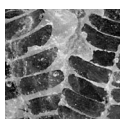# A large specimen and cuticles of *Paripteris gigantea* (Sternberg) Gothan from its type area Žacléř (Pennsylvanian, Czech Republic)

ZBYNĚK ŠIMŮNEK

An exceptionally well preserved, large fragment of *Paripteris gigantea* frond with "pseudo-pinnate" organization was found in Žacléř, Lampertice Member, Žacléř Formation (Intrasudetic Basin, Czech Republic). The single distal dichotomy of several basal "ultimate" pinnae is documented. The adaxial cuticle has elongated tetragonal cells oriented parallel to veins. The cells of the abaxial cuticle are probably polygonal with faintly discernible anticlinal walls; the haplocheilic stomata are sunken, partly covered by the proximal papillae of the subsidiary cells. Stomata are 22–30 µm long and 10–14 µm wide. Trichom bases are present on the pinnule margin and in the intercostal field of the abaxial cuticle. There are two concepts in the infrageneric classification of *Paripteris.* In contrast to traditional binomical classification (*e.g.*, Cleal & Shute 1995), Zhang *et al.* (1993) preferred to provisionally interpret all the so far described species as forms of *Paripteris gigantea.* • Key words: *Paripteris gigantea,* Pennsylvanian, cuticular analysis, Intrasudetic Basin.

After the closing of the last deep mine, Jan Šverma, in Žacléř in 1992, mining activity restarted in 1999. The residual coal resources have been exploited by five quarries that were successively opened and later closed. Remains of *Paripteris gigantea* (Sternberg) Gothan are very common as isolated pinnules on bedding surfaces of mudstones that comprise the roof rocks and intercalations of the upper coal seams Nos 9, 10 and 11 of the Jan Šverma Coals, Lampertice Member, Žacléř Formation. Most of the finds came from the roof of the 9th coal seam that has been mostly exploited by the quarries.

These remains of *Paripteris gigantea* were not the first finds in the Žacléř area. This species had been reported by Sternberg (1821, 1825), Němejc (1933, 1953), Němejc & Šetlík (1950), Havlena (1953), Šetlík *in* Tásler (1979), Purkyňová (1986) and others from the same area. Additional available data are accessible in the unpublished reports of Rieger & Šetlík, namely from boreholes drilled in the period from 1950 to 1970. Invaluable information about the stratigraphical distribution of *Paripteris gigantea* can be found in the report about the construction of the pit Jan of Šverma mine (Rieger *et al.* 1962). However, we can trace the beginnings of investigation of this species back to the 19th century, when Sternberg (1821) erected *Osmunda gigantea* on the basis of a specimen from the Žacléř area.

This species is very important from the point of view of migration of floral elements from Asia to Europe and North America (Laveine *et al.* 1993, 2000; Laveine 1997). Although this species has been known for nearly 200 years, the first reconstruction of the frond was made by Laveine (1967) and modified by Laveine *et al.* (1993). The specimen found in quarry No. 4 provides additional data on the gross morphology of this plant. The cuticles of *Paripteris gigantea* were firstly studied by Barthel (1961). Pteridosperm pinnules are usually weathered in the area of Žacléř quarries, therefore the cuticles were extracted from a specimen from borehole Š 13, situated less than 2 km SEE from the quarries (Spudil 1999).

Material and methods

Samples were collected in all five quarries in the area, whenever possible, systematically layer-by-layer (Fig. 1). The floras from individual layers were evaluated separately (Libertín *et al.* 2009). The thickness of the individual layers is between 5 to 10 cm. Isolated pinnules of *Paripteris* Gothan have been frequently obtained from the spoil tip of
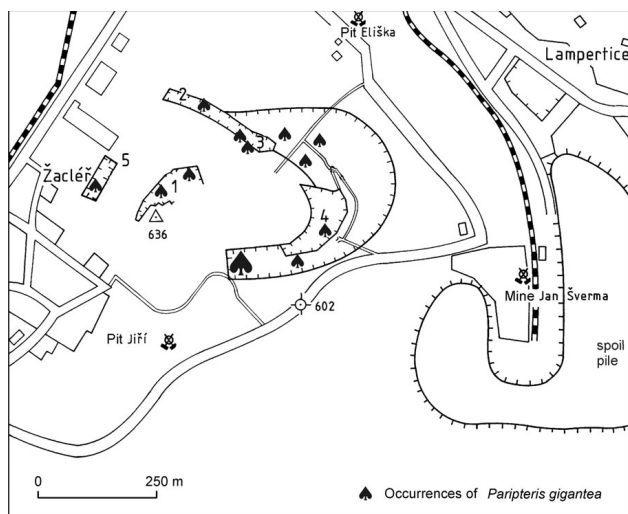
Figure 1. Map of area between Žacléř and Lampertice, the numbers 1–5 represent the quarries.

the Jan Šverma (formerly Marie-Julie) deep coal mine and also in small quarries that started to operate in 1999. The quarries (Nos 1 to 5; Fig. 1) mined the upper coal seams Nos 9, 10, and partly 11 (Fig. 2). Larger fragments of fronds are very rare and the frond fragment from the quarry No. 4 is exceptional. It represents parts of two penultimate pinnae on a slab 75 cm long and 75 cm wide preserved in roof rock mudstone. The studied *Paripteris* frond is from the Duckmantian Substage (Pennsylvanian Subsystem). The large fragment of *Paripteris gigantea* described here was excavated very carefully, and its component parts were wrapped and transported to the Czech Geological Survey building. These small fragments were stuck back together in the lab and studied. Now it is stored there under the No. ZŠ 144a, b.

The sample for cuticular study comes from rocks between the 10th and 11th upper coal seams of borehole Š 13, and is thus from the same stratigraphic level as that exposed in the quarries. Coalified pinnules were separated from the rock matrix by means of hydrofluoric acid (HF), then were bleached in Schulze's reagent (conc., or 20, respectively 40% solution of HNO_3 with crystals of $KClO_3$). The maceration time was 20 hours after which the cuticles were washed in diluted ammonium hydroxide (NH_4OH) or 2% potassium hydroxide (KOH), and finally rinsed in distilled water (see Kerp 1990 and Kerp & Krings 1999). The cuticles were stained with safranin to accentuate cellular structures. The cuticles were embedded in glycerine gelatine slides.

Geological setting

The late Namurian to early Westphalian Žacléř Formation was deposited in the Intrasudetic Basin, one of the basins of the Sudetic area. The Intrasudetic Basin straddles the border between the Czech Republic and Poland. The oldest coal-bearing deposits belong to the Wałbrzych Formation of early Namurian age, and are preserved only in the Polish part of the Intrasudetic Basin. The sedimentation in the Czech part starts with the Błażkow Formation that was formed by coloured (mauve or maroon) rocks with a dominance of conglomerates. The thickness of this formation is several tens to a few hundreds of meters and its age is probably late Viséan to early Namurian. The unconformably overlying Žacléř Formation typically shows a cyclic development. Havlena (1956) defined 64 cycles of conglomerates, sandstones, siltstones, claystones and coal seams in the Lampertice Member, the oldest subdivision of this formation. The maximum thickness of this member is 680 m (Tásler *et al.* 1977). The thickness of a cycle varies from 3 to 30 m and the average thickness of a cycle is 11 m. The Intrasudetic Basin is a typical intermountain basin without any marine influence (the Viséan marine influence is known only in a small area of the Polish part). The basement is formed by the Proterozoic and Early Palaeozoic crystalline rocks. The thickness of the Lampertice Member is approximately 550 m in the Jan pit (crossed hammers at "Mine Jan Šverma" in Fig. 1). The rocks exposed in quarries 1–5 belong to the upper part of this unit.

Origin and terminology of the frond

The frond architecture was designated and described by Laveine *et al.* (1993) and Laveine (1997) as "pseudo-pinnate". The frond is quite large, differing from other neuropteroid groups. The above-mentioned authors explained such a frond as having originated from repeated bifurcations of a "fundamental rachis" (primary entity, bearing simple entire pinnules) by an overtopping process. Therefore, all rachises, whatever their apparent variable order of subordination, are fundamentally homologous. The compound frond is developed through exclusively dichotomous and dichotomous-anisotomous bifurcations of rachises without any pinnatifid segmentation of the lamina. This means that lobate pinnules do not occur in this species. On the other hand "intercalated" pinnules are present on all rachises.

The terminology for a "pseudo-pinnate" frond is not satisfactory. The frond could be called a "partly ante-antepenultimate" frond, because only its proximal parts are ante-antepenultimate, whereas its distal parts are antepenultimate. Similarly, a lateral pinna could be called a "partly antepenultimate" pinna, because its proximal part is antepenultimate and its distal part is only penultimate. This is maybe a little bit confusing, because it is difficult to determine which part of frond the incomplete pinna comes from.

Systematic palaeobotany

Class Pteridospermopsida
Order Medullosales (Trigonocarpales)

Genus *Paripteris* Gothan, 1941

Type species. – Paripteris gigantea (Sternberg, 1821) Gothan, 1941.

Paripteris gigantea (Sternberg, 1821) Gothan, 1941
Figures 3–10

- 1821 *Osmunda gigantea* Sternberg; Sternberg, vol. I, 2: tent. 33, pl. 22.
- 1825 *Nevropteris gigantea* (Sternberg). – Sternberg, vol. I, 4: tent. 16.
- 1831 *Neuropteris gigantea* (Sternberg) Sternberg. – Brongniart, vol. I, 5, p. 240, pl. 69.
- 1933 *Neuropteris gigantea* (Sternberg). – Stockmans, pp. 41–45, pl. 13, figs 1, 1a, 1b, pl. 14, figs 1–4, pl. 15, figs 1–2b.
- 1941 *Neuropteris gigantea* Sternberg. – Arnold, p. 70, pl. 1, fig. 5.
- 1944 *Neuropteris pseudogigantea* Potonié. – Bell, pp. 80, 81, pl. 33, figs 1, 2.
- 1953 *Paripteris gigantea* (Sternberg). – Gothan, p. 61, pl. 34, figs 1, 2, pls 35, 36.
- 1953 *Neuropteris gigantea* (Sternberg). – Havlena, pp. 44–51, pl. 4, pl. 5, figs 1, 1a, 2.
- 1959 *Neuropteris gigantea* (Sternberg). – Crookall, pp. 132–139, fig. 47, pl. 54, fig. 3.
- 1961 *Neuropteris gigantea* (Sternberg). – Barthel, pp. 830, 831; pl. 3, figs 6–13, pl. 4, figs 1, 2.
- 1967 *Paripteris gigantea* (Sternberg). – Laveine, pp. 250–259, pls 70–72.
- 1993 *Paripteris gigantea* (Sternberg). – Laveine *et al.*, pl. 1, figs 1, 3, 4, pl. 4, fig. 9, pl. 7, fig. 1, pl. 8.
- 1993 *Paripteris gigantea* f. *gigantea* (Sternberg). – Zhang *et al.*, p. 27, pl. 24, figs 1–3, pl. 29, fig. 7.
- 1995 *Paripteris gigantea* (Sternberg) Gothan. – Cleal & Shute, p. 28.
- 1997 *Paripteris gigantea* (Sternberg). – Laveine, pp. 160, 161.
- 2003 *Paripteris gigantea* (Sternberg) Gothan f. *gigantea*. – Laveine *et al.*, p. 510, pl. 11, figs 1–4, 6–9.

Description of the holotype. – The holotype comes from Žacléř and is stored in the National Museum in Prague under the No. E 4672 (see Fig. 3). It is preserved in grey micaceous mudstone. The slab is 380 mm long and 280 mm wide. This specimen was figured by Sternberg (1821) on pl. 22, but only part of the specimen was shown. On Sternberg's illustration, only five "ultimate" pinnae are
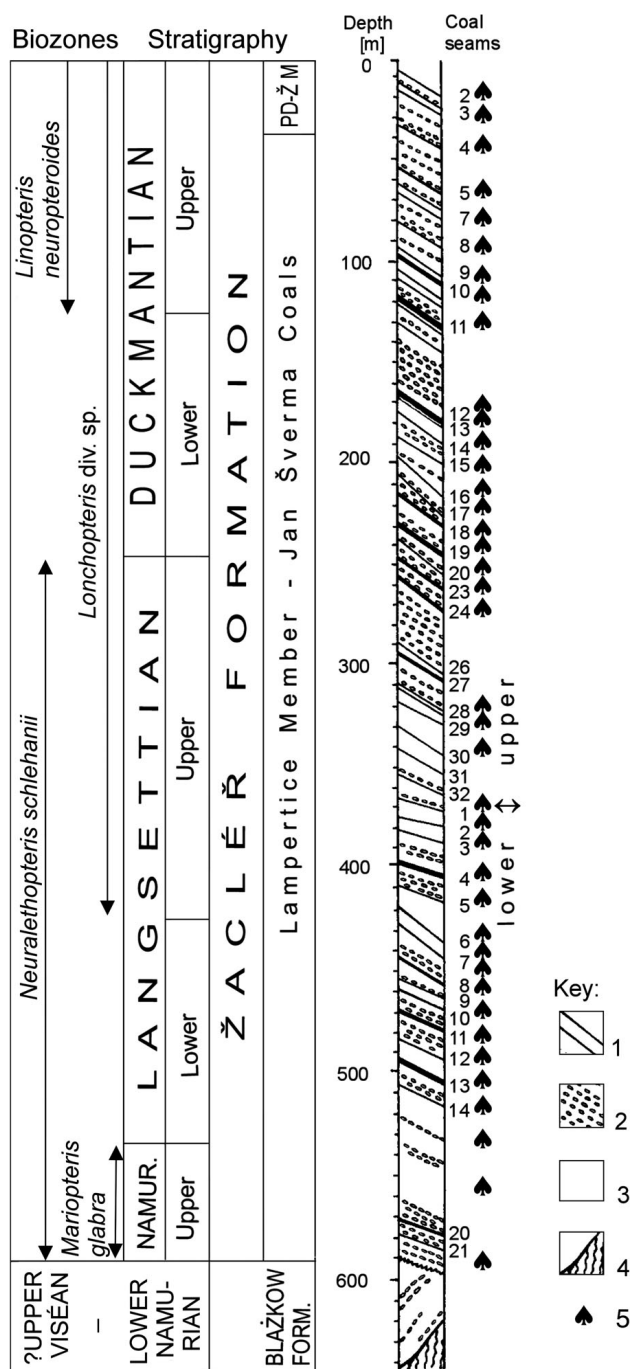

Figure 2. A simplified stratigraphic column of the Žacléř Formation in the pit Jan Šverma (crossed hammers near "Mine Jan Šverma" in Fig. 1). Key: 1 – coal seams, 2 – conglomerate, 3 – claystone, siltstone and sandstone, 4 – crystaline basement; 5 – occurrences of *Paripteris gigantea* according to Z. Rieger. Namur. – Namurian, PD-Ž M – Prkenný Důl–Žďárky Member. (Lithology simplified according to Rieger *et al.* 1962, floral zones according to Purkyňová 1986.)

shown on each side of the "penultimate" rachis. Havlena (1953) noticed that there are in fact seven "ultimate" pinnae on the right side and six on the left side of the "penultimate" rachis.

The "ultimate" pinnae are 170–180 mm long and 60–70 mm wide (see Fig. 3), and are elongatedly triangular. Their insertions on opposite sides are invariably shifted by 2–10 mm. The pinnules grow close to each other or overlap by 1–2 mm. They are attached almost opposite to each other or are mutually offset by 1–5 mm. The pinnules are almost straight, tongue-shaped at the base of the "ultimate" pinnae. After 3–5 pairs they change into sickle-shaped arched pinnules with parallel margins. The sickle-shaped arching becomes more intense towards the apex of the "ultimate" pinna. The pinnules are 22–24 mm long and 8–9 mm wide in the middle of the pinna. The pinnules are concave on the basiscopic side and 40–45 lateral veins per cm occur along the margin, whereas only 36–40 veins per cm of the margin occur on the acroscopic side. The flat midrib is visible to one-half of the pinnule lengths. The lateral veins are fine, several times forked, arching gently from the midrib and reach the pinnule margin at an angle of 50–70°.

The terminal pinnules are preserved only in two pinnae, but they are incomplete in one pinna. The complete terminal pinnules are unevenly developed, the larger pinnule being elliptic, 11.5 mm long and 4 mm wide, whilst the smaller pinnule is only 6.5 mm long and 3 mm wide. The intercalary pinnules are preserved only fragmentarily on the "penultimate" rachis. A very interesting feature is the bifurcating of the lowest left "ultimate" pinna (Fig. 3A, arrow). The two pinnules just above the bifurcation are small, rounded or suboval 6–7 mm in diameter. They are very similar to intercalary pinnules of other samples.

Emended diagnosis. – Pseudo-pinnate frond architecture, pinnules straight or sickle shaped, oblong-linear or oval-lanceolate with slightly cordate base and obtuse to bluntly pointed apex. Midrib reaches up to 2/3 of the pinnule blade. Lateral veins very fine and dense, arising from the midrib at very sharp angles and dividing several times. Intercalary pinnules small orbicular, oval, rounded, triangular or tongue-shaped.

Adaxial cuticle is formed by oblong, tetragonal to hexagonal elongated cells. anticlinal cell walls of abaxial cuticle are slightly cutinised, stomata are sunken with papillate subsidiary cells. Pinnule margin with numerous trichome bases.

Description of the specimen ZŠ 144a. – Specimen No. ZŠ 144a represents fragments of two partly "ante-penultimate" pinnae (Figs 4, 5). The largest pinna has an "ante-penultimate" rachis 700 mm long. It is around 5 mm wide along its entire length. It bears 11 or 12 "ultimate" pinnae on each side, even though they are not fully traceable due to preservation. The distance between rachises increases from 55 to 65 mm proximo-distally in the basal part of the pinna and from 48 to 55 mm in the terminal part of the pinna fragment. The pinnae are opposite or subopposite. The longest "ultimate" pinna is known from the basal acroscopic side – 260 mm, "ultimate" pinnae on the basiscopic side are up to

240 mm long. Only a few pinnae are complete and terminated by two small pinnules (Fig. 8C, D). Two "ultimate" pinnae on the acroscopic side and one "ultimate" pinna on the basiscopic side show a single distal dichotomy (Figs 5, 6, 7D, 8A, B). This dichotomy can be equal (second proximal acroscopic pinna) or unequal. The bifurcation in this specimen starts 90 to 140 mm from the base of the rachis and the parts above the dichotomy are 130–180 mm long, respectively. The dichotomy angle is 45 to 60°. The remaining four proximal pinnae on the left (basiscopic) side of the specimen in Figs 5 and 6 show several anisotomous dichotomies on their basiscopic side only. The left side shows higher proximo-distal differentiation than the right side (Fig. 6).

The second fragment of the "penultimate" pinna is only 300 mm long. Six "ultimate" pinnae are preserved only on one (left) side in their incomplete length as the contact of both "penultimate" pinnae is somewhat obscure. The "ultimate" pinnae of the opposite side are turned down and hidden in the rock. The distances of "ultimate" pinnae increase proximo-distally and are from 45 to 52 mm.

The "ultimate" pinnae are up to 260 mm long and 80 mm wide (in the middle). They taper slightly towards the base and apex.

Pinnules are very variable in shape and dimensions (Figs 7A, B, 8E, F). The "ordinary" pinnule shape is oblong-linear, or oval-lanceolate, perpendicular (in the basal and middle part of pinna) or slightly oblique (in the terminal part) to the rachis (*Paripteris gigantea* "forma *typica*", Fig 8F, or *Paripteris gigantea* "forma *lingua*" Fig. 7B). They can be sickle-shaped (mostly in the pinna terminal part) or straight (basal part), with a slightly cordate base. The "intercalated" pinnules are small orbicular, oval, rounded, triangular or tongue-shaped near the insertion (Fig. 8E); further on they are similar to the "normal" pinnules (Fig. 8E). The longest pinnule reaches 36 mm, whereas the pinnules from smaller pinnae are only 25 mm in length. The width of pinnules is 8–12 mm.

The venation is open, pinnate. The midrib is flat, traceable to half of the pinnule length (Fig. 8F). The lateral veins are fine, several times forked, and arise at a very sharp angle from the midrib. They bend and reach the pinnule margin at an angle of about 50–60°. The veins are relatively dense, 35–45 veins per cm on the pinnule margin.

Cuticles. – Cuticles (slides No. 158/1–2 and 476/1–10) were prepared from a specimen that originated from the borehole Š 13 (Žacléř locality), depth 489.85–490 m (between the 11th and 10th upper coal seams of the Šverma mine, Fig. 7C).

Pinnule adaxial epidermis (Fig. 9A, D): Costal and intercostal fields are weakly differentiated. Intercostal cells (Fig. 8A, B) are longitudinally tetragonal (oblong or trapezoidal), 60–120 μm long and 12–20 μm wide, with straight to slightly bent anticlinal cells and parallel to the veins.
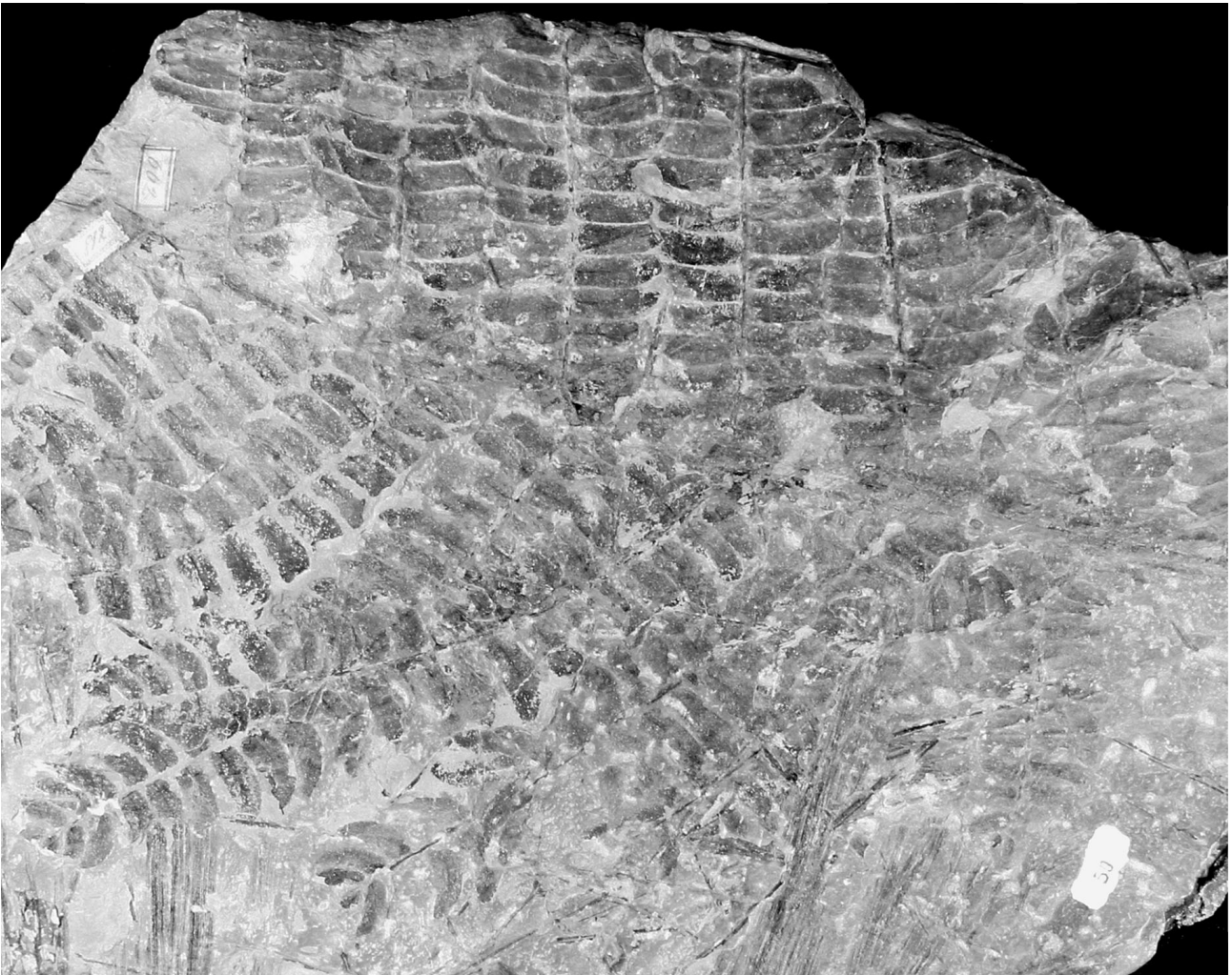
Figure 3. *Paripteris gigantea* (Sternberg) Gothan. Holotype, Sternberg (1821, pl. 32), Žacléř locality. National Museum, Prague, No. E 4672. × 0.5.

Shape and size of the costal cells are the same as in the intercostal ones. Only the adaxial cuticle of the midrib differs (Fig. 9D). The cells are oriented parallel to the midrib, and are square to oblong, 30–50 μm long and 25–40 μm wide.

Pinnule margin epidermis (Fig. 9E–H): The cells differ from cells of the adaxial and abaxial epidermis by being strongly cutinised and also by their shape. The band of these cells is 200–300 μm wide. The cells are elongated, oblong, tetragonal or trapezoidal. The anticlinal walls are prominent, straight, or only slightly bent. The cells are 30–70 μm long and 10–20 μm wide. The structural holes occur relatively densely among these cells. They are relatively small, circular to oval, 20–25 μm in diameter (Fig. 9E–H). Their function is not certain, but most probably they are trichome bases, where trichome remnants, such as cutinised collars, were not preserved. Trichomes were probably actively abscissed from the plant during life at the cuticle surface, which would mean that no cutinised collar was left. The trichome base density varies from place to place, but it is usually within 120–200 trichome bases per mm^2.

Pinnule abaxial epidermis (Figs 9B, C, 10A–C): The anticlinal walls and cell outlines are very weak and therefore it is difficult to trace any difference between costal and intercostals fields. The intercostal cells are polygonal, partly elongated, with straight to slightly curved anticlinal walls. The cells (Fig. 10A, B) are 22–35 μm long and 16–20 μm wide. Monocyclic stomata (Figs 9B, C, 10B, C) occur in the intercostal field. Pairs of guard cells, 22–30 μm long and 10–14 μm wide, are elliptical, sunken and partly covered by proximal papillae of the subsidiary cells (Figs 9B, C, 10C), and orientated parallel to the veins. The subsidiary cells are polygonal to trapezoidal, five to six in number around each stoma. The anticlinal walls are only partly visible. The estimated stomatal density is 220–260 stomata per mm^2 and the stomatal index is approximately 10. There are circular or oval structures in the costal field of the abaxial cuticle, which are 25–35 μm in diameter. Some

Figure 4. *Paripteris gigantea* (Sternberg) Gothan, Žacléř, Quarry 4, roof of the 9th upper coal seam, Duckmantian. Czech Geological Survey, Prague, No. ZŠ 144 (1–4). Fragments of a partly "ante-penultimate" and two partly "penultimate" pinnae, × 0.25.

of the cells have a smaller circular to oval hole in the middle (Fig. 10C). They are probably trichome bases. The density of trichome bases is 8–16 per mm^2.

Cuticles of the species *Paripteris gigantea* have already been studied by Barthel (1961), from a specimen from the Langsettian (Westphalian A) of the Upper Silesian Basin. Barthel (1961) described adaxial cuticles with putative papillae on the cells (his fig. 5); however, he figured only a small fragment (his pl. 3, fig. 9). Papillae are not visible there. Moreover, it seems that this cuticle is from the midrib, because the cells are relatively wide and resemble the midrib cuticle described here (Fig. 9D).

Barthel (1961) in fact did not figure any intercostal field of an adaxial cuticle. Barthel (1961) described and figured a "papilla" on an adaxial cuticle on his pl. 3, fig. 8. The cuticular specimen from Žacléř possesses similar structures in the costal fields of the abaxial cuticle and in the location of the midrib (Fig. 10B, C). These structures were classified as trichome bases. Barthel (1961) mentioned papillary subsidiary cells of stomata on the abaxial cuticle. The same papillae also occur in the Žacléř specimen. The only difference is in the dimensions of the guard cells. Barthel (1961) mentioned 15–20 μm long and 12–15 μm wide pairs of guard cells from the Upper Silesian specimen, whereas the pairs of guard cells from the Žacléř sample are 22–30 μm long and 10–14 μm wide. The presence of the same type of trichome bases and papillary stomata, and the same pattern of abaxial cuticle cells shows that Barthel's (1961) and these specimens belong to the same species, *Paripteris gigantea.*

The cuticles of other "*Paripteris*" species have not been studied yet in detail. Cuticles of the related "species" *Paripteris linguaefolia* P. Bertrand from Central Bohemia near Rakovník were studied by Šimůnek (2007). Its adaxial cuticle is not preserved. Abaxial cuticles of *Paripteris linguaefolia* also have very slightly prominent anticlinal walls; the stomata are deeply sunken and covered by the proximal papillae of the subsidiary cells (Šimůnek 2007). This feature is not so strongly developed in *Paripteris gigantea*.

Discussion

The taxonomy of the genus *Paripteris* Gothan, 1941 is still not satisfactorily solved. Gothan (1941) placed in his genus *Paripteris* the following species: *Paripteris gigantea* (Sternberg, 1821) Gothan, 1941, *P. pseudogigantea* (Potonié, 1897) Gothan, 1941 and *P. lunata* White, 1900. Daber (1963) transferred *Neuropteris schuetzei* Potonié, 1903 to *Paripteris*. Laveine (1967, 1971) classified the species *Neuropteris linguaefolia* Bertrand, 1930 and *Neuropteris linguaenova* Bertrand, 1930 also as *Paripteris*. Moreover, many forms and varieties of *P. gigantea* have been described when it was still placed in *Neuropteris*: *N. gigantea* forma *typica, N. gigantea* var. *abbreviata* Stockmans, 1933, *N. gigantea* forma *arcuata* Novik, 1952, *N. gigantea* forma *lingua* Novik, 1952, and *N. gigantea* forma *triangularis* Bertrand, 1930. Havlena (1953) came to the conclusion that up to three forms can occur in one frond of *Paripteris gigantea* – formas *typica, triangularis* and *lingua.* Crookall (1959) included practically all *Paripteris* species in the species "*Neuropteris*" *gigantea* as is evident from his synonymy and remarks. Since that time the name *Paripteris* has become more common and the species *Paripteris gigantea, P. pseudogigantea* and *P. linguaefolia* have become the most used names in the European literature (*e.g.*, Laveine 1967, 1971; Josten 1991). In the 20th century,
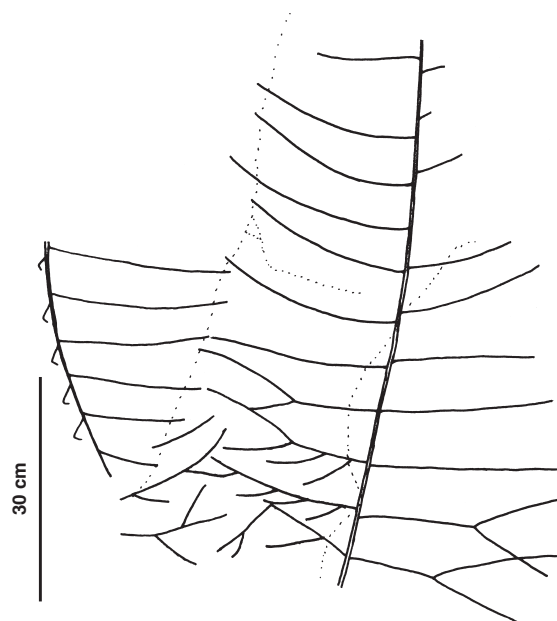

Figure 5. Drawing of "ultimate" and "ante-penultimate" rachises of *Paripteris gigantea* (Sternberg) Gothan, according to fragment figured in Fig. 4. Note the dichotomy of some "ultimate" pinnae.
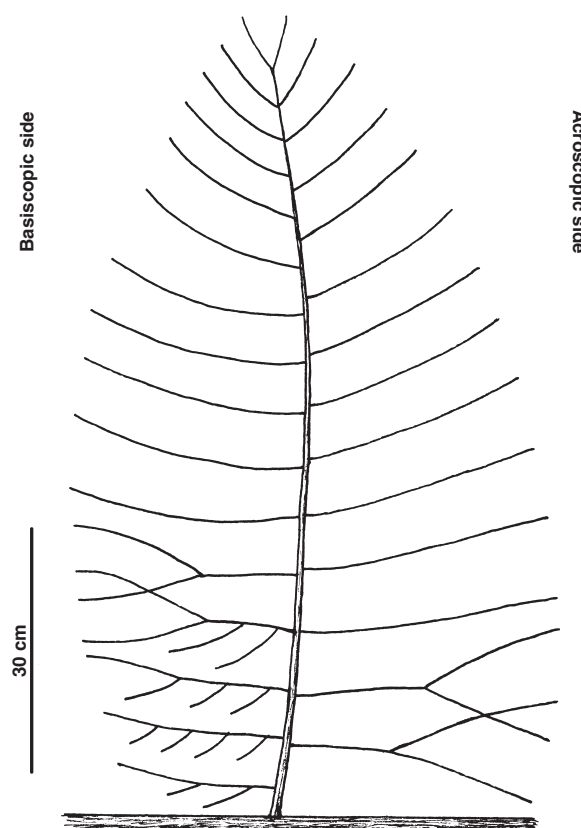

Figure 6. Reconstruction of about 1 m long partly "ante-penultimate" pinna from the central part of an "ante-ante-penultimate" frond. The basal basiscopic pinnae show anisotomous dichotomies on their basiscopic surface (see Laveine *et al*. 1993, text-fig. 9). Two basal acroscopic pinnae show single distal dichotomy.
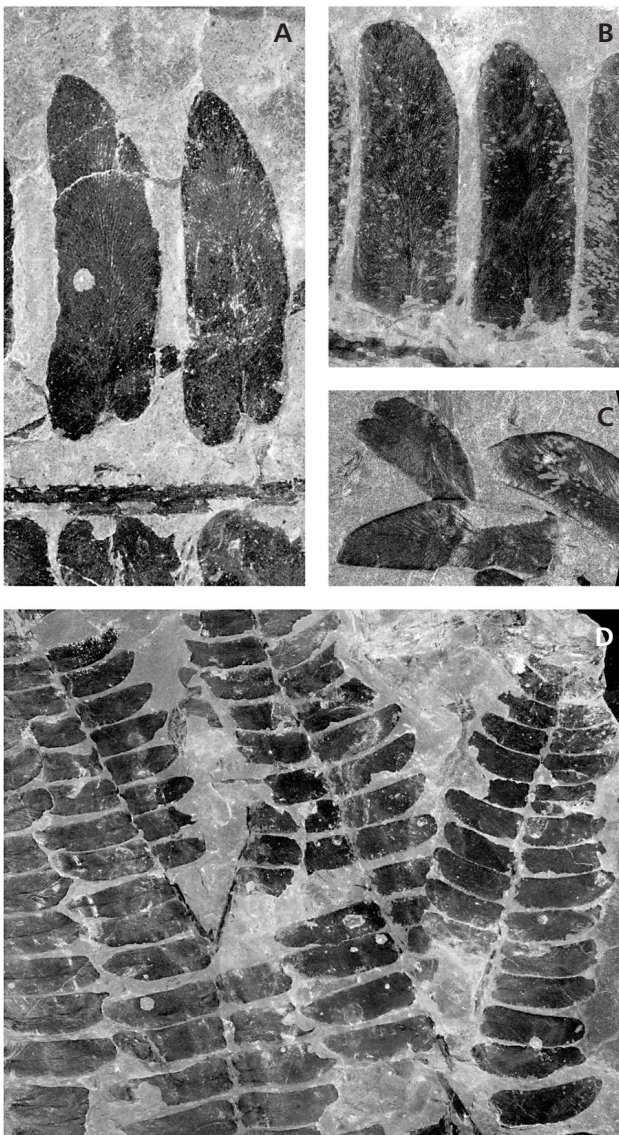
Figure 7. *Paripteris gigantea* (Sternberg) Gothan, Žacléř, Quarry 4, roof of the 9th upper coal seam, Duckmantian. • A, B – details of pinnules (B – "forma *lingua* Betrand"), × 1.5. • C – isolated pinnules – material for cuticles in Figs 9, 10. Loc. Lampertice near Žacléř, borehole Š 13, depth 489.85–490 m, 10th overlying seam of the Šverma Mine Coals. Coll. Z. Rieger, Czech Geological Survey, Prague, No. ZŠ 19, × 1. • D – detail of frond showing bifurcated "unipinate" pinnae, × 0.5.

many specimens belonging to *Paripteris* were described from Asia as species of the genus *Neuropteris* Brongniart: Zhang *et al.* (1993) concluded that *Neuropteris kaipingiana* Sze, 1930, *N. otozamioides* Sze & Lee, 1946 and "*N.*" *cardiopteroides* Bohlin, 1971 from Asia belong to the genus *Paripteris.* It must be noted that "*Neuropteris*" *cardiopteroides* Bohlin, 1971 is a younger homonym of *Neuropteris cardiopteroides* Schmalhausen, 1879. Zhang *et al.* (1993) faced the great variability of paripterid pinnules from China: lingular, subtriangular, triangular pinnules with a straight, subfalcate or falcate outline. Because

they found transitions among these morphotypes, they provisionally considered all these pinnules as belonging to one species – *Paripteris gigantea* (Sternberg) Gothan with many forms that reflect the variability of the pinnules: *P. gigantea* f. *gigantea, P. gigantea* f. *lunata* (White) Zhang *et al.*, *P. gigantea* f. *kaipingiana* (Sze) Zhang *et al.*, *P. gigantea* f. *abbreviata* (Stockmans) Zhang *et al.*, *P. gigantea* f. *linguaefolia* (Bertrand) Zhang *et al.*, *P. gigantea* f. *pseudogigantea* (Potonié) Zhang *et al.*, *P. gigantea* f. *cardiopteroides* (Bohlin) Zhang *et al.*, *P. gigantea* f. *otozamioides* (Sze & Lee) Zhang *et al.* and the new formae *P. gigantea* f. *acuminatissima* and *P. gigantea* f. *longifolia.* The same trinomial concept was used in Laveine *et al.* (2003).

Laveine *et al.* (1993) emphasized that the genus *Paripteris* had the greatest variability in China during the late Viséan and early Namurian. According to Laveine *et al.* (1993), it is the time when this genus originated and reached the greatest diversity and disparity, but later selection pressure caused diminished diversity. For example, acuminate forms known from the lower Namurian of China do not occur in the middle and upper Namurian of Europe. Moreover, Laveine *et al.* (1993) found a large frond with pinnules similar to the typical *Paripteris gigantea* in one part and pinnules similar to *Paripteris pseudogigantea* in another part of the frond. Laveine *et al.* (1993) concluded that the local Spanish species, *Paripteris asturiana* (Jongmans) Wagner, 1962, also belonged to *Paripteris pseudogigantea*, the only difference is that *Paripteris asturiana* has pinnules of about a half the size of those of *Paripteris pseudogigantea.* Laveine *et al.* (1993) are of the opinion that *Paripteris asturiana* is an ecoform or geographically restricted form. Only the following forms of *Paripteris gigantea* introduced by Zhang *et al.* (1993) were recognized in Europe: *P. gigantea* f. *gigantea*, *P. gigantea* f. *abbreviata*, *P. gigantea* f. *linguaefolia* and *P. gigantea* f. *pseudogigantea.* The forms *P. gigantea* f. *linguaefolia* and *P. gigantea* f. *pseudogigantea* were originally described as species of the genus *Neuropteris* Brongniart and are characterized by morphological features of the pinnules (Table 1). Individual forms also have different stratigraphical ranges. The forms *P. gigantea gigantea* and *P. gigantea abbreviata* occur in the Namurian and Lower Westphalian and the forms *P. gigantea linguaefolia* and *P. gigantea pseudogigantea* usually occur first in the Westphalian and the last record of these forms is before it ends. In particular, *P. gigantea* f. *linguaefolia* is important for Bolsovian (Westphalian C) floras. Wagner (1984) considers this "forma" as the index species of the *Paripteris linguaefolia* Zone. However, Brousmiche Delcambre *et al.* (1996) found this "species" together with *Neuralethoptreis schlehanii* (Stur) Cremer in the Namurian strata of Briançonais (France). They used the trinomial system of classification – *Paripteris gigantea* (Sternberg) forma *linguaefolia* (Bertrand) Zhang *et al.*
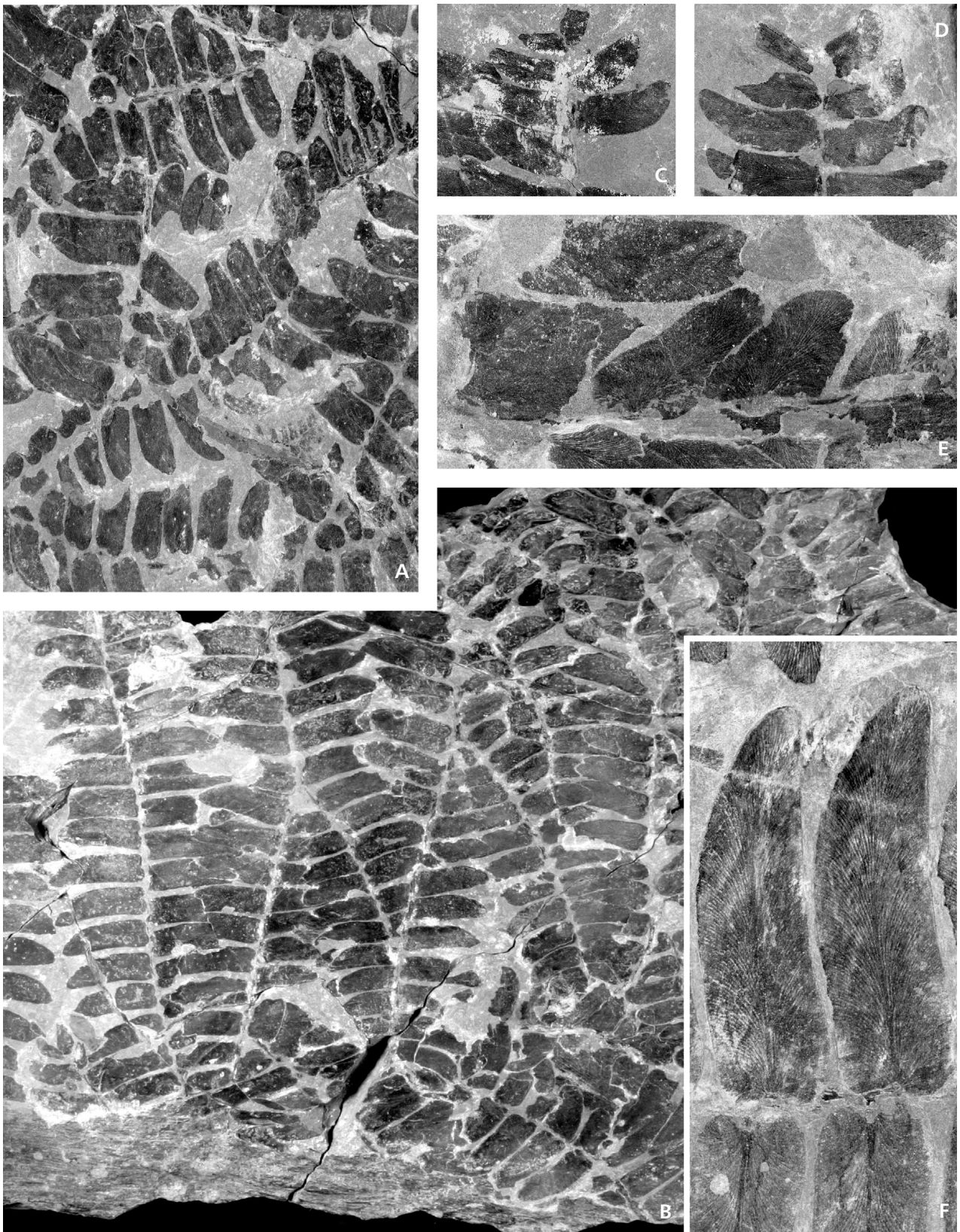
Figure 8. *Paripteris gigantea* (Sternberg) Gothan, Žacléř, Quarry 4, roof of the 9th upper coal seam, Duckmantian. • A – fragments of repeatedly bifurcating pinnae from Fig. 8B, × 0.7. • B – fragment of "penultimate" pinna showing bifurcated "ultimate" pinnae, × 0.5. • C, D – terminal parts of pinnae with pairs of apical pinnules, × 1. • E – rachis with "intercalated" pinnules, × 1.5. • F – detail of two "normal" pinnules (forma *typica*), × 2.

Table 1. Comparison pinnule morphology of three *Paripteris* "species". According to Josten (1991) and the author's observation. 1 – pinnule length [mm], 2 – pinnule width [mm], 3 – midrib, 4 – vein density, 5 – form of pinnule

	P. gigantea	*P. pseudogigantea*	*P. linguaefolia*
1	25–40	< 20	30–45
2	10–15	5	10–20
3	up to 1/2 of the pinnule	up to 4/5 of the pinnule	without or only 1–2 mm
4	35–50 veins per cm	cca 30 per cm	30–35 per cm
5	sickle-shaped, tongue-shaped	tongue-shaped	tongue-shaped

The situation in the Bohemian part of the Intrasudetic Basin is not so complicated, as in the Žacléř area only one species of *Paripteris – Paripteris gigantea –* is known. According to Havlena (1953), it is possible to distinguish three forms of this species, *viz. typica, triangularis* and *lingua.* Pinnules of all these forms can be found in a single pinna, and therefore these forms have no taxonomic significance. Zhang *et al.* (1993) did not consider these "forms" in their taxonomy. The age of these samples ranges from late Namurian to early Duckmantian. However, Havlena (1953) found both "species" or "forms" *P.* (*gigantea* f.) *gigantea* and *P.* (*gigantea* f.) *linguaefolia* at several localities (Markoušovice, Žďárky u Hronova) of late Duckmantian age. He explained this situation with partial overlap of the species "*Paripteris gigantea*", which was approaching extinction at that time, and "*Paripteris linguaefolia*" which originated not long before. The difference between these species is mainly in the length of midrib (Table 1). "*Paripteris linguaefolia*" is without a midrib, or with only a very short one, "*Paripteris gigantea*" should have the midrib at least to ½ of the pinnule blade. Havlena (1953) classified the isolated pinnules with a longer midrib as *Neuropteris gigantea.* It seems that there also exists variation in the length of the midrib. The presence of *Paripteris pseudogigantea* in the Intrasudetic Basin has not been recorded.

Now we return back to our sample. Its left side shows a higher proximo-distal differentiation than the right side (Fig. 6), and therefore must be basiscopic. The penultimate rachis is slightly bent to the base of the frond. The correct position of this pinna within the frond is not known. Either it represents a lateral, not very differentiated pinna from the basal part of a small frond, in which the basal lateral fronds were bent basally, or, more probably, it represents a lateral, partly "penultimate" pinna from the terminal (distal) part of the frond (see Laveine *et al.* 1993, fig. 11). The slightly proximally turned rachis can be explained by taphonomy. Laveine *at al.* (1993, fig. 11) showed a reconstruction of a frond up to 6 m long and 4 m wide. The "lateral" pinnae with a similar segmentation as in Laveine's reconstruction are less than 1 m long. The described pinna must have been more than 1 m long. Laveine's pinnae do not show such a distal dichotomy of the "ultimate" pinnae as in the sample described here. Nevertheless, this specimen can be fitted into Laveine's *et al.* (1993) reconstruction.

Cleal & Shute (1995) followed the traditional binomial classification and used the following *Paripteris* species names: *P. gigantea* (Sternberg) Gothan, *P. linguaefolia* (Bertrand) Laveine, *P. linguaenova* (Bertrand) Cleal & Shute, *P. pseudogigantea* (Potonié) Gothan and *P. schuetzei* (Potonié) Daber.

It is difficult to decide which concept is better. If we have typical samples, we can distinguish the above mentioned "species". However, there are localities, where large pinnule variability can be seen and more *Paripteris* "species" seem to be present in a single locality. It is really unusual that several related species can occur together, which tends to fit in better with Laveine's *et al.* (1993) concept.

The adaxial cuticle of *Paripteris gigantea* has oblong, tetragonal to hexagonal elongated cells and thus resembles some neuropterid species: *Neuropteris neuropteroides, Neuropteris tennuifolia* and *Neuropteris obliqua* (Barthel 1962), *Neuropteris scheuchzeri* (Barthel 1961, Cleal & Zodrow 1989), *Neuropteris rarinervis* Bunbury, *N. flexuosa* (Cleal & Zodrow 1989) and *Neuropteris terminiscus* (Cleal 2002). Of course, cuticles of individual species differ slightly in shape and dimension of cells.

The abaxial cuticle of *Paripteris gigantea* is typified by slightly cutinised anticlinal cell walls and sunken stomata with papillate subsidiary cells. Such cuticles can be observed in some linopterids: *Linopteris weigelii* and *L. neuropteroides* and neuropterids: *Neuroteris obliqua* and *Neuropteris tennuifolia* (Barthel 1961), *Laveineopteris loshii* (Cleal & Shute 1992) and *L. rarinervis* (Cleal & Zodrow 1989).

However, the typical feature of *Paripteris gigantea* cuticles is a more cutinised rim at the pinnule margin with numerous trichome bases. Such a feature has not been observed in any other medullosan species and neither in *Paripteris linguaefolia* (Šimůnek 2007). A comparison of these two species is not possible because the cuticles of *Paripteris linguaefolia* are poorly preserved. Further observation of other *Paripteris linguaefolia* cuticles are required for a detailed comparative analysis.

Paleoecology

Paripteris gigantea (Sternberg) Gothan, is the most common species in the Žacléř Formation of the Žacléř area. It was found by Rieger *et al.* (1962) associated with nearly all coal seams there, mostly in roof rocks (Fig. 2). It is also the dominant species in many of the studied quarries (Fig. 1). However, large frond fragments are very rare, and the described specimen is exceptional, even when compared to
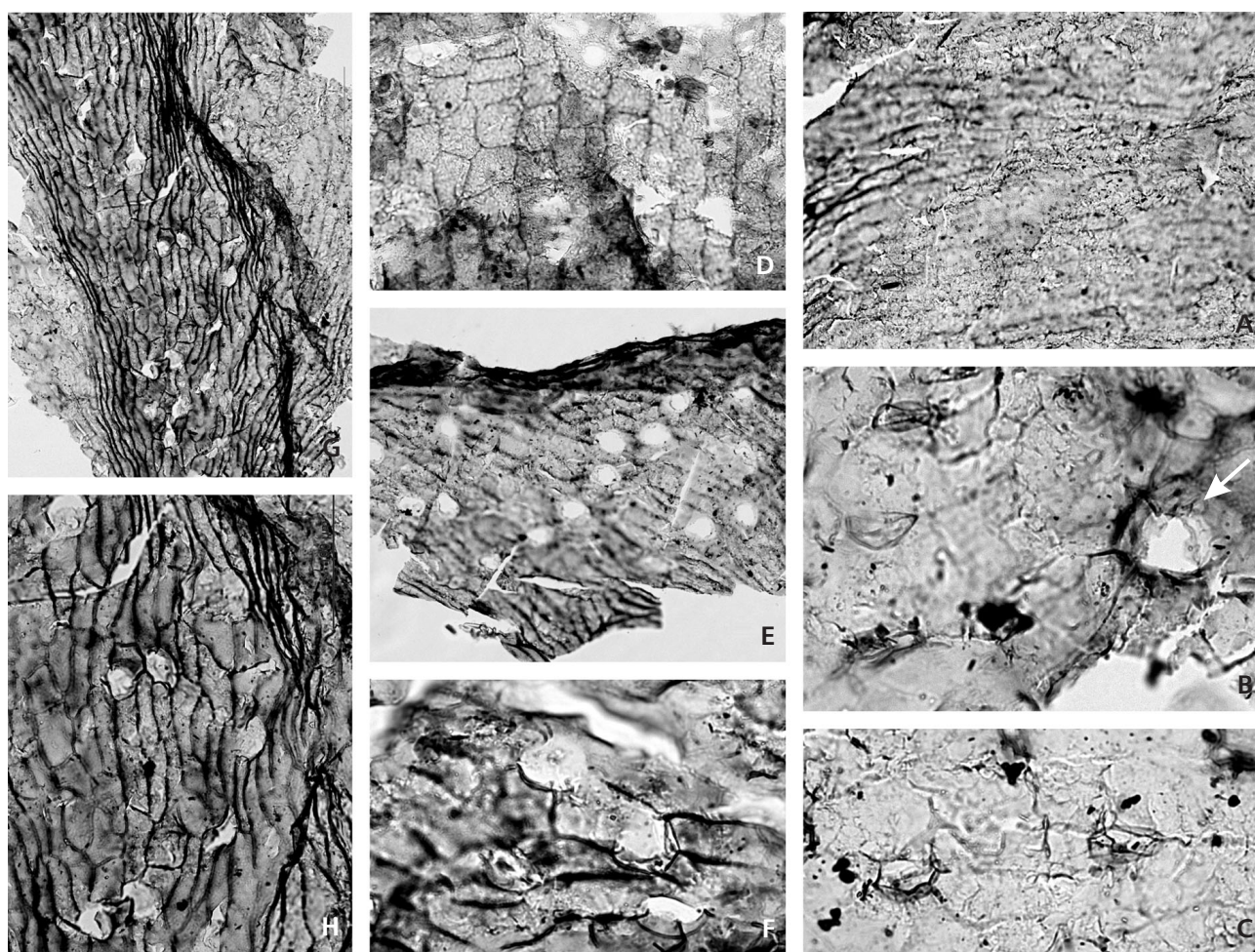
Figure 9. *Paripteris gigantea* (Sternberg) Gothan, Lampertice near Žacléř, borehole Š 13, depth 489.85–490 m. 10th overlying seam of the Šverma mine, Lampertice Member, Duckmatian. (Specimen on Fig. 7C.) • A – adaxial cuticle. Slide 476/8, × 200. • B – a detail from Fig. 10A with a trichome base (arrow) and 3 stomata, × 500. • C – abaxial cuticle in the intercostal field with two stomata. Slide 476/5, × 500. • D – adaxial cuticle in the place of midrib. Slide 158/1, × 200. • E – pinnule margin with trichome bases. Slide 476/6, × 200. • F – detail of trichome bases. Slide 476/8, × 500. • G – pinnule margin with trichome bases. Adaxial cuticle is in the upper right corner, abaxial cuticle is in the lower left corner. Slide 476/10, × 150. • H – detail of trichome bases from Fig. 9G, × 300.

Laveine's specimens (Laveine 1967, pls 70–72). *Paripteris gigantea* obviously had few ecological demands, because it spread throughout Europe very quickly after overcoming the barrier between Asia and Europe during the Kinderscoutian and Marsdenian (Namurian B) (Laveine *et al.* 1993). The presence of isolated pinnules in different types of sediment can be explained by primarily large fronds, up to 6 m long (Laveine *et al.* 1993), bearing many pinnules with a constricted cordate base, that could be easily abscised. Cleal & Laveine (1988) described juvenile fronds of *Paripteris gigantea* with partly preserved pinnules on a petiole, but pinnules from the petiole had abscised already even in the juvenile stage of the frond. Probably, when the mature fronds died, they disintegrated very quickly into rachises and individual pinnules; the latter could be transported through wind and water very easily (Wnuk & Pfefferkorn 1984).

Riverbanks were probably the natural habitat of *Paripteris gigantea* (Sternberg) Gothan. Vegetation of riverbanks grew on elevated (levee), well-drained substrates with a high nutrient level supply. These substrates were inundated only during floods and the presence of some tree or liana-like pteridosperms is a typical feature (Iwaniw 1985). The most common are fragments of fronds of *Mariopteris muricata* (Schlotheim) Zeiller and isolated pinnules of *Paripteris gigantea* concentrated on bedding surfaces in association with trigonocarpid seeds (Libertín *et al.* 2009). Less common species in this community are: *Alethopteris valida* Boulay, *Linopteris neuropteroides* Gutbier f. *major* Potonié, *Lonchopteris rugosa* Brongniart, *Pecopteris plumosa* (Artis) Brongniart, *Annularia radiata* (Brongniart) Sternberg, *Palmatopteris furcata* (Brongniart) Potonié, *Sphenophyllum cuneifolium* (Sternberg) Zeiller, *Trigonocarpus noeggerathii* Sternberg and *Calamites* (*Diplocalamites*) *carinatus* Sternberg.
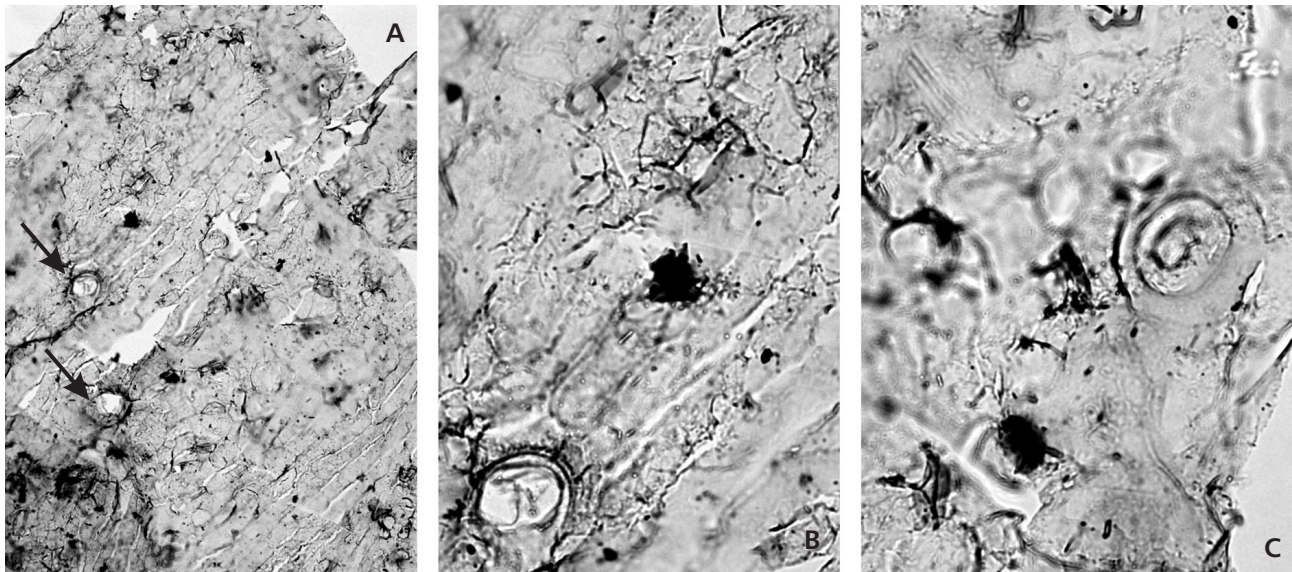
Figure 10. A – abaxial cuticle with two trichome bases (arrows) and alternating costal fields and intercostal fields with stomata. Slide 476/5, × 150. • B – abaxial cuticle with a trichome base and a stoma from Fig. 10A, × 500. • D – a detail of abaxial cuticle with a trichome base and stomata. Slide 476/9, × 500.

Paripteris gigantea (Sternberg) Gothan was also an important element of the plant assemblage growing on well-drained substrates. Pteridosperms, some ferns and calamites are typical for well-drained substrates in the Žacléř locality. Sphenophytes are represented especially by the genera *Calamites* Brongniart and *Sphenophyllum* Brongniart, which occur as pioneer vegetation in places with an unstable substrate (Behrensmeyer *et al.* 1992). Dominant species here are *Pecopteris plumosa* (Artis) Stur, a lianescent fern, and the already mentioned medullosan pteridosperm *Paripteris gigantea*, which preferred well-drained nutrient-rich substrates. *Neuropteris obliqua* (Brongniart) Zeiller also had similar ecological demands. Cordaitaleans grew on both well-drained and poorly drained substrates probably due to their physiological xeromorphism (Wardtmann 1969). The recently described species *Cordaites schatzlarensis* Šimůnek & Libertín, 2006 with about 50 cm long leaves is associated with seeds of *Samaropsis newberryi* (Andrews) Seward.

Other elements of this assemblage are *Palmatopteris furcata* (Brongniart) Potonié, *Annularia radiata* (Brongniart) Sternberg, *Eusphenopteris obtusiloba* (Brongniart) Novik, *Calamostachys intermedia* Němejc and *Calamites* (*Diplocalamites*) *carinatus* Sternberg.

Based on previous studies and on new data from open-cast mines in the Žacléř area, it is possible to interpret sediments of the Lampertice Member as the fill of a tectonically controlled system of piedmont river valleys, drained generally to the NE (Libertín *et al.* 2009). These valleys were occupied by a fluvial system, which is interpreted as a low-sinuosity braided river and wandering gravel-bed river (Miall 1985). This fluvial style is characterized by the well-developed floodplain with clastic to peat swamps.

Taphonomy

Three plant associations, autochthonous, parautochthonous and allochthonous were recognized, based on taphonomic research of the assemblage of plants from one lithofacies. However, only two species of pteridosperms – *Paripteris gigantea* (Sternberg) Gothan and *Mariopteris muricata* (Schlotheim) Zeiller were more tolerant to different ecological conditions and occur in most of the studied taphocenoses. This is in accordance with DiMichele *et al.* (2006) who stated that most early and middle Pennsylvanian arborescent medullosan species lived in clastic floodplain environments, but only a few could tolerate areas of long-persistent standing water.

Conclusions

Newly prepared cuticles of *Paripteris gigantea* from the type area resemble the cuticles prepared by Barthel (1961) from a specimen from the Upper Silesian Basin. The structures he described as epidermal papillae are interpreted here as trichome bases. New information on the cells and trichome bases on the pinnule rim of *Paripteris gigantea* is given. This plant grew in different habitats, ranging from well-drained substrates to clastic floodplain environments with short-term standing water. Up to now, very little information is known about the epidermal structures of other species of the genus *Paripteris*.

To date, two different concepts of classification of the genus *Paripteris* Gothan are used: 1. The trinomial classification of Zhang *et al.* (1993) that accommodates all the so-far recognized paripterid species as forms of the species *Paripteris gigantea.* This classification reflects morpho-

logical differences (variability or polymorphism) that sometimes prevent distinguishing individual species and formae, therefore all species are formae in this classification. 2. The traditional binomial classification (*e.g.*, Josten 1991, Cleal & Shute 1995) leaves the taxonomic entities at their original value – species. This paper does not deal with this problem. Maybe cuticular analysis of other paripterid species and forms will help to solve this problem in the future.

Acknowledgements

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