, 1982). In this last species, the leaf dimensions and the width ratio of the costal and stomatal zones exactly match the Lebanon species.

Monocotyledons

*Phragmites* sp.  
**Figure 2A, B**

*Description.* A ribbon-shaped leaf, more than 155 mm long (apex lacking), 13 mm wide at the base, expanded to 16 mm slightly below the middle, gradually

---

**Figure 3. Nammouria gracilis** gen. et sp. nov., aquatic fern (?) from the Cenomanian of Nammoura, Lebanon: sketch drawing of holotype, $\times$ 1.5.
tapering toward the apex. The base is slightly concave, thickened along the abscission line. The veins are straight, parallel, 1–0.7 mm apart, with the interstitial veins traceable for a short distance. Epidermal cells are arranged in files parallel to the veins (Figure 2B).

Remarks. This leaf is of the same type as the widespread Late Cretaceous and Cenozoic remains traditionally assigned to *Phragmites* (e.g. *Phragmites alaskana* Heer: Hollick, 1936), but their affinities to this genus and to gramineous monocots have yet to be proved.

Dicotyledons

*Nupharanthus* Krassilov gen. nov.

*Derivation of name.* From extant genus *Nuphar* (Nymphaeaceae), and *anthus*, flower.
Type species. *Nupharanthus cretacea* sp. nov.

**Diagnosis.** Flower solitary, perfect actinomorphic. Five sepals, free, imbricate, with subparallel venation. Petals smaller than sepals in more than one circle, heteromorphous. About ten stamens, spirocyclic, leaving elongate scars with pits of vascular bundles. Stigmatic disk faintly striated radially.

*Nupharanthus cretacea* Krassilov, sp. nov.  
*Figures 5A, B, 6*

**Derivation of name.** From the Cretaceous.

**Holotype.** Palaeontological Institute, Moscow, Catalogue no. 4799-11, Nammoura locality, Lebanon.

**Diagnosis.** As for the genus.

**Description.** The flower is preserved as a pale yellowish impression showing a radially symmetrical calyx 25 mm in diameter, with five sepals spreading in the bedded plane, slightly imbricate proximally, distally spreading, with broadly rounded apices. The sepal venation is clearly marked, consisting of thick subparallel veins, with indistinct cross veins. Intersecting vein patterns are seen in the marginal overlap areas, indicating the membranous texture of the sepals.

The petals are of variable shapes and dimensions ranging from semicircular to lingulate, 3.5–5 mm long. They are either distinctly or faintly impressed upon the sepals, apparently arranged at different levels in a spirocyclic series. The petal venation is thin, digitate, with oblique anastomoses.

The stamens are shed, but about ten scars are conspicuous in the peripheral zone of the receptacle *(Figure 5A)*. The scars are arranged in an irregular spirocyclic series, and are elongate, slightly curved, with rounded pits apparently left by vascular bundles. The central part of the receptacle is occupied by a disk 2 mm in diameter, with a slightly undulating margin. The disk surface shows faint radial striations.

**Remarks.** Distinguishing features of the flower are its pentameric actinomorphic structure, distinct sepals, and spirocyclic arrangement of small petals and stamens which, judging by the scars, might have been laminar. These features indicate affinities with the Nymphaeaceae, in particular with the extant genus *Nuphar*, which has thin membranous sepals and reduced petals *(Mosley, 1972)*. No fossil genus matches the description. The Palaeogene *Florissantia*, assigned to the Malvales, is similar in general shape, dimensions and the relative development of sepals and petals *(Manchester, 1992)*, but the sepals are connate, with a distinct reticulate venation.

*Figures 7*


**Description.** A compound leaf with four alternate leaflets and a sheathing stipule at the base. The leaflets are linear-lanceolate, about 65–80 × 7 mm, slightly asymmetrical at the base, decurrent, with stout midrib, thin secondaries and a prominent intramarginal vein. The stipule is ovate, 15 × 6 mm, with subparallel veins converging to the apex.

**Remarks.** This species differs from the contemporaneous North American *Sapindopsis* *(Huang & Dilcher, 1994)* by its better-developed intramarginal vein, which gives the venation a myrtaceous aspect. In leaf shape and venation it is also comparable with *Halyserites reichii* Sternberg from the Cenomanian of the Bohemian Massif *(Knobloch, 1978)*.

*Sapindopsis lebanensis* Krassilov & Maslova, sp. nov.  
*Figures 8, 9A–D*

**Holotype.** Palaeontological Institute, Moscow, Catalogue no. 4799-11, Nammoura locality, Lebanon.

**Diagnosis.** Leaf lobate-palmate, stipulate, with a basal leaflet distinct, the rest increasingly fused over the leaf. Leaflets linear-lanceolate, about 40 × 4 mm, acutely pointed. Midrib prominent, secondaries thin, faintly marked, eucamptodromous, joining intramarginal vein. Stipule sheathing ovate-lanceolate, parallel-veined, with free part triangular, 1 mm long. Leaf compression thick, with stomatal pits distinct at low magnification, and with transverse striation reflecting paliсаде mesophyll structure. Leaf blade hypostomatic, with hair bases and large spherical glands *(Figure 9B)* on both sides. Secondary veins scarcely reflected in the epidermal cell patterns. Ordinary epidermal cells polygonal, irregularly disposed or radiating from a larger, rounded cell. Stomata scattered, irregularly orientated, anomocytic to weakly cyclocytic, with typically five trapezoid subsidiary cells that are slightly sunken below the level of ordinary cells. Some guard cells show long, T-shaped polar thickenings. Hair bases small, elliptical, encircled by a variable number (up to ten) epidermal cells.

**Remarks.** This species belongs to a xeromorphic group of *Sapindopsis* with narrow leaflets, a thick, probably...
Figure 5. Cenomanian plants of Nammoura, Lebanon. A, B, *Nupharanthus cretacea* gen. et sp. nov., nymphaeaceous flower, holotype no. 4799/9, showing large, imbricate sepals and smaller, indistinctly marked petals (arrows), × 2.5 and × 10; insertion, top right corner, shows central part differently illuminated with distinct scars of stamens. C, *Aryskumia* sp. cf. *A. zelkovifolia* Shilin, serrate angiosperm leaf with a short twisted petiole, no. 4799/12, × 1. D, E, *Nammourophyllum altingioides* gen. et sp. nov., serrate angiosperm leaf, holotype no. 4799/11, × 1, and detail of marginal serration, × 7.
coriaceous leaf blade, indistinct venation, amphistomatic epidermis and sunken stomata. In contrast, *Sapindopsis anhouryi* Dilcher & Basson represents a relatively mesomorphic type of leaf with much broader leaflets and well-marked venation. *Sapindopsis lebanensis* differs from the North American species in its relatively smaller dimensions, better developed intramarginal vein and stipule characters. Their cuticular structures are similar (see Upchurch, 1984), although in the Lebanese species the lateral to polar differentiation of subsidiary cells is less distinct. *Proteophyllum laminarium* Velenovsky from the Cenomanian of Bohemia has a slightly broader lamina which is similar in its coriaceous texture, indistinct secondaries and cuticular structure (Němejc & Kvaček, 1975). *Proteophyllum* conventionally includes simple leaves, some of which, however, appear as *Sapindopsis*-type leaflets.

*Proteophyllum* laminarium Velenovsky from the Cenomanian of Bohemia has a slightly broader lamina which is similar in its coriaceous texture, indistinct secondaries and cuticular structure (Němejc & Kvaček, 1975). *Proteophyllum* conventionally includes simple leaves, some of which, however, appear as *Sapindopsis*-type leaflets.

*Nammourophyllum* Maslova & Krassilov gen. nov.

**Derivation of name.** From Nammoura locality.

**Type species.** *Nammourophyllum altingioides* Maslova & Krassilov sp. nov.

---

**Figure 6.** *Nupharanthus cretacea* gen. et sp. nov., nymphaeaceous flower from the Cenomanian of Nammoura, Lebanon: sketch of holotype, × 2.5.

**Figure 7.** *Sapindopsis anhouryi* Dilcher & Basson, 1990, compound stipulate angiosperm leaf, no. 4799/14, from the Cenomanian of Nammoura, Lebanon, × 1.
Diagnosis. Leaf small, elliptical, long-petiolate, base slightly asymmetrical, margin irregularly serrate, with rare additional serrations. Larger serrations glandular. Venation pinnate, brochidodromous. Midrib stout, secondaries thin, irregularly spaced. Intrabasal secondaries short, recurved. Subsequent secondaries curved upwards, looping far from the margin, their distal branches terminating in sinuses of the marginal serration.

*Nammourophyllum altingioides* Maslova & Krassilov sp. nov. Figures 5D, E, 10

**Derivation of name.** From extant genus *Altingia* (Hamamelidales).

**Holotype.** Palaeontological Institute, Moscow, Catalogue no. 4799-7, Nammoura locality, Lebanon.

**Diagnosis.** As for the genus.

**Description.** A single complete leaf with a blade 32 mm long, reaching 15.5 mm in maximum width slightly above the middle. The petiole is 13 mm long, 1 mm thick, expanded to 1.5 mm at the abscission line. The leaf base is broadly cuneate, asymmetrical, with the halves of the blade slightly displaced against each other. The apex is a short point, appearing as a larger marginal tooth. The margin is serrate from the base up. The serration is somewhat irregular, with the teeth tending to increase distally. Larger teeth in the distal part of the blade bear a small additional serration (Figure 5E). The marginal glands are conspicuous in the larger teeth (Figure 10).

The midrib starts as a direct continuation of the petiole, gradually attenuating to the apex. Both the petiole and midrib are longitudinally striate. The secondaries are thin and indistinct, arising at variable angles and not quite parallel to each other. The lower secondaries are short, not ascending above the basal quarter, recurved. The next pair ascends at a more acute angle giving off a few basiscopic branches. These and subsequent secondaries loop irregularly well before the margin. Short branches ascending from the loops terminate in the sinuses of marginal serrations.

**Remarks.** This leaf represents a distinct morphotype with no close allies in Cretaceous leaf floras. *Crassidenticulatum* Upchurch & Dilcher, 1990 is similar in the glandular serration and irregular brochidodromous venation, but the marginal teeth are much smaller and of chloranthoid morphology, while the secondaries are far more numerous. *Hamamelites* Saporta is similar in leaf shape (though more conspicuously asymmetrical in the type species *H. clarus* Saporta, 1868) and secondary venation, but the petiole is typically short and the marginal teeth are non-glandular.

The marginal features of *Nammourophyllum* are rather altingioid, with the secondaries or their derived veins ending in the sinuses. In herbarium material of *Altingia excelsa* we observed rare additional teeth over the typically simple marginal serration. The striate petiole (long in *A. gracilis*) continuing into the blade as a similarly striate midrib is also an altingioid feature. However, in modern Altingiaceae the secondaries are far more regular, loop closer to the leaf margin.
Figure 9. *Sapindopsis libanensis* sp. nov., from the Cenomanian of Nammoura, Lebanon, holotype no. 4799/7, SEM micrographs of abaxial cuticle with stoma (A), epidermal gland (B), and hair bases (C, D).
Description. An infructescence of bracteate fruits 30 mm long, 10 mm wide, dense, with a short, stout peduncle. The bracts are crowded, showing obliquely spreading acuminate beaks that emerge from the mass of intact fruits (Figure 11B–C). The latter are poorly preserved, some showing relatively broad, membranous lateral wings that spread over the bedding plane.

Remarks. The infructescence is of a general juglandaceous aspect and resembles Platycarya americana from the Lower Eocene of North Dakota (Wing & Hickey, 1984), but details of the nutlet morphology are scarcely discernible.

Aryskumia sp. cf. A. zelkovifolia Shilin

Description. A poorly reserved leaf with ovate blade, 50 × 20 mm, showing a doubly serrate margin and craspedodromous venation in the proximal part of the blade. The leaf base is slightly cordate, with a short (4 mm), stout, twisted petiole.

Remarks. In the marginal characters and venation this leaf resembles Aryskumia zelkovifolia, a primitive ulmaceous morphotype, but is somewhat smaller and with a denser serration than the type material from the Santonian of Kazakhstan (Shilin, 1986).

Parvileguminophyllum sp.

Figure 11D

Description. A complete leaflet, oblanceolate, 30 × 10 mm, gradually tapering to the base, apparently with a short petiole, and with a bluntly pointed apex. The margin is entire, indistinctly undulate, incised by a marginal gall (at left side near the apex in Figure 10D). The midrib extends to the apex. The secondaries are thin, eucamptodromous.

Remarks. The leaf genus Parvileguminophyllum was erected by Herendeen & Dilcher (1990) for compound leaves and small inequilateral leaflets which could be assigned to the Leguminosae. The leaf from Nammoura is considerably broader than the Eocene species and lacks a mucronate apex, which is characteristic of the latter (Call & Dilcher, 1994).

3. Discussion

The Nammoura florule appears to represent a distinct stage of floristic evolution in the Middle East. It is fairly different from both the Early Cretaceous and Turonian–Maastrichtian regional floras. No elements are shared with the widespread Jurassic–Early Cretaceous Piazopteris-Brachyphyllum assemblages (e.g., El Chair et al., 1995; Barale et al., 1997), which suggests a major mid-Cretaceous floristic change. The Nammouran ferns and gymnosperms are morphologically modern, with the mid-Mesozoic elements represented by Pseudotorellia alone. The Early Turonian flora of Israel is comparable on account of the putative gramminoid elements (Krassilov & Dobruskina, 1998), but is dominated by the broad-leaved platanoid morphotypes (Dobruskina, 1996) that are lacking in the Nammoura locality.

The Nammouran angiosperm affinities are with the Cenomanian Sapindopsis of North America and their coeval Proteophyllum of Central Europe. Aryskumia is a modern-looking Paratethyan element previously described from western Kazakhstan and the Crimea (Shilin, 1986; Krassilov, 1984).

The Nammoura assemblage is too small for a comprehensive palaeoecological analysis. However, some preliminary considerations seem justified by the material. Most importantly, the Cenomanian assemblage gives no evidence of a tropical climate. It is
relatively small-leaved, with a distinct xeromorphic component (*Pseudotorellia* with thick, narrow, resiniferous leaves; *Sapiondopsis lebanensis* with narrowly dissected, thick, coriaceous, thickly cutinized, amphistomatic glandular leaves; even the fern leaves are quite small, with resistant cuticle). In comparison with the dry mid-Cretaceous regional vegetation recognized by Schrank (1994 and elsewhere) the Nammoura assemblage is relatively rich in ferns and conifers suggesting that aridity was not severe, perhaps expressed in a fairly dry mid-summer season. Morphologically, the assemblage hosts two groups of angiosperms: those with compound leaves (*Sapindopsis, Parvileguminophyllum*, the Platycaрейae) and those with simple serrate leaves (*Aryskumia, Nammourophyllum*). The compound leaf morphotypes have narrow, entire leaflets. The simple leaf morphotypes are small with peltate blades, and with petioles that are either short and twisted (*Aryskumia*) or long, with a distinct abscission line (*Nammourophyllum*). These features typically are associated in deciduous angiosperm leaves. The Nammouran biserrate leaves are

Figure 11. Cenomanian plants of Nammoura, Lebanon. A–C, Platycaрейae gen. sp., juglandaceous catkin, no. 4799/8, × 3, and details of bracts (B) and nuts (N), × 10 and × 15. D, *Parvileguminophyllum* sp., legume leaflet with a marginal gall (arrow), no. 4799/2, × 2.
among the earliest records of this morphotype that in most regions of the world first appeared no earlier than the Turonian (Krassilov, 1997).

It does not seem productive to single out extant ecological equivalents because they can be found in various climatic zones. Modern ecological equivalents of the assemblage as a whole may prove more instructive. In a search for such the following features of the Nammoura assemblage seem significant: (1) it contains a subordinate, yet prominent, fern-gymnosperm component; (2) the conifer remains, though rare, might come from an abundant up-slope source; (3) compound leaves predominate among angiosperm morphotypes; (4) the morphology of simple leaves indicates deciduousness; (5) the leaf blade units (simple leaves and leaflets of compound leaves) are small, with xeromorphic features; and (6) the leaf margins are serrate in the simple leaves, entire in the leaflet component; (2) the conifer remains, though rare, might come from an abundant up-slope source; (3) compound leaves predominate among angiosperm morphotypes; (4) the morphology of simple leaves indicates deciduousness; (5) the leaf blade units (simple leaves and leaflets of compound leaves) are small, with xeromorphic features; and (6) the leaf margins are serrate in the simple leaves, entire in the leaflets. A combination of these features is characteristic of the present day Mediterranean vegetation of the same territory (Krassilov, 1975, 1984).

Sedimentological features of the locality may add to the climatic interpretation of the floristic assemblage. The fish beds of Lebanon are considered to be deposits of an anoxic sedimentary environment, the origin of which was ascribed to a number of tectonic and/or palaeogeographic factors, such as synsedimentary downfaulting or upwelling (recently reviewed in Schram et al., 1999). An alternative explanation is prompted by the transported plant material that was found not only at Nammoura but also at Haquel from which indeterminable plant remains were reported by Hückel (1970). Their constant, though scattered, occurrence indicates a considerable influx of terrestrial organic debris. A dilution of marine surface waters by a discharge of fresh waters carrying organic material might have caused anoxia down the water column. In the Mediterranean Sea such anoxic events correlate with increased mid-latitude precipitation (Rossignol-Strich et al., 1982). At the same time, the thinly laminated limestones of the Nammoura fish bed indicate a pronounced seasonality of precipitation, which concurs with palaeocological aspect of the plant assemblage.

References


