A new Late Cretaceous ginkgoalean reproductive structure *Nehvizdyella* gen. nov. from the Czech Republic and its whole-plant reconstruction[1]

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During the Mesozoic Era, gingkoaleans comprised a diverse and widespread group. Here we describe ginkgoalean fossils in their facies context from the Late Cretaceous (Cenomanian) Peruc-Korycany Formation of the Czech Republic and present a reconstruction of tree architecture and ecology. Newly described in this study is the ovuliferous reproductive structure, *Nehvizdyella bipartita* gen. et sp. nov. (Ginkgoales). This ovuliferous organ consists of a bifurcating axis, terminated by large cupule-like structures, probably homologous to the collar of the recent *Ginkgo*. Each cupule encloses an orthotropous ovule. In specimens with the early developmental stages preserved, the entire ovule and young seed, with the exception of the micropylar area, is embedded in the cupule. Mature seeds consist of sclerotesta and sarcotesta. Monosulcate pollen grains of *Cycadopites*-type are found adhering to the seeds. Although similar to *Ginkgo* in terms of its large size and reduced number of seeds, *N. bipartita* differs from the extant genus in having ovules completely enclosed in a cupule-like structure. The co-occurrence of *N. bipartita* with ginkgoalean leaves of *Eretmophyllum obtusum* (Velenovský) Kvaček, J., ginkgoalean short shoots of *Pecinovicladus kvacekii* Falcon-Lang, and ginkgoalean trunk wood of *Ginkgoxylon gruettii* Pons and Vozenin-Serra in monodominant taphocoenoses at four geographically distant localities suggests that these remains all belong to one plant. This is supported by the close morphological and anatomical similarity between the different organs. Facies analysis of plant assemblages indicates that our Cretaceous tree occupied a water-stressed coastal salt marsh environment. It therefore represents the first unequivocal halophyte among the Ginkgoales.

Key words: Cenomanian; *Cycadopites*; *Eretmophyllum*; Ginkgoales; *Ginkgoxylon*; Late Cretaceous; *Nehvizdyella*; *Pecinovicladus*.

The order Ginkgoales contains a single extant species, *Ginkgo biloba*, but fossil studies demonstrate that this group of plants has, at certain times during its 200-million-year history, possessed much higher levels of diversity (Zhou, 1997). Peak diversity was attained in the Mesozoic Era, when ginkgoaleans comprised more than 13 genera (Tralau, 1968) and grew over much of the Pangean supercontinent (Royer et al., 2003). Although sterile ginkgoalean foliage is very common in Mesozoic strata, associated reproductive structures have only been documented very rarely. Furthermore, although fossil assemblages comprising both vegetative and reproductive organs are documented at some sites, only a few Mesozoic gingkoaleans have been reconstructed to date.

In this paper, we describe a new genus of ginkgoalean ovuliferous reproductive structure, *Nehvizdyella bipartita* gen. et sp. nov., from the Late Cretaceous (Cenomanian) of the Czech Republic. These fertile remains occur in facies-association with several other ginkgoalean morphotaxa, which all show strong morphological and anatomical similarities. Associated morphotaxa include tongue-shaped leaves referable to *Eret-mophyllum obtusum* (Velenovský) Kvaček, J., pollen of *Cycadopites*-type, woody short shoots of *Pecinovicladus kvacekii* Falcon-Lang, and mature trunk wood of *Gingkoxylon gruettii* Pons and Vozenin-Serra (Uličný et al., 1997; Kvaček, 1999; Falcon-Lang, 2004). Based on these additional materials, we propose a whole-plant reconstruction for the ginkgoalean tree and utilize facies data to assess its paleoecology.

MATERIALS AND METHODS

The ginkgoalean plant material described here was collected at localities within the Peruc-Korycany Formation, the basal lithostratigraphic unit of the Bohemian Cretaceous Basin in the Czech Republic (sensu Čech et al., 1980). Palynological data indicate a late middle Cenomanian age for these beds (Pacltová, 1977, 1978). The four main sites are Hloubětín Brickpit (50°06′45″ N, 14°32′02″ E), a disused brick pit in the eastern part of Prague (material collected by Hluštík, 1973–1974), and three large working quarries, Pecínov Quarry near Rynholec (50°08′00″ N, 13°54′34″ E), Kamenná Panna Quarry near Horoušany (50°07′17, 14°44′09″ E), and Vyšehořovice Brickpit (50°07′17″, 14°45′12″ E) east of the village of the same name (Fig. 1).

Geological mapping and sequence stratigraphic analysis has shown that the Peruc-Korycany Formation infills a series of palaeovalleys (Uličný and Špičáková, 1996). Palaeovalley-fill successions (Uličný et al., 1997; Uličný and Nichols, 1997) comprise the deposits of a variety of continental (braided rivers, meandering streams and floodplains, and anastomosed fluvial systems) and coastal environments (tidally influenced braided rivers, supratidal marshes, tidal flats, ebb-tidal deltas, estuaries, and lower shoreface). The ginkgoalean plant fossils were extracted from mudstone units interpreted as supratidal marsh facies at all four sites (Nguyen Tu et al., 2002). Ginkgoaleans form the dominant fossil component of these beds, which also contain the remains of the conifer *Frenelopsis alata* (K. Feistmantel) Knobloch, a few angiosperms, and a putative gnetalean (Uličný et al., 1997; Falcon-Lang et al., 2001).

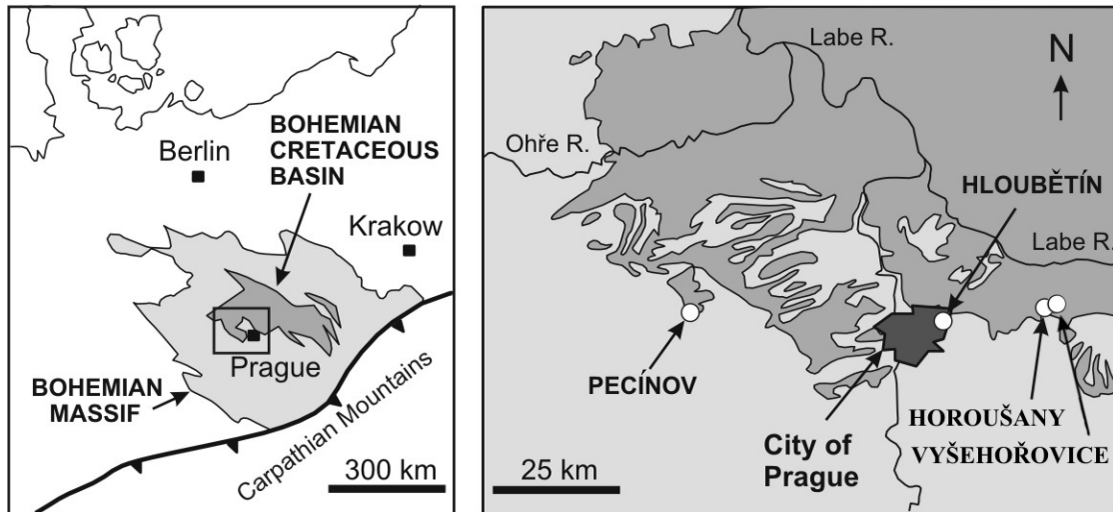Mudstone specimens dominated by ginkgoalean foliage (*Eretmophyllum*)

Fig. 1.   Geological setting. Location of the Bohemian Cretaceous Basin in Central Europe (left) and location of the four fossil sites mentioned in this paper, surrounding Prague, Czech Republic (right). Dark grey area indicates Cretaceous Basin; light grey area indicates Bohemian Massif (after Uličný et al., 1997).

were treated in a solution of natrium carbonate. Other specimens were macerated for 8 h in diluted Schulze's solution and then stored in glycerine. After approximately 1 month, macerated specimens became partially translucent, although optimum translucence was not obtained until after 5 months of maceration and treatment in glycerine. Cuticles from the seed integument were then prepared using standard Schulze techniques (Kvaček, 1999, 2000). In addition to the ovules themselves, pollen grains that adhered to the seeds after maceration were separated using a dissecting needle with a human hair glued to its tip (Zetter, 1989; Zetter et al., 2002). Associated lignified and charred wood was also collected, and treated using standard HF techniques (Falcon-Lang et al., 2001). Resultant material was examined using an Olympus (Japan) SZX 12 binocular microscope, an Olympus (Japan) BX 50 light microscope, a Phillips (Germany) 515 SEM, and a Hitachi (Japan) S-3200 SEM. All specimens and preparations were deposited in the palaeobotanical collections of the National Museum, Prague (F 00003–15, F 00112–133, F 00189–191, F 02281, F 02293, F 02481–2483, F 02497–2500, F 02856, F 02886, F 02910–13, F 02926, F 02958, F 02972, F 03010–18, F 03038).

SYSTEMATICS

Genus—*Nehvizdyella* gen. nov. (Figs. 2–11)

Etymology—Diminutive drived from Nehvizdy, the village near where the fossils were found.

Type—*Nehvizdyella bipartita* gen. et sp. nov.

Generic diagnosis—Compound ovuliferous reproductive organ consisting of a main axis and two short secondary axes, each terminated by a large cupule-like structure. Each cupule encloses one orthotropous ovule. Seeds consist of sclerotesta and sarcotesta.

Species—*Nehvizdyella bipartita* gen. et sp. nov. (Figs. 2–11)

Synonym—*Nehvizdya obtusa* (Velenovský) Hluštík pro parte—seeds, megasporangiophores, Hluštík 1986: 100, pl. 1, figs. 1, 2, 6, text-fig. 8.

Specific diagnosis—Compound ovuliferous reproductive structure consisting of a main axis, stout and thick, which bears two short, apical secondary axes, each terminated by a cupule-like structure enclosing an ovule. In early developmental stages, the entire ovule, except the micropylar area, is embedded in the cupule. Ovule is orthotropous with micropyle facing distally. Seeds ovoid, having sclerotesta and sarcotesta. Remains of sarcotesta consisting of putative parenchymatous tissue. Outer cuticle of sarcotesta thick, bearing polygonal cells and stomata. Inner cuticle of sarcotesta very thin, bearing elongated cells. Sclerotesta hard and fragile. All the ovuliferous organs including main axis contain numerous resin bodies.

Holotype—Designated here F 03010, National Museum, Prague, (Figs. 3–5).

*Paratype*—Designated here F 03011, National Museum, Prague, (Fig. 2).

Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

Type locality—Horoušany, Kamenná Panna Quarry near Nehvizdy (holotype F 03010, paratype F 0301, F 03012–14, F 03018), Czech Republic (50°07′17″, 14°44′09″ E).

Other material—Prague, Hloubětín Brickpit (F 00189–91); Pecínov, unit 3 (F 03015–17), Vyšehořovice Brickpit (F 02497–99).

Etymology—Derived from bipartite nature of the organ.

Description—The holotype of *Nehvizdyella bipartita* (F 03010) is a 15 mm long ovuliferous reproductive structure bearing two cupules (Fig. 3). The main axis is 6 mm long and 2 mm in diameter and has fine longitudinal striations. Secondary axes, 3–5 mm long and 2 mm in diameter, are dichotomously attached to the terminal part of the main axis. Each secondary axis is wrinkled, and its apical part gradually passes into the cupule-like structure. The holotype shows two cupules. The larger cupule is 8.5 mm in diameter and bears the remains of a seed. The smaller cupule (Figs. 4–6) is 4.5 mm in diameter encloses an orthotropous ovule (2.5 mm in di-
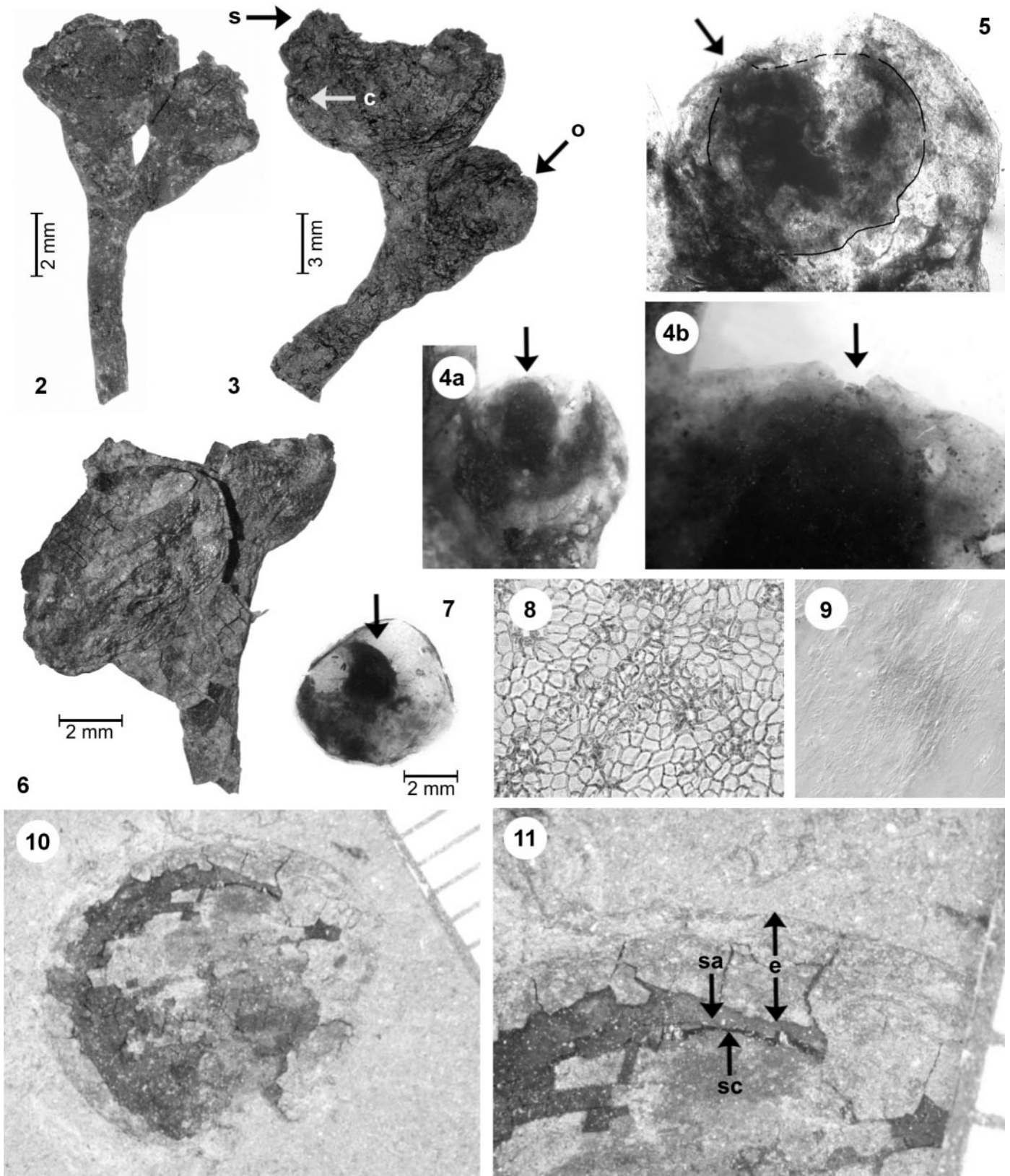
Figs. 2–11. *Nehvizdyella bipartita* gen. et sp. nov. Horoušany, Kamenná Panna Quarry, general morphology. **2.** Paratype, ovuliferous organ, each secondary axis terminating with a cupule-like structure enclosing an ovule, F 03011, ×4. **3.** Holotype, ovuliferous organ showing partly preserved seed and one ovule. c = cupule, o = ovule, s = seed. F 03010.×4. **4a.** Ovule with micropyle (arrowed) enclosed in a cupule-like structure, detail of Fig. 3, holotype, macerated. F 03010. ×6.5. **4b.** Detail of micropyle (arrowed), detail of Fig. 3, holotype. F 03010. ×25. **5.** Detail of macerated ovule, full/deshed line indicating presumed boundary of ovule, detail of Fig. 3 (presumed micropyle arrowed), holotype. F 03010. ×15. **6.** Empty cupules attached to the main axis. F 03014. ×6.

ameter). There is an ovoid mass of tissue (1 mm in diameter), which differs from the surrounding cells (Fig. 5). It is interpreted as a nucellus or proembryo. The micropyle and pollen chamber are situated in the terminal part of the ovule (Fig. 4a, b). Other studied material includes five additional reproductive axes with or without seeds or ovules. They vary in length from 11 mm up to nearly 20 mm (paratype F 03011, Fig. 2). Their main axes are 5–9 mm long and 1–2 mm in diameter. Secondary axes are 2–3 mm in length. Cupule-like structures bearing mature seeds are 4–8 mm in diameter and have a well-cutinized rim (Fig. 6). All the ovuliferous organs except sclerotesta contain numerous resin bodies (Fig. 5).

Where the seeds are attached to an axis, they are always aborted at some stage of maturation. Fully mature seeds only occur in a detached state, typically filled with sediment (Fig. 10), which probably penetrated through the broken sclerotesta after burial. Furthermore, mature seeds are not usually preserved intact and therefore rarely occur in bulk-macerated material. The generally poor preservation of mature seeds is probably linked to the development of the sclerotesta, which would have accentuated fragmentation during attrition resulting from sedimentary transport, maceration, and postsedimentary compression. Another similar case of differences between the preservation of immature and mature seeds has been noted by Rothwell and Holt (1997) in Maastrichtian assemblages from Alberta, Canada.

The detached seed compressions (Fig. 10) are circular or slightly elliptic, 9–10 mm in diameter. They show two layers of coalified matter (Fig. 11). The inner layer, consisting of shiny black coalified matter, is usually 0.1 mm thick. It is interpreted as sclerotesta. The outer layer, consisting of faint (porose) matter, 0.2–4 mm thick, is interpreted as sarcotesta. It is covered by a thick cuticle (Fig. 11). The outer cuticle of the sarcotesta is easily macerated and comprises stomata surrounded by 6–7 subsidiary cells (15–25 μm by 20–35 μm) interspersed between isodiametric cells (10–25 × 20–35 μm, Fig. 8). The inner cuticle of the sarcotesta is poorly preserved and has elongated cells (Fig. 9). The sclerotesta is fragile and has a thin cuticle, which is difficult to prepare.

Some seeds are preserved intact (e.g., F 03018, Fig. 7), but do not possess sclerotesta, and when macerated, have a short, central stalk (2–3 mm). These fossils are interpreted as immature seeds.

GINKGOALEAN AFFINITY

The ovuliferous structure, *Nehvizdyella bipartita*, bears diagnostic characters of both living and fossil representatives of the Ginkgoales (e.g., Page, 1990; Stewart and Rothwell, 1993). The ovuliferous organ is characterized by bifurcating axes, that each bear one ovule; seeds with haplocheilic stomata, axes and seeds bearing resin bodies; and associated leaves having two vascular bundles in petioles and dichotomizing venation. Further evidence for ginkgoalean affinity is given by the facies-association of this ovuliferous organ and foliage with a variety of unequivocally ginkgoalean organs including pollen, foliage, woody short shoots, and trunks (details discussed later). The

most remarkable feature of *Nehvizdyella* is the upward-oriented cupule-like structure. It is striated and probably built of nonwoody tissues. It encloses the ovule, and in later developmental stages supports a seed. Based on its position and function, we suggest that it is homologous with the collar of extant *Ginkgo*.

Similarity of *Nehvizdyella* to extant *Ginkgo* is evident in terms of the number of seeds per axis and their large size (length 20–22 mm in *Ginkgo*, 9–10 mm in *Nehvizdyella*). However, *Nehvizdyella* differs from *Ginkgo* in having ovules, which are mostly enclosed in a cupule-like structure, and in being facies-associated with the *Eretmophyllum* type of leaves (details discussed later). Although morphologically similar, *Nehvizdyella bipartita* is probably only distantly related to extant *Ginkgo biloba*. Reduction of the number of seeds per ovuliferous structure, the increasing size of the seeds, and the unification and expansion of the leaf lamina are probably general trends in several lineages of the Ginkgoales.

Nehvizdyella is most similar to ovuliferous reproductive structures associated with the genus *Grenana* Samylina from the Middle Jurassic of Angren, which have similarly sized seeds embedded in a large cupule (Appendix S1, see Supplemental Data accompanying online version of article). *Grenana* was originally described as a pteridosperm (Samylina, 1990), but later Zhou (1997) reinterpreted it as a member of the Ginkgoales. Although *Nehvizdyella* could be closely related to *Grenana*, detailed comparison between these two taxa is problematic because the holotype of *Grenana angrenica* Samylina (number 813/1N13) is a sterile leaf compression (Samylina, 1990). Although the aforementioned reproductive structures, including seeds and cupules, are facies-associated with the leaves, they never occur in an attached state. It is important to note that fig. 1 of Samylina (1990) is merely a hypothetic reconstruction and does not represent an actual specimen. Consequently, we consider the reinterpretation of *Grenana* by Zhou (1997, p. 185) to be misleading. We maintain that the genus *Grenana* is best reserved for the foliage alone and that the facies-associated reproductive structures should be classified as a new taxon.

The genus *Nehvizdyella* is also similar to the ginkgoalean ovuliferous reproductive structures *Umaltolepis* Krassilov from the Lower Cretaceous of Siberia (Krassilov, 1972) and *Toretzia* Stanislavski from the Triassic of Ukraine (Stanislavsky, 1973); they all have one or two ovules per axis (Appendix S1). However, *Umaltolepis* differs from *Nehvizdyella* in having a bract supporting the ovule, in having bracts at the base of the seed-bearing axis, and by the absence of a cupule-like structure. *Toretzia* differs from *Nehvizdyella* in having inverted anatropous seeds and in lacking cupule-like structures. Additionally, both *Toretzia* and *Umaltolepis* differ from *Nehvizdyella* in having linear ribbon-like leaves named *Pseudotorellia*.

Of the other fossil ginkgoalean reproductive structures described in the literature, all differ substantially from *Nehvizdyella* (Appendix S1). *Schmeisneria* Kirchner and Van Konijnenburg-Van Cittert from the Jurassic of Germany has small

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7. Dispersed seed with stalk (arrowed), macerated. F 03018. ×4. **8.** Outer cuticle of sarcotesta showing stomata. F 03018c. ×100. **9.** Inner cuticle of sarcotesta. F 03018b ×100. Figs. 10–11. *Nehvizdyella bipartita* gen. et sp. nov. Hloubětín Brickpit, seed morphology. **10.** Dispersed seed compression, F 00189. ×5. **11.** Detail of seed anatomy showing sarcotesta (sa), epidermis of sarcotesta (e), and sclerotesta (sc), detail of Fig. 10. F 00189. ×15.
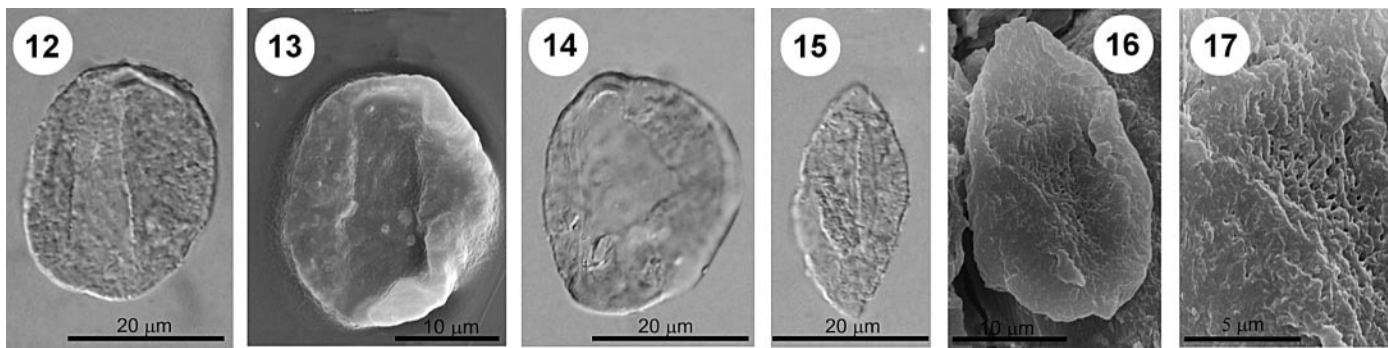
Figs. 12–17.   *Cycadopites* sp. Horoušany, Kamenná Panna Quarry, pollen morpology. **12.** Pollen grain showing concave sulcus, light microscopy (LM). F 03018c. ×1000. **13.** The same pollen grain as in Fig. 12, SEM. F 03018c. ×1000. **14.** Pollen grain showing irregularly open sulcus, LM. F 03018d ×1000. **15.** Boat-shaped pollen grain showing narrow sulcus, LM. F 03018e, ×1000. **16.** Partly fragmented pollen grain showing intrareticulate sculpture of sulcus, SEM. F 03018f ×1000. **17.** Detail of exine in sulcus, detail of Fig. 16, SEM. F 03018f. ×4000.

orthotropous ovules, and is locally attached to short shoots of *Glossophyllum* or *Eretmophyllum* type (Kirchner and Van Konijnenburg-Van Cittert, 1994). *Yimaia* Zhou and Zhang from the Middle Jurassic of China shows eight to nine sessile anatropous ovules, attached to or facies-associated with *Baiera* and *Ginkgoites* foliage (Zhou and Zhang, 1988, 1992). *Karkenia* Archangelsky from the Lower Cretaceous of Argentina has numerous small anatropous ovules per axis and is facies-associated with a variety of foliage types including *Sphenobaiera*, *Ginkgodium*, and *Eretmophyllum* (Archangelsky, 1965; Del Fueyo and Archangelsky, 2001). It probably represents a distinct, perhaps ancestral, lineage within the Ginkgoales, together with the Palaeozoic genus *Trichopitys* (Zhou, 1997).

FACIES-ASSOCIATED PLANT REMAINS

A variety of other unequivocally ginkgoalean morphotaxa co-occur in the same depositional facies as *Nehvizdyella bipartita* at four widely spaced localities. This assemblage comprises a single morphotaxon of pollen, sterile foliage, short shoot, and trunk wood, with fossil remains being preserved both as compressions and charcoal. The facies association, together with close anatomical similarities, strongly suggest that all these organs belonged to the same plant.

Pollen—*Cycadopites* sp. (Figs. 12–17)

Material studied—F 03018 c, d, e, f, National Museum, Prague.

Horizon and locality—Late Cretaceous (Cenomanian) Peruc-Korycany Formation, at Horoušany, Kamenná Panna Quarry near Nehvizdy.

Description—Eleven pollen grains and their fragments were found adhering to the exterior of the seed of *Nehvizdyella bipartita*. They were the only pollen grains adhering on seed no. F 03018. Pollen grains were photographed during maceration of the seed cuticle, so they are in various modes of preservation and fragmentation.

Pollen grains are boat shaped with a single sulcus, not more than 30 μm in diameter (Figs. 12–16). The sulcus occupies the entire length of the grain and is slightly concave (Figs. 12, 13). The pollen surface is scabrate, and microverrucate (Fig.

12). Auricular projections observed by Sahashi and Ueno (1986) are visible and have a reticular-like sculpture on the germinal aperture. This sculpture is also present in an internal part of the sulcus (Fig. 17).

Discussion—The pollen grains attached to seeds of *Nehvizdyella bipartita* agree with the genus *Cycadopites* Wodehouse (ex Wilson and Webster, 1946) in having the same size and shape and one colpus and a similar exine pattern. The genus was based on material from the Palaeocene of Red Lodge, Carbon County in Montana, USA (Wodehouse, 1933; Wilson and Webster, 1946) and later emended by Krutzsch (1970) and Nichols et al. (1973). The type species, *Cycadopites follicularis* Wilson and Webster 1946, differs from the present *Cycadopites* sp. in larger size and rather smoother surface. The most similar pollen taxa to *Cycadopites* sp. are *Cycadopites fragilis* Singh and *Cycadopites nitidus* (Balme) de Jersey (1964), which are commonly encountered in the same supratidal marsh facies that contain *N. bipartita* in the Bohemian Cretaceous Basin (e.g., Pacltová and Svobodová, 1993; Svobodová, 1990, 1992; Svobodová et al., 1998; Uličný et al., 1997). They both agree in general morphology with the material described herein attached to *N. bipartita*, having nearly smooth or faintly granulate exine.

Cycadopites fragilis was originally described from the Lower Cretaceous of Alberta (Singh, 1964) and is characterized by a sulcus extending the whole length of the grain and a smooth surface. *Cycadopites nitidus* was originally described from the Lower Cretaceous of Australia (Balme, 1957). It is characterized by a narrow sulcus extending the full length of the distal surface, which is slightly expanded at the extremities, and a faintly granulate exine. These two types of pollen primarily differ only in terms of size, and we therefore suggest that the two Czech species likely represent taphonomic or ontogenetic variants. This view has been previously discussed by Norris (1967), who identified a similar intergradational relationship between two other *Cycadopites* pollen species. In summary, we suggest that *C. fragilis* and *C. nitidus* in the Cretaceous Bohemian Basin of the Czech Republic were probably produced by the same species that bore *N. bipartita* organs.

According to the morphological classification scheme introduced by Thomson and Pflug (1953) the pollen grains described here are also similar to the genus *Monocolpopollenites* Pflug and Thomson in Thomson and Pflug 1953. However, *Monocolpopollenites* differs from our material in its shorter

sulcus and in having marginal folds. It is also smaller and confined mostly to pollen derived from monocots.

Foliage—*Eretmophyllum obtusum* (Velenovský) Kvaček, J., 1998 (Figs. 18–24)

Holotype—F 00003, Velenovský 1885, pl. 1, fig. 8, National Museum, Prague, refigured herein (Fig. 18).

Type locality—Nehvizdy (old sandstone quarry in east surroundings of the village).

Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

Other material—Nehvizdy (holotype F 00003, F 00004–7, F 00012, 13); Prague, Vysočany (F 00010); Lipenec (F 00008, 9); Kralupy and Vltavou (F 00014, 15); Prague, Hloubětín (Velenovský type collection-F 00011); Prague, Hloubětín Brickpit (F 00112–133, F 00189–191, F 02856); Horoušany, Kamenná Panna Quarry (F 02886, F 02958, F 02972); Pecínov Quarry, unit 3 (F 02281, F 02293, F 2481–3, F 02497–2500, F 02856).

Description—Leaves of *Eretmophyllum obtusum* are large (up to 11 cm long and up to 2.5 cm at their widest point), tongue-shaped, coriaceous, and entire-margined with a typically obtuse apex and cuneate base (Figs. 18, 19). The massive well-pronounced petiole (3 mm in diameter) contains two veins (Fig. 19). The veins dichotomously branch near the base of leaf, run subparallel to leaf lamina, and converge near the apex at a high angle. Up to 8–12 veins per cm occur in the medial part of the leaf. The adaxial cuticle is very heavily cutinized, composed of polygonal, isodiametric to slightly elongate cells, that are arranged in longitudinal rows with anticlinal walls that are straight or slightly bent (Fig. 23). The abaxial cuticle is also heavily cutinized, with costal and intercostal bands (Fig. 20). Intercostal cells are polygonal, elongate, and occur in longitudinal rows. Costal bands are constructed of strongly cutinized polygonal, isodiametric cells, and stomata, which are randomly scattered or arranged in short rows (Fig. 24). Stomata are haplocheilic, deeply sunken, and surrounded by 4–6 subsidiary cells (Fig. 22). Subsidiary cells are strongly cutinized and typically bear papillae that form a raised coronal rim (Fig. 21). Numerous circular or spindle-shaped resin bodies occur in the mesophyll tissue (Fig. 20).

Discussion—These tongue-shaped leaves were first described from the Cenomanian of Bohemia as *Podozamites obtusus* (Velenovský, 1885), but their ginkgoalean affinity was later established by Velenovský and Viniklář (1926, 1927). Believing that the leaves were not arranged in bundles and given their superficial similarity to *Glossophyllum*, Hluštík (1977) erected the genus *Nehvizdya* for this foliage type. In his revision of gymnosperm foliage from the Bohemian Cenomanian, Kvaček (1998, 1999) transferred these fossil leaves to the genus *Eretmophyllum*, introducing a new combination *Eretmophyllum obtusum* (Velenovský) Kvaček J. (2000). Gomez et al. (2000) attempted to distinguish *Eretmophyllum* from *Nehvizdya* on the basis of the presence or absence of papillae on subsidiary cells as the differential character. However, this character is variable among genera in the Ginkgoales, and the suggested splitting of *Nehvizdya* and *Eretmophyllum* is con-

sequently not accepted herein. The ginkgoalean affinity of *Eretmophyllum* is based on its dichotomous venation, which arises from the two main petiole veins, and its cuticle having haplocheilic stomata (Thomas, 1913).

Short shoots—*Pecinovicladus kvacekii* Falcon-Lang, 2004 (Figs. 25–34)

Holotype—F 02912; National Museum, Prague, refigured herein (Fig. 25).

Type locality—Pecínov Quarry, unit 3.

Type horizon—Late Cretaceous (Cenomanian), Peruc-Korycany Formation.

Other material—Pecínov Quarry, unit 3, F 02910, F 02911, F 02913-F 02926.

Description—*Pecinovicladus kvacekii* consists of 7–13 mm diameter shoots comprising pith, xylem, periderm, leaf traces, and branch traces (Fig. 25). The 1.6–2.2 mm diameter pith is parenchymatous. The xylem layer is 0.5–1.8 mm in radius (Fig. 26). Mucilage ducts (70–110 μm in diameter, >1.1 mm high) surrounded by axial parenchyma occur in the inner part of the secondary xylem (Fig. 27). Xylem comprises scalariformly-thickened primary and metaxylem succeeded by pycnoxylic secondary xylem composed of irregularly arranged tracheids (7–26 μm in diameter). Tracheids have 1–2-seriate, alternate or mixed, circular, bordering pitting on the radial walls (Fig. 28). Cross-fields comprise 1–6 taxodioid or cupressoid pits per field (Fig. 29). Axial parenchyma, arranged in vertical files may locally contain inflated cells, 25–45 μm in diameter, containing crystalline molds (Fig. 30). Rays are very short (1–7 cells high) and uniseriate, being spaced 5–11 tracheids apart (Fig. 31). The cambial zone, 55 μm radius, contains inflated parenchyma and rhombic crystal molds. The 2.5 mm radius periderm comprises parenchyma, resin-filled fibers and sieve cells.

Leaf traces, comprising an oval adaxial xylem strand and a crescent-shaped abaxial phloem strand, are 1.0–1.5 mm in diameter at the point of departure from the secondary xylem, and arranged with a 5/13 helical phyllotaxy (Figs. 25, 32). Leaf bases preserved on the exterior of the axis, 2.7–3.5 mm wide and 1.45 mm thick, comprise xylem, phloem, mesophyll and epidermis (Fig. 33). The vascular bundle ramifies into >6 veins at the leaf base. Some shoot specimens have fewer leaf traces, but have secondary branch traces (1.8–2.1 mm diameter) comprising a 0.8 mm diameter pith and a 0.8 mm radius secondary xylem layer. A few secondary branches are positioned in the leaf axil (bracts) and may represent the detached peduncle of reproductive structures (Fig. 34).

The ginkgoalean affinity of this morphotaxon is indicated by a combination of features including, most importantly, the presence of inflated axial parenchyma in the secondary xylem, which demonstrably once contained crystalline druses (Gunckel and Wetmore, 1946; Greguss, 1955; Scott et al., 1962). Additional ginkgoalean features are irregularly arranged files of wide and narrow tracheids in the secondary xylem (Srivastava, 1963), and very short rays (Mastogiuseppe et al., 1970).
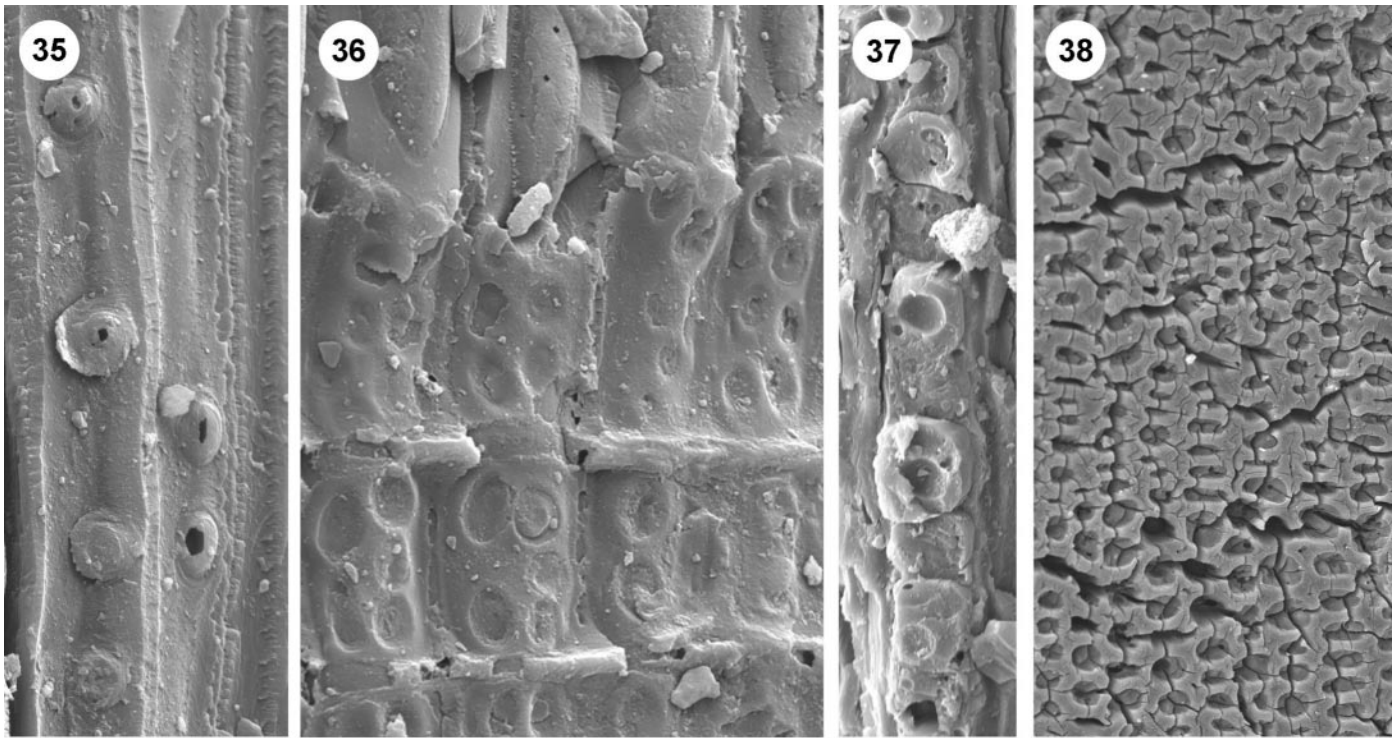
Mature wood—*Ginkgoxylon gruettii* Pons and Vozenin-Serra 1992 (Figs. 35–38)
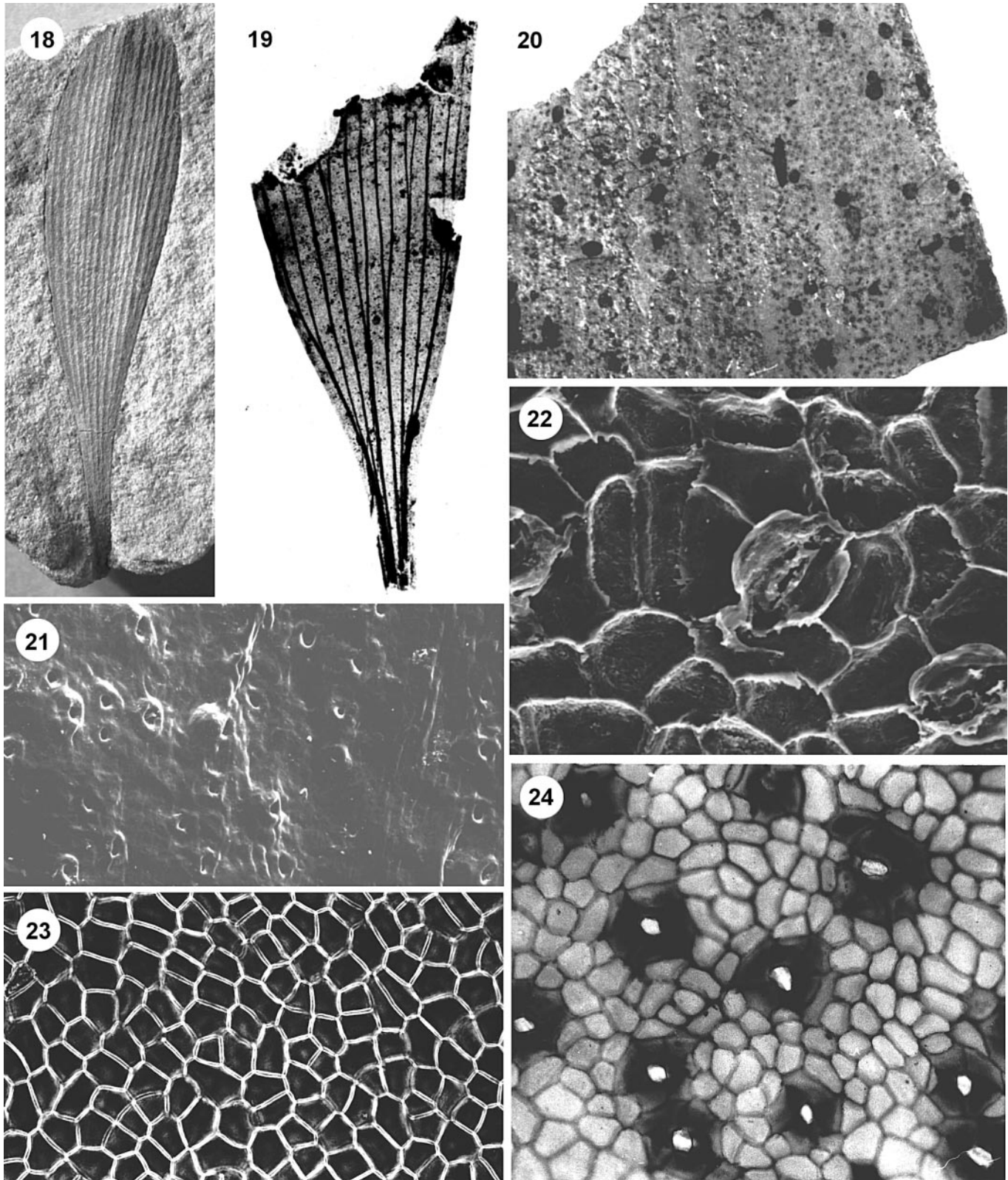
Figs. 18–24. *Eretmophyllum obtusum* (Velenovský) Kvaček, J., leaf morphology and anatomy. **18.** Holotype, leaf impression, Nehvizdy. F 00003. ×1. **19.** Basal part of naturally translucent leaf showing venation pattern, Prague, Hloubětín Brickpit. F 00116. ×2.5. **20.** Macerated leaf showing resin bodies, Pecínov Quarry, unit 3. F 02483. ×10. **21.** Outer part of abaxial leaf cuticle, SEM, Pecínov Quarry, unit 3. F 02481b. ×100. **22.** Inner part of abaxial cuticle, SEM, Pecínov Quarry, unit 3. F 2481b. ×500. **23.** Adaxial cuticle, type collection of Velenovský, LMM, Prague, Hloubětín. F 0008. ×200. **24.** Abaxial cuticle, type collection of Velenovský, LMM, Prague, Hloubětín. F 0008. ×200.
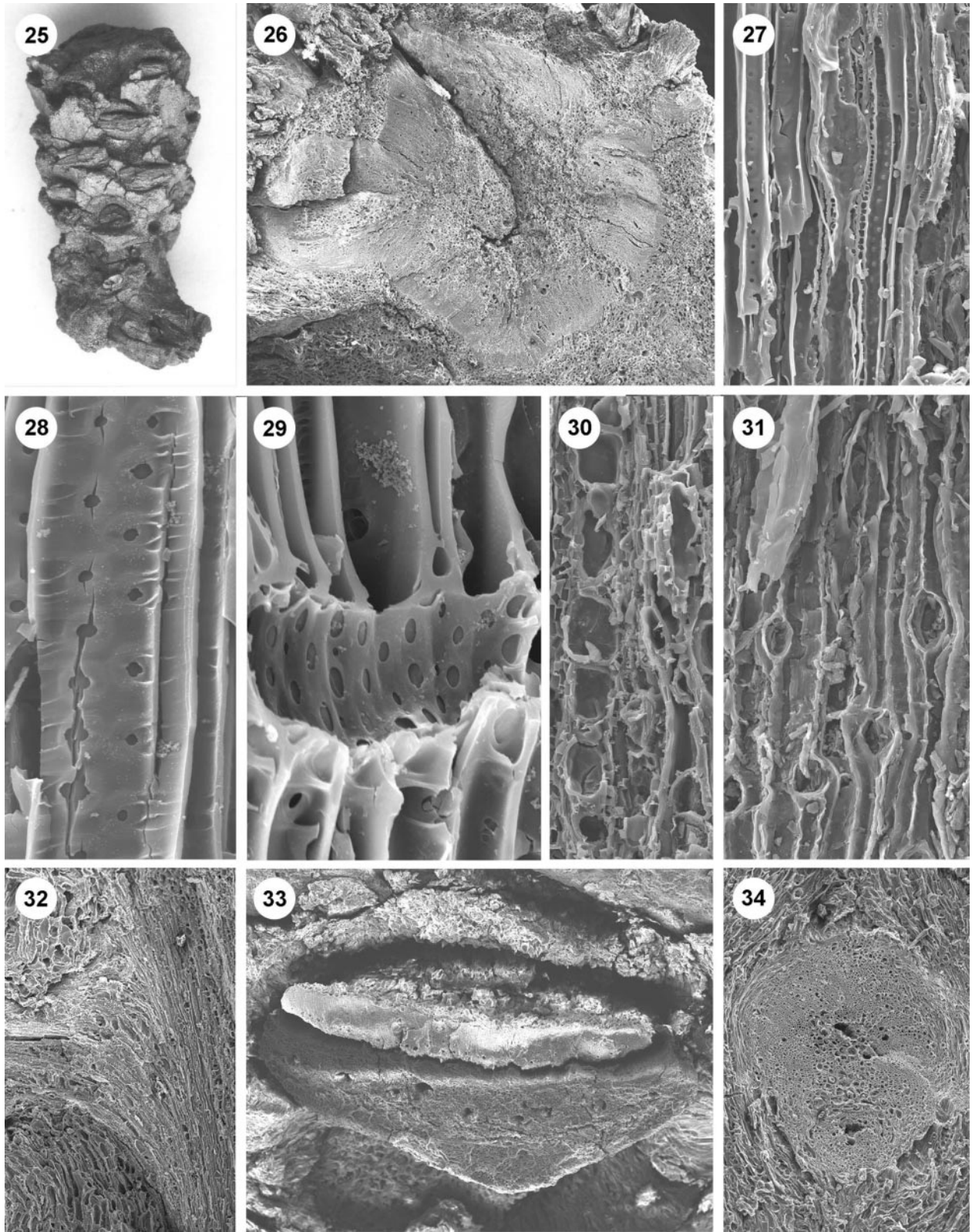
Figs. 25–34.   *Pecinovicladus kvacekii* Falcon-Lang, anatomy. **25.** Holotype, longitudinal view of branch, Pecínov. F 02912, ×2.5. **26.** Primary branch in transverse section (TS) with secondary branch, Pecínov. F 02912. ×10. **27.** Mucilage duct surrounded by epithelial cells, Pecínov, radial longitudinal section (RLS). F 02909. ×180. **28.** Tracheid with alternate and opposite bordered pits, Pecínov, RLS. F 02910. ×650. **29.** Cross-field pitting, Pecínov, RLS. F 02909. ×1000. **30.** Inflated axial parenchyma, Pecínov, tangential longitudinal section (TLS). F 02909. ×150. **31.** Uniseriate rays, Pecínov, TLS. F 02910. ×300. **32.** Departing leaf trace, Pecínov, RLS. F 02910. ×30. **33.** Leaf trace showing xylem and phloem bundles, Pecínov, TLS. F 02910. ×18. **34.** Reproductive axis (penducle) embedded in branch, position in leaf axil, Pecínov, TLS. F 02911. ×40.

Figs. 35–38. *Ginkgoxylon gruettii* Pons and Vozenin-Serra, wood anatomy, Hloubětín Brickpit. **35.** Uniseriate, spaced tracheid pits, radial longitudinal section (RLS). F 03038. ×1000. **36.** 2–8 cupressoid cross-field pitting, RLS. F 03038. ×1250. **37.** Chains of inflated axial parenchyma, RLS. F 03038. ×200. **38.** Tracheids in transverse section (TS) showing faint growth interruption. F 03038. ×250.

Holotype—10532, Palaeobotany Laboratory, Pierre and Marie Curie University, Paris.

Type locality—Carrière du Bouillard, Nord d'Angers, France.

Type horizon—Late Cretaceous (Cenomanian), Jumelles and Brissac Formation.

Material studied—F 03038, National Museum, Prague.

Horizon and Locality—Late Cretaceous (Cenomanian) Peruc-Korycany Formation, at Prague, Hloubětín Brickpit.

Description—Mature ginkgoalean wood is known from a single trunk specimen, 13 cm in diameter and >1.09 m in length, preserved in the salt marsh peat facies at Hloubětín Brickpit. Anatomically, the wood is pycnoxylic, consisting only of tracheids and rays. In radial longitudinal section (RLS), tracheids are characterized by uniseriate bordered pits which are typically spaced at least one pit diameter apart (Fig. 35). Both borders (9–10 μm in diameter) and apertures (2–3 μm in diameter) are circular. Rays are composed of parenchyma cells that are 50–75 μm long, 20–30 μm high, and 20–30 μm wide, and have well-preserved cross-field pitting. Typically 2–8 circular cupressoid pits, each 5–6 μm in diameter, occur clustered in the cross-field region (Fig. 36). Chains of inflated axial parenchyma, 3–12 cells in length are common (Fig. 37). Axial parenchyma cells are large (25–45 μm in diameter), locally thick-walled (up to 8 μm thick), and may contain moldic preservation of crystalline druses. In tangential longitudinal section (TLS), rays are uniseriate and short (1–12

cells high). Tangential tracheid pits are absent. In transverse section (TS), rays are spaced 90–210 μm apart, and may be up to 3–4 mm long. Tracheids have tangential diameters of 14–22 μm and radial diameters of 12–21 μm. Middle lamellae are present between adjacent trachieds indicating that the wood is lignified, not charred. Growth rings are absent over several centimetres, but subtle growth interruptions do locally occur with an irregular spacing (Fig. 38).

This wood corresponds closely to *Ginkgoxylon gruettii* Pons and Vozenin-Serra from the Cretaceous (Cenomanian) of Anjou, France. This species differs from the Czech specimens in exhibiting rare biseriate trachied pitting, rare biseriate rays that are 1–26 cells high, and fewer cross-field pits (1–6). Such differences are of little taxonomic significance and likely reflect ontogenetic variability (Falcon-Lang, 2005a). For these reasons, our mature woods are assigned to *Ginkgoxylon* cf. *G. gruettii*. This morphotaxon has also recently been discovered in Cenomanian deposits at Charente in western France (Perrichot, 2000). One of the key features that allows this morphotaxon to be referred to the Ginkgoales is, as previously noted, the presence of druse-filled, inflated axial parenchyma chains (Gunckel and Wetmore, 1946; Greguss, 1955; Scott et al., 1962).

WHOLE-PLANT RECONSTRUCTION

Despite the abundance and diversity of Cretaceous ginkgoalean remains, assemblages of isolated morphotaxa have rarely been reconstructed in terms of a whole-plant. However, it is important that such attempts are made in order to gain a true sense of ginkgoalean diversity and phylogeny (Tralau, 1968; Zhou, 1997; Czier, 1998). Some ginkgoalean taxa show

a high degree of polymorphism with up to three genera of sterile foliage associated with one reproductive structure, and locally one genus of sterile foliage may have several associated reproductive structures (Zhou, 1997). Consequently, analysis of isolated morphotaxa may result in either an overestimate or underestimate of biological diversity.

Whole-plant reconstruction—In this paper we demonstrate the common affinity of *Nehvizdyella bipartita* ovuliferous organs, *Cycadopites* pollen, *Eretmophyllum obtusum* leaves, *Pecinovicladus kvacekii* short shoots, and *Ginkgoxylon gruettii* trunk wood based on (1) the facies co-occurrence of parautochthonous remains at four sites, and (2) the precise anatomical correspondence between adjacent morphotaxa.

Specifically, *Cycadopites* pollen is found adhering to *Nehvizdyella*, whereas other pollen morphotaxa are absent. Furthermore, *Cycadopites* pollen is always highly abundant in the salt marsh facies dominated by *Eretmophyllum*. Leaf bases preserved on the external surface of *Pecinovicladus* are anatomically and morphologically identical to the leaf bases of *Eretmophyllum*, indicating a close association between the two morphotaxa (Falcon-Lang, 2004). Furthermore, secondary axes preserved in leaf axils (bracts) on *Pecinovicladus* are of identical size and shape to the main axis of *Nehvizdyella*, and closely correspond anatomically. The secondary wood of *Pecinovicladus* is almost identical to *Ginkgoxylon* wood, the only minor differences probably being related to wood ontogeny (Falcon-Lang, 2005a). Finally, *Nehvizdyella* bears the same type of stomata and contains the same type of resin bodies as leaves of *Eretmophyllum*, indicating a common affinity (compare Fig. 8 and Figs. 5, 20, 24).

Previous studies have also hinted at this same association, although only in part. For example, Velenovský and Viniklář (1926, 1927) described poorly preserved isolated axes (putative long shoots) and seeds, which they tentatively associated with *Eretmophyllum* foliage. Preliminary cuticular studies of seed sarcotesta were carried out by Hluštík (1986), who also noted an association with *Eretmophyllum* foliage. In both cases, the seeds were of the same type as those described herein as *Nehvizdyella bipartita*. Hluštík (1986) attempted a partial reconstruction of these remains, depicting them in terms of a long shoot with helically arranged leaves, a reconstruction based on Velenovský and Viniklář (1926)'s poorly preserved specimen (which is now lost). During the course of our investigation, we did not find similar long shoot material. It is possible that the *Nehvizdyella* whole-plant possessed both short shoots and long shoots, as in recent *Ginkgo*, but in the absence of well-preserved long shoot material we are unable to confirm Hluštík's reconstruction.

Based on the fossil assemblage described, we maintain that the *Nehvizdyella* whole-plant was a small tree or large shrub. The maximum recorded trunk diameter of only 13 cm suggests a height of no more than a few meters given biomechanical considerations (Niklas, 1994). Lateral branches with short shoots, and possibly long shoots, bore helically arranged tongue-shaped leaves up to 11 cm long with ovules locally positioned on stalks within the leaf axils. A representative branch of *Nehvizdyella* whole-plant is illustrated in Fig. 39.

Paleoecology—The ginkgoalean assemblage is exclusively associated with salt marsh peat facies at four different localities spanning the entire basin (Uličný and Nichols, 1997). These units were formed during periods of marine transgres-

Fig. 39. Reconstructed short shoot bearing *Nehvizdyella* reproductive structures by Jiří Svoboda. ×0.5.

sion and represent a saline, water-stressed environment (Uličný et al., 1997). Tree-rings in facies-associated woods additionally suggest a seasonally dry subtropical climate (Falcon-Lang et al., 2001). The ginkgoalean remains, especially *Eretmophyllum obtusum* leaves, occur in very high concentrations in these units, locally forming the dominant component of the peat (Kvaček, 1999). These data, together with presence of roots below the peat and the taphonomic co-occurrence of organs with varying hydrodynamic properties (Nichols et al., 2000), indicate that this is an autochthonous or parautochthonous assemblage. Therefore, the ginkgoaleans, together with co-occurring cheirolepid conifers, putative gnetaleans, and a few angiosperms, are best characterized as a mangrove or salt marsh community (Hluštík, 1986) with trees adapted for growth in saltwater environments (Tomlinson, 1994). No modern coniferopsids utilize the mangrove or saltmarsh strategy (Hogarth, 1999), although rare putative examples have been reported from the fossil record (Falcon-Lang, 2005b).

Carbon isotopic studies of plants from the salt marsh peat facies allow more detailed palaeoecological interpretation. The angiosperm, gnetalean, and cheirolepid conifer remains have highly positive δ^{13}C values (-23‰) compared to the mean value for the whole Peruc-Korycany Formation, consistent with growth under highly water-stressed conditions (Nguyen Tu et al., 1999, 2002). Additionally, these plants have very thick cuticles and show a variety of xerophytic characters including deeply sunken stomata (Uličný et al., 1997). In contrast, δ^{13}C values for *Eretmophyllum* are consistently more negative (-25.5‰) than the other salt marsh plants, although more positive than for plants in freshwater facies (-27‰). Furthermore, *Eretmophyllum*, being a broadleaf, is less characteristically xeromorphic, although such characters as sunken, papillate stomata certainly suggest xeromorphy (Kvaček, 1999). An additional xeromorphic character in *Nehvizdyella* is the enclosure of ovules in sterile tissues (presumably to limit water loss), a feature also seen in *Alvinia bohemica*, the ovuliferous cone of *Frenelopsis alata* (Kvaček, J., 2000). Isotopic data perhaps imply that the *Nehvizdyella* tree grew in less saline regions of the salt marsh, either in a supratidal setting landward of the other trees, or adjacent to lower salinity drainage channels that locally cut into the salt marsh peat facies (Uličný et al., 1997).

The absence of tree-rings in the woody cylinder of *Peci-*

novicladus may suggest that all of the short shoots were less than 1 year old and were therefore seasonally shed as in *Metasequoia*. However, tree-rings are also absent in the mature wood, *Ginkgoxylon gruettii* so the age at which short shoots were shed cannot be assessed with certainty. Nor can the occurrence of discrete *Eretmophyllum*-rich laminae be used as an indicator of seasonal leaf shedding because this may simply represent a taphonomic phenomenon. Furthermore, *Eretmophyllum* leaf bases and leaf scars attached to *Pecinovicladus* show evidence for mechanical breakage rather than abscission, perhaps indicating an evergreen habit. Whilst the phenology of the *Nehvizdyella* tree cannot be determined with certainty, it is worth noting that all modern trees adapted to salt marsh or mangrove settings have a physiological necessity for an evergreen canopy. It is therefore likely that our Cretaceous ginkgoalean tree was similarly evergreen, in contrast to its nearest living relative, *Ginkgo biloba*.

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