

Fruit structure and microsculpture in the annual species of the genus *Bupleurum*, section *Perfoliata* (*Umbelliferae*)

Tatiana A. Ostroumova & Eugene V. Kljuykov

Botanical Garden, M.V.Lomonosov Moscow State University, 119234, Moscow Russia,
e-mail: ostroumovata@gmail.com (corresponding author)

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Abstract. Fruit morphology, anatomy and micromorphology were studied of all eight species of the *Bupleurum* section *Perfoliata*. Fruit structure seems to be rather diverse. The surface is smooth, or has multicellular emergences 50–300 µm high, fruits of *B. lophocarpum* have unique for the *Umbelliferae* winged ribs with hemispheric expansions. There is often a wax layer, densely covered by very thin vertical wax platelets, 2–4 µm in diameter. Exocarp looks different under SEM and light microscope. Mesocarp cells are large, in some species inner mesocarp is collenchymatous, secretory ducts are small or absent, but in *B. schistosum* the ducts are large. Fruit characters revealed in this study can be used for species identification and taxonomy.

Key words: *Apiaceae*, *Bupleurum*, fruit anatomy, micromorphology, *Umbelliferae*

Introduction

As part of our extensive carpological analysis of the Old World *Umbelliferae*, we have studied fruit morphology, micromorphology and anatomy of some annual species of the genus *Bupleurum* L. Although the latter's fruits had already been the subject of anatomical studies by Kozo-Poljansky (1914), Klan (1947), Larrival (1952), Gorovoy (1966, 1990), Pimenov & Sdobnina (1983), Gorovoy & Volkova (1987), Kim & Yoon (1990); Krasnoborov (1998), Pimenov & Kljuykov (2002), those studies focused mainly on the perennial species. As for annuals, only *B. gerardii* All., *B. pachnospermum* Pančić, *B. prealtum* L., *B. rotundifolium* L., *B. semicompositum* L., and *B. tenuissimum* L. have been so far described in detail. Additionally, fruit micromorphology for some *Bupleurum* species from Turkey was described by Özcan (2002).

Umbelliferae fruits (*Turgenia latifolia* (L.) Hoffm.) were among the first plant structures studied by SEM (Heywood 1969), to be followed by other genera, including *Geocaryum* Coss., *Bunium* L., and *Conop-*

odium W.D.J.Koch by Engstrand (1973), *Ammi* L. and *Visnaga* P. Gaertn. by Cappelletti (1979), *Ammodaucus* Coss. & Durieu by Tejera (1983), *Daucus* L. by Živković (1984); *Eryngium* L. by Tamamschian & Pimenov (1987), *Tordylium* L. by Al-Eisawi & Jury (1988), *Pastinaceae*; by Menemen & Jury (2001), *Ferula* L. by Sağıroğlu & Duman (2006), and *Lichtensteinia* Cham. & Schldl. by van Wyk & Tilney (2008). Mention deserves the fact that micromorphological traits are of taxonomic importance.

To present our material, we have used the worldwide generic system of Wolff (1910), with some nomenclatural changes. We accept *B. rigidum* L. as the lectotype of the genus (Britton & Brown 1913; Pimenov & Tikhomirov 1979; Pimenov & Leonov 1993).

Diagnostic characters of the section *Perfoliata* Gord. are perfoliate upper leaves and lack of involucral bracts; involucre bracts are usually large (10–15 mm long) but in *B. wittmannii* they are ca. 6 mm, and in *B. schistosum* 1–2 mm. *B. rotundifolium* is distributed in Europe, Southwest and North Asia, North Afri-

ca, secondary areas being East Asia, N. America, Africa, Australia and Oceania. Other species have smaller areas of distribution in the Mediterranean, Azerbaijan, Armenia, Iraq, Iran, and Turkmenistan. Wolff (1910) accepted three subsections. 1) Subsection *Laevia* Briq. (valleculas and commissure smooth) – *B. rotundifolium*, *B. schistosum*, *B. croceum*, *B. wittmannii*. 2) Subsection *Rugosa* Briq. (valleculas and commissure granulate, tuberculate or rugate) – *B. heldreichii*, *B. subovatum*, *B. lancifolium*. 3) Subsection *Lophocarpa* Briq. (ribs broadly winged, wings thin with semi-spherical expansions) – *B. lophocarpum*. We have studied fruit anatomy and micromorphology of all species of section *Perfoliata*.

Material and methods

SEM investigations were carried out with a CamScan S–2 (accelerating voltage 15 kV and working distance 56 mm), at magnification of 15–3000×. Dry fruits were placed on aluminium stubs and sputter-coated with gold or gold-palladium to a thickness of ca. 25 nm.

For anatomical investigation, fruits were softened in hot water or in glycerol-alcohol-water; free-hand sections were processed with phloroglucinol – hydrochloric acid, and kept in glycerol. Microphotographs were made with Olympus BX41 microscope and Olympus DP25 camera; RA-4 device was used for drawings. Mention deserves the fact that the epidermis cell structure is different in dry and hydrated states.

Application of micromorphological characters for taxonomy is rather difficult, due to the absence of a generally accepted terminology. Other challenges are the wide magnification range achieved with SEM, and similarity of details at different magnifications. Therefore, it seemed worthwhile to describe the cell pattern and microstructure within three categories: cell shape (the primary sculpture), fine relief of the cell wall (the secondary sculpture), and epicuticular secretions (the tertiary sculpture) as suggested by Barthlott & Ehler (1977) and Barthlott (1981). On the basis of these two papers, as well as on Heywood & Dakshini (1971), Bosewinkel & Bouman (1984), Al-Eisawi & Jury (1988), Stearn (1983), and Murley (1951), we compiled a glossary to describe the fruit microsculpture (Ostroumova & al. 2010, 2011). For the fine relief of cell wall we have

used palynological terminology (Kremp 1965; Hesse & al. 2009) wherever possible; plant cuticle and sporoderm are not homologous structures.

Material studied: *Bupleurum croceum* Fenzl – Iran, Pimenov & al. 19.06.2001, N 480 (MW); Turkey, Pimenov & al. 12.07.1994 N 870 (MW); Turkey, Pimenov & al. 10.07.1994 N 641 (MW). *B. heldreichii* Boiss. & Balansa – Turkey, Pimenov, Kljuykov 08.08.2008 N 40 (MW). *B. lancifolium* Hornem – Turkmenistan, Ikonnikov 08.06.1974 N 3041 (MW); Turkmenistan, Popov 07.05.1931 (LE). *B. lophocarpum* Boiss. & Balansa – Turkey, Ermenek N 145 (P). *B. rotundifolium* L. Turkey, Pimenov & Kljuykov 08.08.2008 N 45 (MW); Azerbaijan, Kreczetowicz 10.06.1901 (MW); Georgia, Hryniewiecki 30.07.1900 (MW); BG MSU No 1996-252. *B. schistosum* Woronow – Turkey, Pimenov & al. 07.07.1994 N 352 (MW). Turkey, Nydegger 24.05.1990 N 45528 (MHA); *Sebzeciber* 07.07.1994 N 352 (G). *B. subovatum* Link ex Spreng. Italy, Galliano & Vieldes 09.06.1970 (MHA); BG Lissabon N 368; BG Tel-Aviv; Iran, Scott 11.06.1986 N 61, 11.06.1986 (GAZI); Italy, Fiori 04.07.1906 N 1319 (MW); *B. wittmannii* Steven – Georgia, Kolakovsky 20.07.1926 N 214 (LE); Georgia, Smirnov 1884 (LE).

Results

All studied fruits were dry, separating into 2 mericarps with carpophore bifid to the base; beak absent; mericarps homomorphic; terete; with five equal primary ribs; ribs filiform, keeled, narrow winged or broadly winged; calyx teeth obsolete; stylopodia with a thin margin, discoid or dish-shaped, flat or low-conical; styles shorter of equalling stylopodium radius, recurved; exocarp (outer epidermis) cells small, up to 25 µm; commissure narrow, exocarp nearly reaches carpophore; inner fibrous mesocarp obsolete; mesocarp parenchyma not lignified; outer mesocarp parenchymatic, contains large cells, inner mesocarp parenchymatic or collenchymatic; vascular bundles compact; vittae obsolete in mature fruit, or vittae solitary in furrows, and two on commissural side, or vittae solitary in furrows and obsolete on commissure; rib secretory ducts obsolete; endocarp not lignified; crystals obsolete; endosperm flat, slightly convex or slightly concave on commissural side; embryo with two cotyledons.

Subsect. *Laevia* Briq.

B. croceum (Figs. 1, 2, 9). **Morphology:** Mericarps smooth, $3.5\text{--}4.5 \times 1\text{--}2$ mm, elliptic or ovate in outline, styles shorter than stylopodium. Ribs keeled. **Micromorphology:** On the rib crest – cell boundaries invisible, surface undulate. On the rib slopes and in vallecules – the boundaries inconspicuous in some parts, surface irregularly rugate, cell boundaries conspicuous in some parts, the cell pattern random, cells isodiametric $20\text{--}25$ μm , anticlinal walls straight, cell boundaries raised, outer periclinal walls concave or cell boundaries sunken, outer periclinal walls flat with central depression. Wax forms dense vertical platelets *ca.* $2\text{--}3$ μm . **Anatomy:** Pericarp thin, $60\text{--}80$ μm in vallecules. Exocarp cells slightly compressed $10\text{--}25$ μm wide, outer walls $5\text{--}7$ μm thick. Outer mesocarp cells thin-walled, up to 50 μm in diam. Inner mesocarp consists of smaller and partly compressed cells, some cells thick-walled, unligified and resembling the colenchyma. Secretory ducts absent.

B. rotundifolium (Figs. 4, 5, 6, 10). **Morphology:** Mericarps smooth, straight or slightly curved, $2.5\text{--}4 \times 1\text{--}1.5$ mm, elliptic or ovate in outline, styles shorter than stylopodium radius, ribs filiform or narrow winged. Vallecules with whitish coat, with low longitudinal cushions and grooves that do not correspond to secretory ducts. **Micromorphology:** On the rib crest – cell boundaries invisible, surface smooth. On the rib slopes and in vallecules – cell boundaries conspicuous, cell pattern is random, cells isodiametric $15\text{--}20$ μm , anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. The wax layer is rather thick and continuous, with grains and platelets *ca.* $2\text{--}3$ μm on its surface. The wax can be removed with hot water and with diethyl ether, cuticular surface is smooth. **Anatomy:** Pericarp thin, $80\text{--}100$ μm in vallecules. Exocarp cells compressed or retaining their shape, $8\text{--}20$ μm wide, outer walls thin in vallecules (*ca.* 2 μm) and thick on the rib crest (5 μm). Mesocarp cells thin-walled, often with brown walls, outer cells small, cells of the middle mesocarp zone large, up to 30×60 μm . Secretory ducts absent. Seed coat is of a single cell layer.

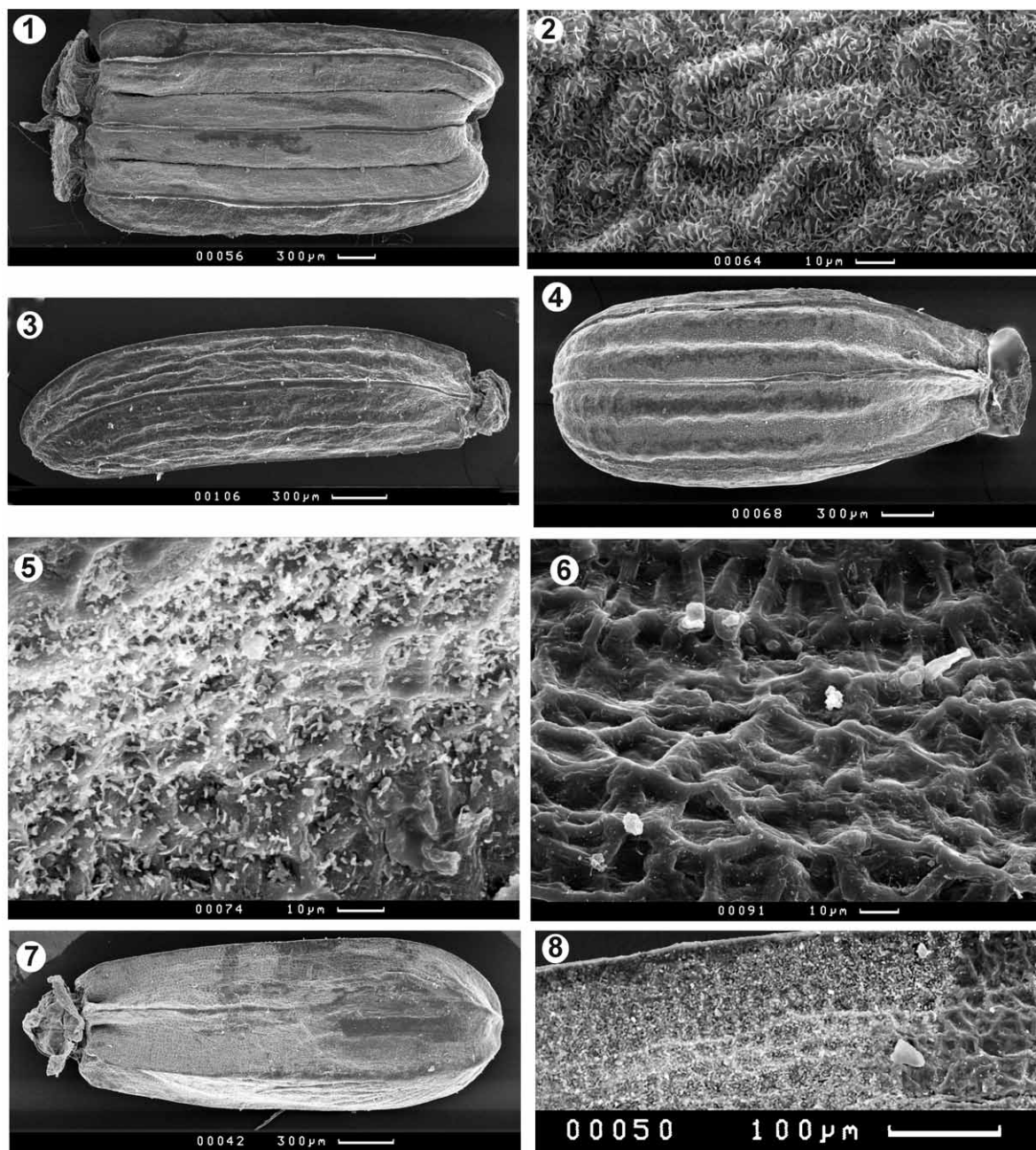
B. schistosum (Figs. 3, 11, 18). **Morphology:** Mericarps $2\text{--}3 \times 0.7\text{--}1.2$ mm, elliptic or oblong, styles equalling stylopodium radius or slightly longer. Ribs filiform or keeled. Vallecules with whitish coat, slight-

ly rugate and with weak longitudinal cushions that may correspond to secretory ducts. **Micromorphology:** Cell borders indistinct, rib crest smooth or longitudinally sulcate, vallecules undulate or irregularly rugate. Wax layer rather thick, with few grains and platelets. **Anatomy:** Pericarp thin, $60\text{--}100$ μm thick in vallecules. Exocarp cells compressed or retaining their shape, $5\text{--}15$ μm wide, outer walls thin in vallecules (*ca.* 2 μm) and thick on the rib crest ($4\text{--}5$ μm). Mesocarp cells thin-walled, often with brown walls, outer cells small, cells of the middle mesocarp zone large, up to 40 μm . Secretory ducts with dark-brown content, solitary in vallecules, two on commissural side, orbicular or elliptic in transection, $40\text{--}80$ μm in diameter. Seed coat is of a single cell layer.

B. wittmannii (*B. pseudocroceum* H. Wolff) (Figs. 7, 8, 12, 19, 20). **Morphology:** Mericarps $2.5\text{--}3 \times 0.8\text{--}1.0$ mm, smooth, oblong, styles equalling stylopodium radius. Ribs filiform or keeled. Vallecules with whitish coat. **Micromorphology:** Cell borders distinct, cell pattern random or in longitudinal rows, cells on ribs and vallecules isodiametric, anticlinal walls straight, cell borders raised, outer periclinal walls concave. Cuticular surface smooth or sparsely striate. Wax in vertical platelets $1\text{--}3$ μm diam. **Anatomy:** Pericarp thin, $50\text{--}70$ μm in vallecules. Exocarp cells $15\text{--}20$ μm wide, outer walls thin, *ca.* 2 μm . Mesocarp of $3\text{--}4$ cell layers, cells of the middle layer up to 50 μm long, outer and inner layers consists of small cells. Secretory ducts absent. Cells of the seed coat indiscernible.

Subsect. *Rugosa* Briq.

B. heldreichii (Figs. 15, 21, 22, 23, 32, 33). **Morphology:** Mericarps 3×1.3 mm, outline elliptic or ovate, styles shorter than stylopodium radius. Ribs keeled. In vallecules there are conical multicellular tubercles, $50\text{--}100$ μm in diameter at their base, $50\text{--}70$ μm high, randomly distributed, solitary or connected in groups of two-three. **Micromorphology:** Rib crest – cells indistinct under wax layer or distinct, cell pattern random, cells elongated *ca.* 20 μm long, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. Tubercles and depressions – cells distinct, cell pattern random, cells isodiametric *ca.* 20 μm in diameter, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. Wax in a continuous layer and dense vertical thin plates $3\text{--}4$ μm in

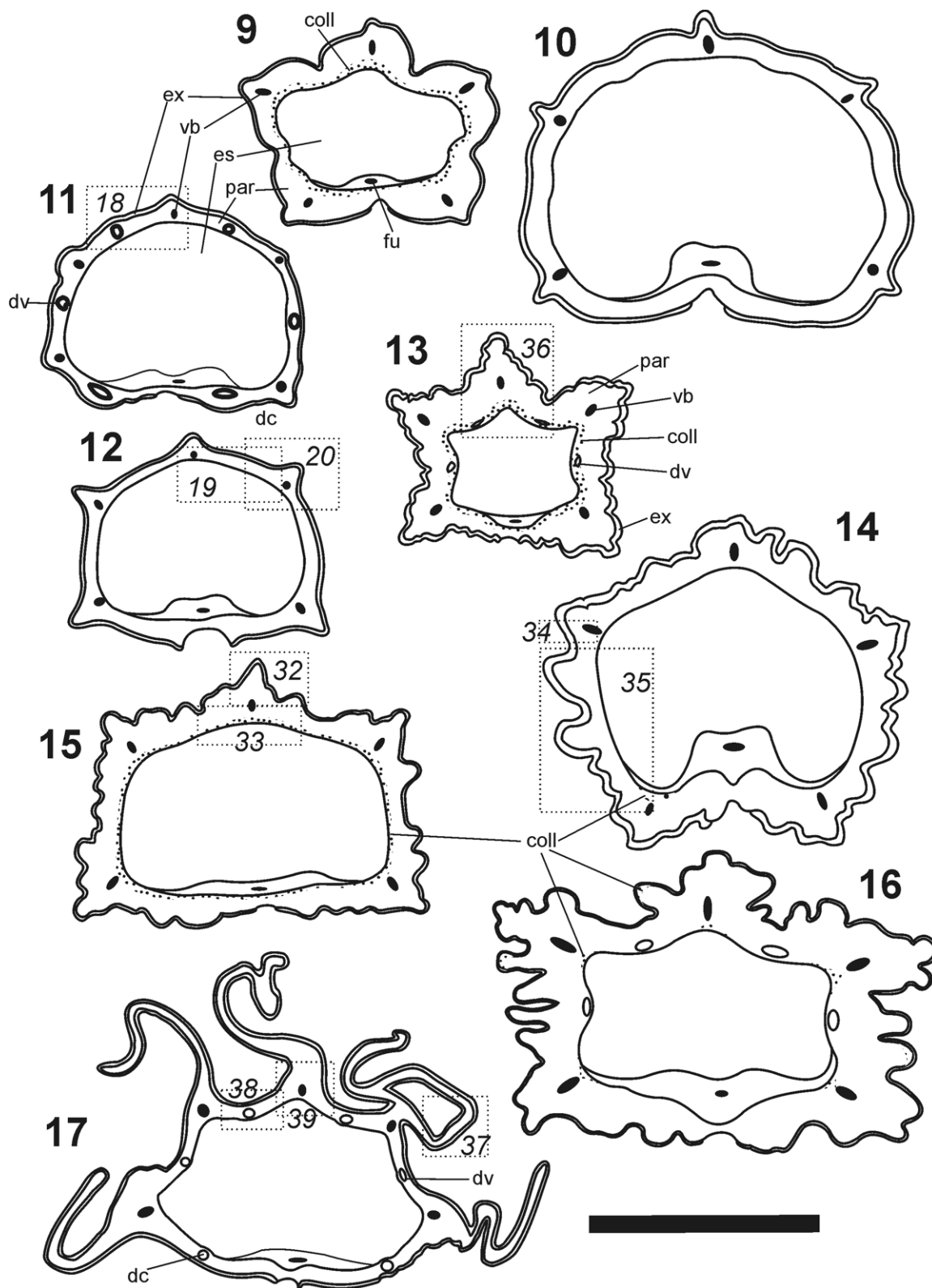


Figs. 1-8. SEM microphotographs. Figs. 1, 2 – *Bupleurum croceum*. Fig. 3 – *B. schistosum*. Figs. 4-6 – *B. rotundifolium*: Fig. 5 – intact surface, Fig. 6 – wax removed. Figs. 7, 8 – *B. wittmannii*.

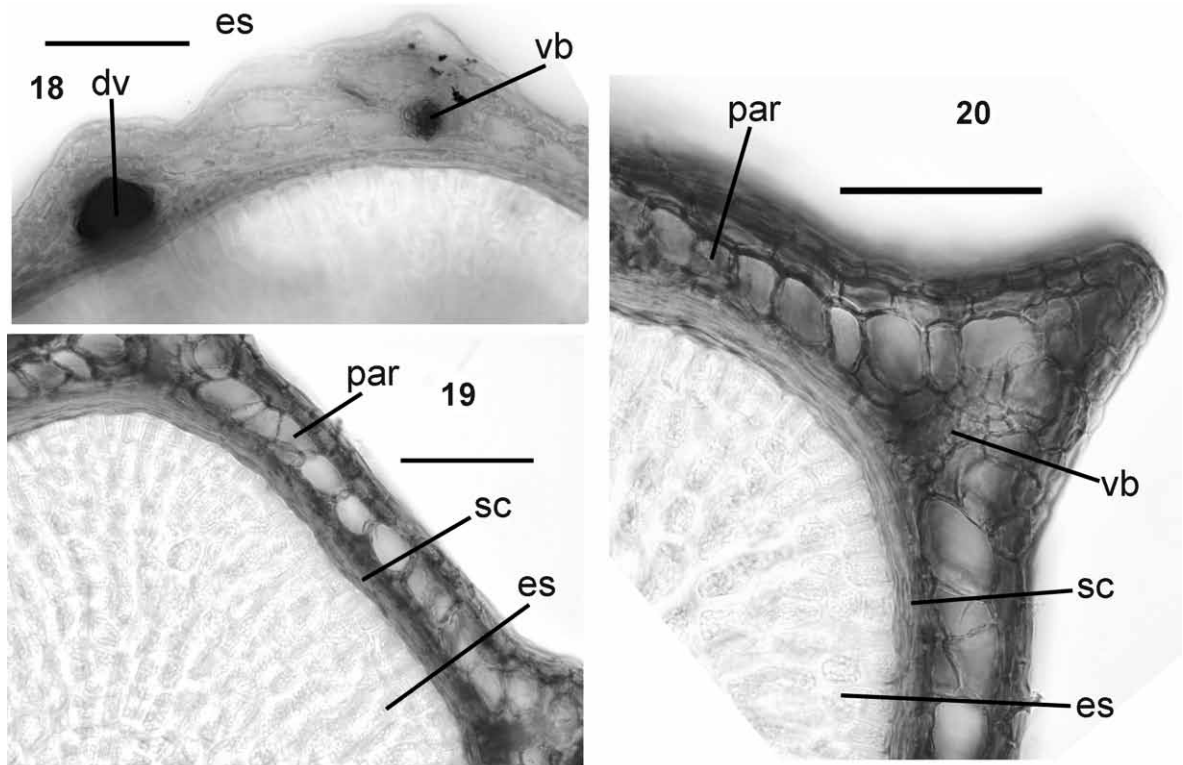
diameter. **Anatomy:** Exocarp cells retained, 10–25 μm wide, outer walls rather thick (4–5 μm). Outer mesocarp parenchymatic, cells up to 60 μm. Inner mesocarp collenchymatic. Secretory ducts absent. Seed coat is of a single cell layer.

B. lancifolium (13, 14, 24, 25, 34, 35, 36). **Morphology:** Mericarps 2–3 × 1.5 mm, elliptic in outline, styles shorter than stylopodium radius. Ribs narrow winged.

In vallecules there are conical multicellular tubercles, 100–150 μm in diameter at their base, solitary or connected in groups of two-three. **Micromorphology:** On rib crest – cell boundaries indistinct, surface longitudinally rugate. Tubercles – in some places cell borders indistinct, surface irregularly rugate, in other places cells visible, cell pattern random, cells isodiametric and oblong, 15 × 15–25 μm, anticlinal walls straight, cell boundaries sunken, outer periclinal walls



Figs. 9-17. Mericarp transections, schematic. Fig. 9 – *Bupleurum croceum*, immature. Fig. 10 – *B. rotundifolium*; Fig. 11 – *B. schistosum*; Fig. 12 – *B. wittmannii*; Figs. 13 & 14 – *B. lancifolium*. Fig. 15 – *B. heldreichii*. Fig. 16 – *B. subovatum*. Fig. 17 – *B. lophocarpum*. Abbreviations: **coll** – collenchyma, **dc** – commissural secretory duct, **dv** – vallecular secretory duct, **es** – endosperm, **ex** – exocarp, **fu** – funicular bundle, **par** – parenchyma, **vb** – vascular bundle. Scale bar: 1 mm. Dotted boxes indicate microphotograph positions and numbers. Scale bar = 1 mm.

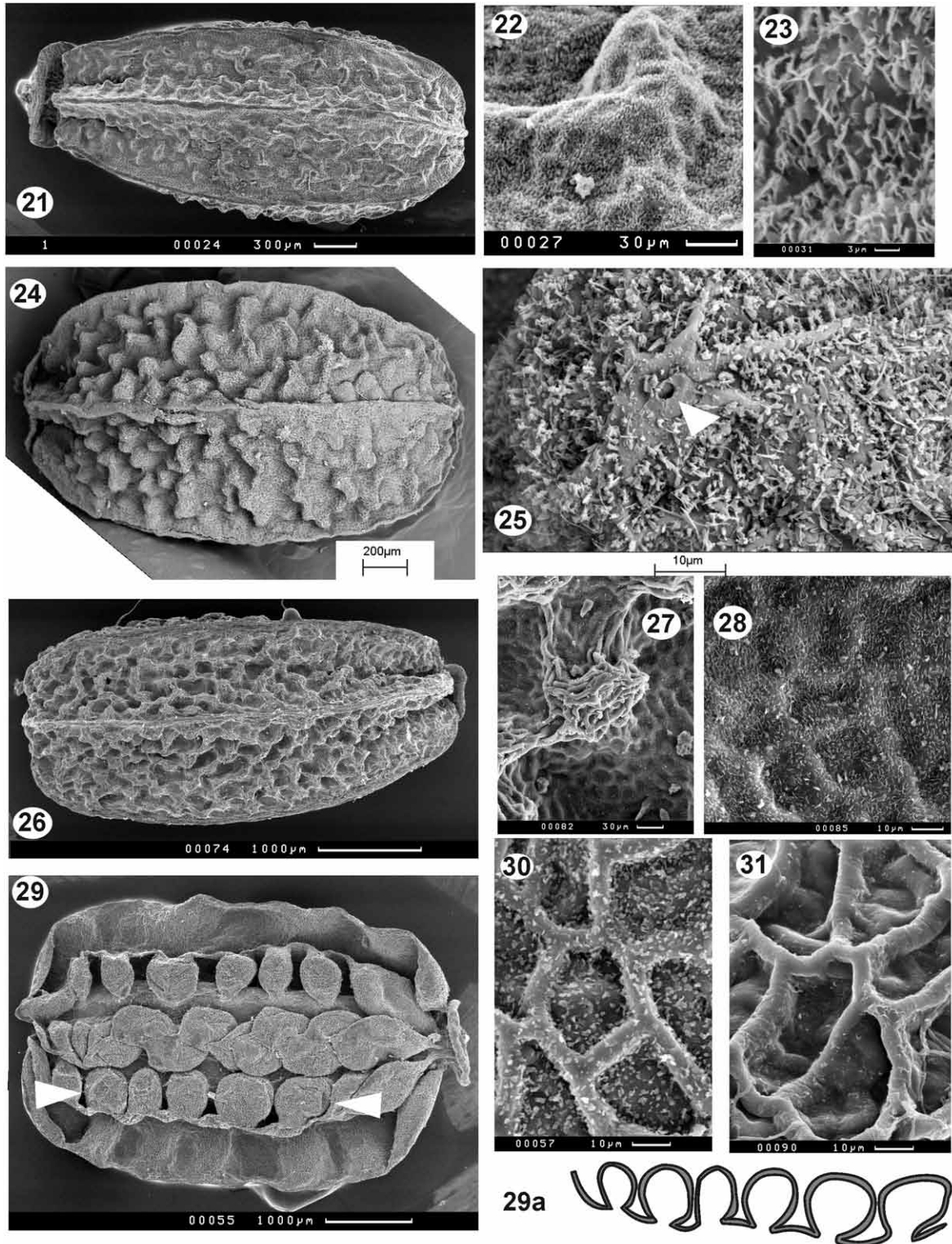


Figs. 18-20. Microphotographs of fruit transections. Fig. 18 – *B. schistosum*, dorsal rib and vallecule. Figs. 19 & 20 – *B. wittmannii*: Fig. 19 – vallecule, secretory ducts absent, Fig. 20 – dorsal rib. Scale bar = 0.1 mm. Abbreviations: **dv** – vallecular secretory duct, **es** – endosperm, **par** – parenchyma, **sc** – seed coat, **vb** – vascular bundle.

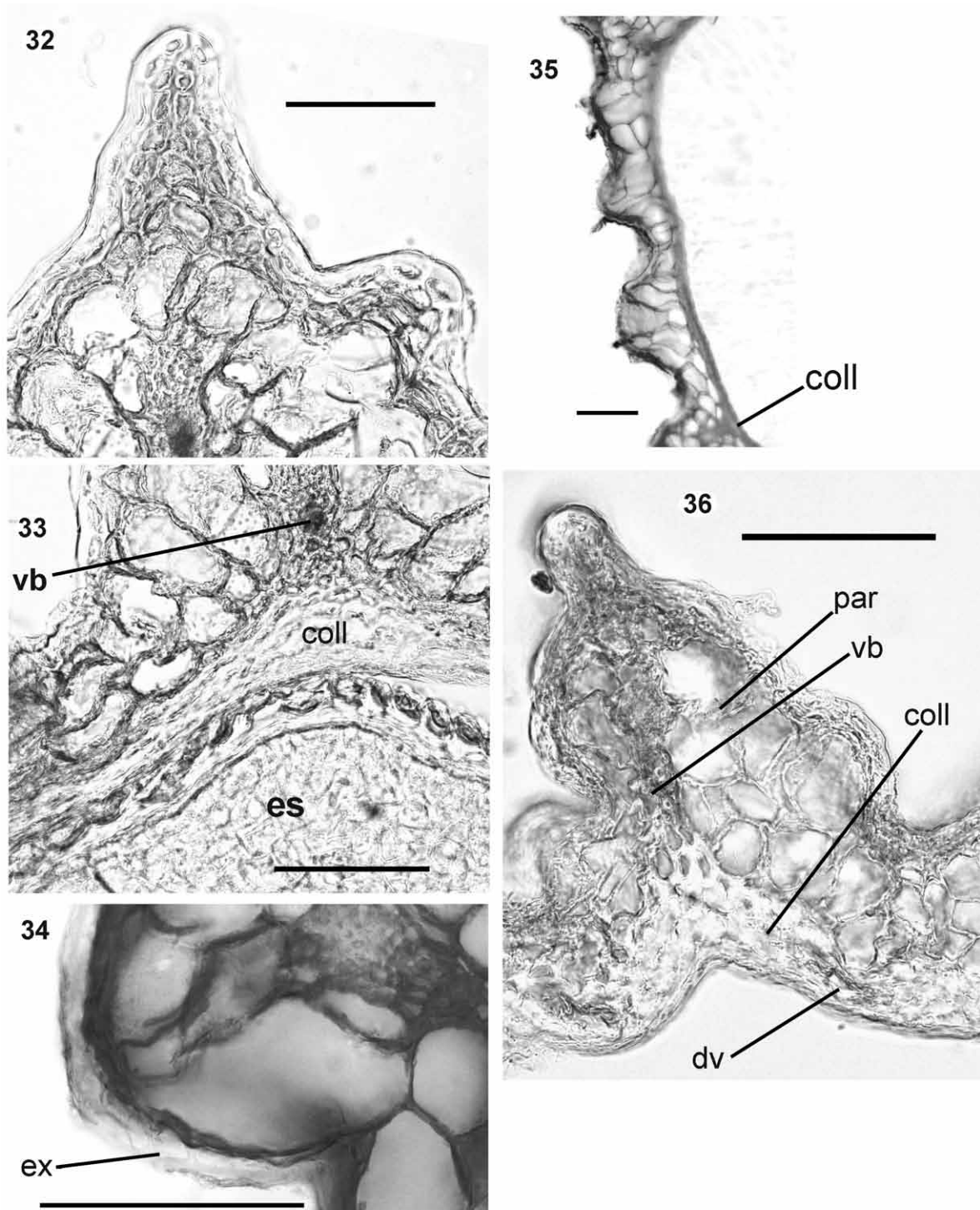
convex or flat; solitary stomata found on tops of some tubercles. In vallecular depressions – cells visible, cell pattern random, cells isodiametric and oblong, $15 \times 15\text{--}25 \mu\text{m}$, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. Wax in dense plates of $2\text{--}3 \mu\text{m}$. **Anatomy:** Epidermal cells on the rib crest $5\text{--}8 \mu\text{m}$, other cells $10\text{--}25 \mu\text{m}$, outer walls thin *ca* $2 \mu\text{m}$. Outer mesocarp parenchymatic, cells up to $50 \mu\text{m}$. Mesocarp structure is variable. In “*Popov 07.05.1931*” (Figs. 13, 36), fruits are immature, inner mesocarp collenchymatic, vallecular secretory ducts solitary, $30\text{--}40 \mu\text{m}$ wide, imbedded in the collenchyma. Commissural ducts absent. In “*Ikonnikov N 3041*” (Figs. 14, 24, 25, 34, 35) fruits are mature, secretory ducts absent, a small collenchyma strand is visible only in one marginal rib. Seed coat of a single cell layer, or cells are indiscernible.

B. subovatum (Figs. 16, 26, 27, 28). **Morphology:** Mericarps $4\text{--}5 \times 2\text{--}2.5 \text{ mm}$, elliptic or oblong, styles shorter than stylopodium radius. Ribs narrow winged or filiform. Vallecules coarsely reticulate with distinct bulges *ca.* $100 \mu\text{m}$ diam. (at their tops) and up

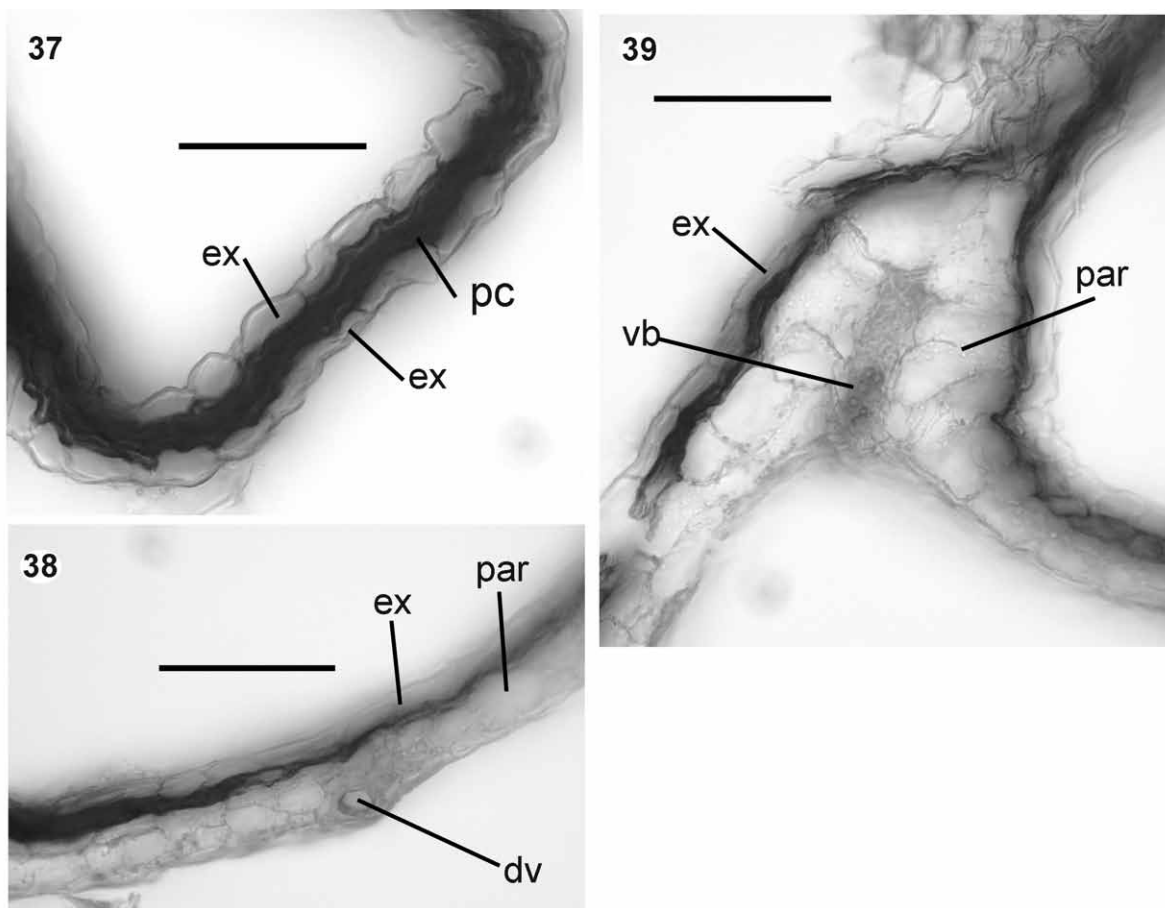
to $300 \mu\text{m}$ high, connected by muri. **Micromorphology:** Rib crest – cells indistinct, surface irregularly sulcate or rugate. Bulges and muri – cell borders indistinct, surface irregularly rugate, wax layer and grains. In depressions – cell borders visible, cell patterns random, cells isodiametric $20\text{--}25 \mu\text{m}$, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave; wax with many plates of $2\text{--}3 \mu\text{m}$. Occasionally (Tel-Aviv) cell borders distinct; on rib crest – cells in rows, on emergences and depressions with a random pattern, cells isodiametric, *ca.* $20 \mu\text{m}$, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. Solitary stomata are found on tops of few bulges in some mericarps. **Anatomy:** Exocarp cells $10\text{--}25 \mu\text{m}$ wide, outer walls thick ($5\text{--}6 \mu\text{m}$) on tops of bulges and thin ($2\text{--}3 \mu\text{m}$) in depressions. On top of bulges, collenchymatous hypoderm occurs occasionally. Mesocarp cells in the middle mesocarp zone up to $100 \mu\text{m}$, outer and inner layers of smaller cells. Beneath vascular bundles a collenchymatous layer is observed. Secretory ducts small – *ca.* $30 \mu\text{m}$ wide, solitary in vallecules, on commissural side obsolete. Seed coat is of a single cell layer, or cells indiscernible.



Figs. 21-31. SEM microphotographs. Figs. 21-23 – *B. heldreichii*: Fig. 23 – detail with wax plates. Figs. 24 & 25 – *B. lancifolium*: Fig. 25 – stoma on a tubercle top (arrowhead). Figs. 26-28 – *B. subovatum*. Fig. 29-31 – *B. lophocarpum*: Fig. 29a – longitudinal section of lateral rib between arrowheads, Fig. 30 – intact surface, Fig. 31 – wax removed.



Figs. 32-36. Microphotographs of fruit transections. Figs. 32 & 33 – *B. heldreichii*, median rib. Figs. 34-36 – *B. lancifolium*: Fig. 34 – lateral rib, Fig. 35 – vallecule, secretory ducts absent, Fig. 36 – dorsal rib and vallecule of immature fruit with collenchyma and secretory ducts. Scale bar = 0.1 mm. Abbreviations: **coll** – collenchyma, **dv** – vallecular secretory duct, **es** – endosperm, **ex** – exocarp, **par** – parenchyma, **vb** – vascular bundle.



Figs. 37-39. Microphotographs of fruit transections. *B. lophocarpum*: Fig. 37 – fragment of wing, Fig. 38 – vallecule, Fig. 39 – the base of dorsal rib. Scale bar = 0.1 mm. Abbreviations: **dv** – vallecular secretory duct, **ex** – exocarp, **par** – parenchyma, **pc** – compressed parenchyma, **vb** – vascular bundle.

Subsect. *Lophocarpa* Briq.

B. lophocarpum (Figs. 17, 29, 29a, 30, 31, 37, 38, 39). **Morphology:** Mericarps 5 × 2.5 mm, elliptic in outline, styles shorter or equal to stylopodium radius. Ribs broadly winged, wings thin, undulate with hemispheric expansions. **Micromorphology:** On wings – cell borders distinct, cell pattern random, cells isodiametric, 20–30 μm, anticlinal walls straight, cell boundaries raised, outer periclinal walls concave. Wax in a dense platelet 2–3 μm. Wax can be removed by ether and xylene. Outer cell walls smooth. **Anatomy:** Pericarp thin, 60–80 μm in vallecules. Epidermal cells 20–40 μm wide, outer walls thin, ca. 2 μm. Mesocarp cells compressed in brown film on wings and retaining their form on the fruit body, up to 40 μm. Wing thickness 50–60 μm. Secretory ducts small (10–20 μm), solitary in the vallecules, two on the commissural side. Seed coat is of a single cell layer.

Discussion

Detailed anatomical descriptions of *B. rotundifolium*, with illustrations, were given by Klan (1947) and Pimenov & Sdobnina (1983), who mentioned thin pericarp, large mesocarp cells, small vascular bundles, and absence of secretory ducts; our data confirm their observations.

The fruit structure in the section *Perfoliata* seems to be rather diverse. In *B. croceum*, *B. rotundifolium*, *B. schistosum*, and *B. wittmannii* the surface of vallecules is smooth, in *B. heldreichii*, *B. lancifolium* and *B. subovatum* vallecules and commissural side have multicellular emergences 50–300 μm high, randomly distributed; in *B. heldreichii* and *B. lancifolium* tubercles are solitary or in groups of two or three, in *B. subovatum* tubercles are connected by muri, the surface being coarsely reticulate. Fruits of *B. lophocarpum* have unique for the *Umbelliferae* winged ribs

with hemispheric expansions. Cell borders are indistinct or distinct, cell pattern random, outer cell walls usually concave, cell borders raised or indistinct, in *B. croceum* and *B. lancifolium* cell boundaries are occasionally sunken. There is often a wax layer densely covered by very thin vertical wax platelets 2–4 µm in diameter, except for *B. rotundifolium* and *B. schistosum* which are with sparse platelets. After removal of the wax layer, smooth cuticular surface is exposed, cuticular folding is absent or (few cells in *B. wittmannii*) sparsely striate.

There are some common traits in the anatomical structure: specifically, exocarp and mesocarp cells mostly retain their shape, and some mesocarp cells are very large (40–100 µm). Inner mesocarp is collenchymatic and continuous in *B. croceum*, *B. heldreichii*, in *B. subovatum* collenchyma is in the base of the ribs, *B. lancifolium* is variable, we have observed both a continuous collenchyma layer and a small cell group in the base of the rib; in *B. rotundifolium*, *B. schistosum*, *B. wittmannii*, and *B. lophocarpum* all mesocarp is parenchymatic. Secretory ducts are obsolete in *B. rotundifolium*, *B. croceum*, *B. heldreichii* and in one specimen of *B. lancifolium*; in *B. subovatum* and *B. lancifolium* there are small ducts in the vallecules, commissural ducts are lacking; in *B. lophocarpum* small secretory ducts are visible in the vallecules and on the commissural side. *B. schistosum* differs from the other studied species with its large ducts with brown secretions in vallecules and on the commissural side, along with tiny involucre bracts.

Mention deserves the fact that exocarp looks different under SEM and light microscope. In the vacuum SEM camera, the surface of dry fruits often has concave outer cell walls, but the material hydrated in glycerol usually exhibits a smooth surface. Cell walls on rib crests and on tops of tubercles are rather thick (5–8 µm), in depressions between the tubercles and in the smooth vallecules cell walls are thin (ca. 2 µm); under SEM these cells have a concave outer wall, except *B. croceum* with 4–6 µm – thick walls and a concave or flat dry surface.

Fruit characters recorded in this study can be used for species identification and taxonomy.

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