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Seed coat morphology and its systematic significance in *Juncus* L. (Juncaceae) in Egypt

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Abstract The seed morphology of nine taxa of *Juncus* from Egypt has been investigated using light and scanning electron microscopy, to determine the importance of seed coat features as taxonomic characters. Macro- and micromorphological characters, including seed shape, color, size, seed appendages, epidermal cell shape, anticlinal boundaries, and outer periclinal cell wall and secondary cell wall sculpture are presented. Four types of seed appendages are recognized: (i) seeds with two appendages; (ii) seeds without appendages; (iii) seeds with minutely a piculate at one end; and (iv) seeds with minutely a piculate at both ends. Two types of anticlinal cell wall boundaries, (i) raised-channeled, straight and (ii) raised, straight or sinuous, and three different shapes of outer periclinal cell wall are described: (i) flat; (ii) concave; and (iii) flat to slightly concave. The secondary sculpture of the cell wall varies from striate to microreticulate or reticulate, and smooth to finely folded. Seed characters provide useful data for formulating the taxonomy of *Juncus* both on the subgeneric and sectional level. A key for the identification of the investigated taxa based on seed characters is provided.

Key words *Juncus*, seed coat morphology, systematic significance.

Juncus L. is a cosmopolitan genus of annual and perennial herbs that reaches its greatest diversity in mesophytic and boreal regions of the world (Buchenau, 1906). The genus *Juncus* was described by Linnaeus (1753), who reported the occurrence of 15 species and divided them into two groups, according to stem type (nodus = node and foliofis = leafy). Boissier (1881) reported 26 species of the genus *Juncus* divided into 8 sections. Buchenau (1875, 1890, 1906) published the most comprehensive systematic account of the Juncaceae. He distinguished 250 species of *Juncus* divided into 8 subgenera. Several studies focused on chromosome morphology of the genus *Juncus* (Snogerup, 1963, 1985, 1993; Taylor & Mulligan, 1968; Zandee, 1981; Cope & Stace, 1985). Brooks & Kuhn (1986) studied seed morphology of 15 species of *Juncus* from Kansas (USA) using scanning electron microscopy (SEM). Novikov (1990) distinguished 350–389 species of *Juncus* divided into 2 subgenera, 14 sections, and 45 subsections and he counted the total numbers of species and subspecies of the flora in the former USSR (75 species and 14–15 subspecies, composing 2 subgenera, 12 sections, and 25 subsections). Kirschner (2002a) said Juncaceae is a cosmopolitan family, comprising 7 genera and 442 species. He counted more than 300 species and divided them into 10 sections, with a nearly worldwide distribution and centers of diversity in the temperate zones. Drábková et al. (2003) carried out a cladistic analysis of *rbc*L nucleotide sequences for 58 species from most subgenera and sections of *Luzula* and *Juncus* and they concluded that *Luzula* is monophyletic and *Juncus* is non-monophyletic. Each of the generally accepted subgenera of *Juncus*, subg. *Juncus* and subg. *Agathryon*, form a clade, but their circumscription differs from the traditional views. Knapp & Naczi (2008) studied taxonomy, morphology, and geography of three species of *Juncus*, *J. marginatus, J. biflorus*, and *J. longii*, and showed that the seeds of the three species differ in shape and size. The numbers of ridges per seed and the presence of white tails are too variable to be useful. Drábková & Vlček (2009) presented a phylogenetic analysis of mitochondrial and plastome genes. They showed that the general resolution of the main topology of the tree is similar to the separate *rbc*L tree (Drábková et al., 2003), and the subgenus *Juncus* is divided into two separate clades, the first closely related to the subgenus *Agathryon* and the second in the most basal part of the tree.

According to Tackholm & Drar (1950), culms of *Juncus* were used for making baskets from the Neolithic period, some 6000 years ago, and they were also used at that time for wrapping the bodies of the deceased. In Egypt *Juncus* is represented by 9 species (Tackholm, 1974; Boulos, 2005). El Husseiny (1980) investigated the morphology and anatomy of the

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Table 1 *Juncus* taxa used for this study

No	Taxon	Voucher	Boissier (1881)	Buchenau (1890, 1906)	Kirschner (2002a, 2002b, 2002c)
1	*Juncus acutus* L.	Egypt: El Dikheila, El Hadidi, M. s.n. (CAI)	Perennes Sect. *Maritimi*	Subgen. *Juncus*	Subgen. *Juncus* Sect. *Juncus*
2	*J. bufonius* L.	Egypt: Giza, Kralik s.n. (WAG)	Annui Sect. *Annui*	Subgen. *Poiophylli*	Subgen. *Agathryon* Sect. *Tenageia*
3	*J. fontanesii* J.Gay subsp. *pyramidatus* (Lah.) Snog.	Egypt: Faiyum, Abdel Khalik s.n. (SHG)	Perennes Sect. *Septati*	Subgen. *Septati*	Subgen. *Juncus* Sect. *Ozophyllum*
4	*J. hybridus* Brot.	Egypt: Giza, Shabetai s.n. (CAI)	Annui Sect. *Annui*	Subgen. *Poiophylli*	Subgen. *Agathryon* Sect. *Tenageia*
5	*J. inflexus* L.	Egypt: South Sinai, Wadi Feiran, Schimper 287 (L)	Perennes Sect. *Communes*	Subgen. *Genuini*	Subgen. *Agathryon* Sect. *Juncotypus*
6	*J. littoralis* C. A. May	Egypt: Cairo– Alexandria road, Wadi Natrun, Abdel Khalik s.n. (SHG)	Perennes Sect. *Maritimi*	Subgen. *Juncus*	Subgen. *Juncus* Sect. *Juncus*
7	*J. punctorius* L.	Egypt: South Sinai, Sant Katrine, Wadi Abo Twita, Abdel Khalik & Osman s.n. (SHG)	Perennes Sect. *Septati*	Subgen. *Septati*	Subgen. *Juncus* Sect. *Ozophyllum*
8	*J. rigidus* Desf.	Egypt: Red Sea coast, Wadi Gemal, Abdel Khalik s.n. (SHG)	Perennes Sect. *Maritimi*	Subgen. *Juncus*	Subgen. *Juncus* Sect. *Juncus*
9	*J. subulatus* Forssk.	Egypt: Alexandria–Matrouh coastal road, Burg El Arab, Abdel Khalik s.n. (SHG)	Perennes Sect. *Subulati*	Subgen. *Subulati*	Subgen. *Agathryon* Sect. *Forskalina*

Taxa arranged in alphabetical order according to Boulos 2005. Location of voucher specimens provided, and herbarium acronyms given in parentheses. The table compares traditional [Boissier (1881), Buchenau (1890, 1906)] and more recent [Kirschner (2002a, 2002b, 2002c)] classifications.

Juncus species in Egypt. She said that *J. rigidus* is a polymorphic species and the anatomical characters of peduncle and leaf characters provided their applicability for the distinction of the Egyptian species of *Juncus*.

The aim of the current study is to investigate the range of variability in seed characters for the *Juncus* species of Egypt in order to elucidate their usefulness in distinguishing them and to verify whether these results correspond to the results of Boissier (1881), Buchenau (1890), Novikov (1990), and Kirschner (2002a, 2002b, 2002c) for *Juncus* sections.

1 Material and methods

Some of the investigated seeds were collected from mature plants in Egypt and others were taken from herbarium specimens. A list of voucher specimens and localities is given in Table 1.

Only mature seeds were taken for investigation. The dried seeds were first examined by dissecting scope (Olympus type BH-2), and 10–15 seeds for each taxon were chosen to cover the range of variation. Seeds were mounted on stubs with double adhesive tape. The stubs were sputter-coated with gold for 5 min in an E1100 (Polaron Equipment). After coating, the specimens were examined with a Jeol JSM 5300 SEM, using accelerating voltages at 20–25 kV. The terminology used here follows authors such as Barthlott (1981, 1984), Abdel Khalik & Maesen (2002), and Abdel Khalik (2006).

2 Results

The seeds of *Juncus* are tightly invested by a layer of nearly translucent and membranous. This layer forms the tails or appendages that can be used as diagnostic characters among species.

The seed morphological characters of the studied taxa of the genus *Juncus* as shown by light microscopy and SEM are reviewed in Table 2 and Figs. 1–9.

2.1 Seed shape

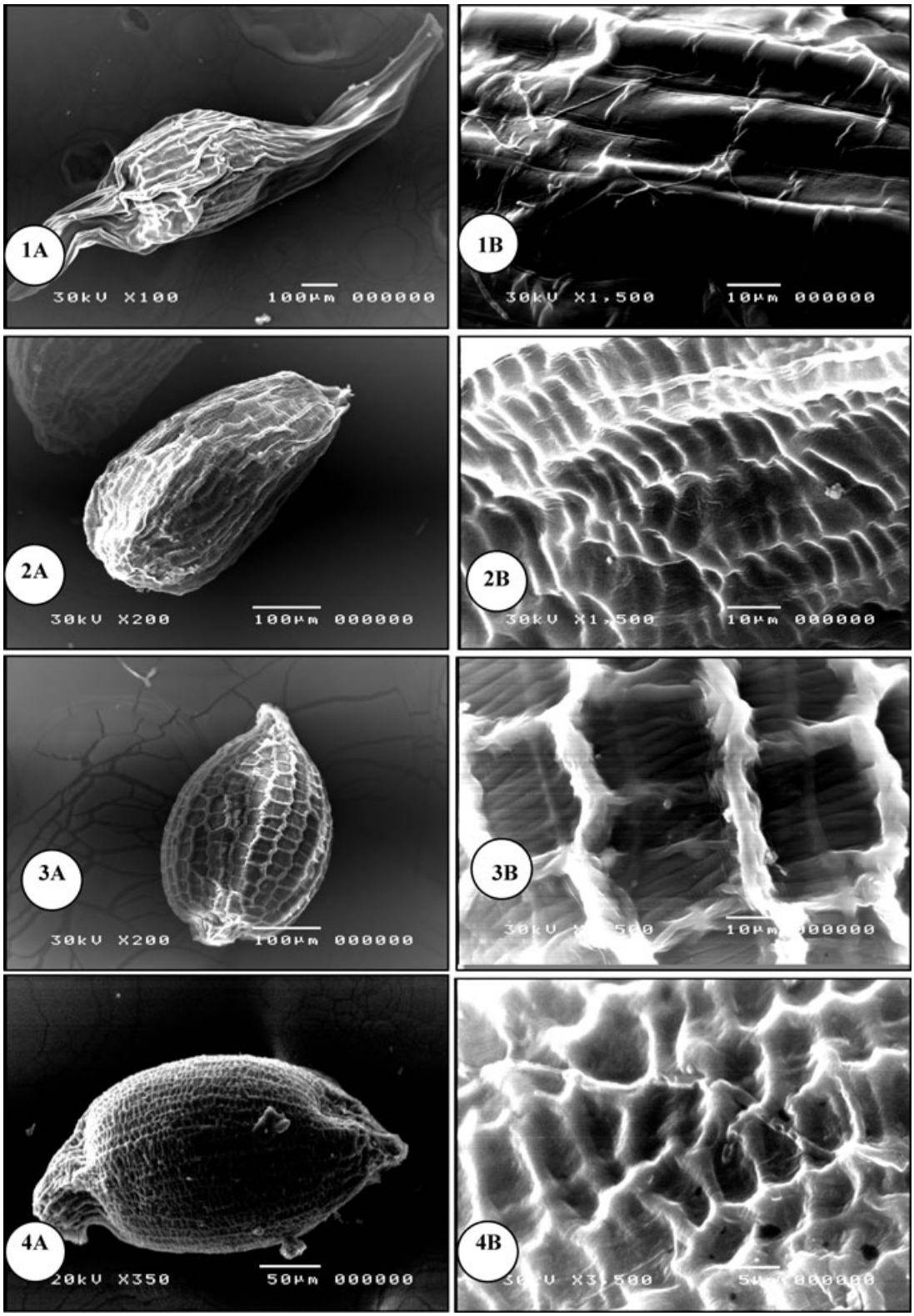
The seed shape varies from fusiform in *J. rigidus* (Fig. 8), ovoid to elliptic in *J. bufonius* and *J. inflexus* (Figs. 2, 5), ovoid in *J. fontanesii* subsp. *pyramidatus* and *J. hybridus* (Figs. 3, 4), to obliquely ovoid in the rest of the *Juncus* species.

2.2 Seed size

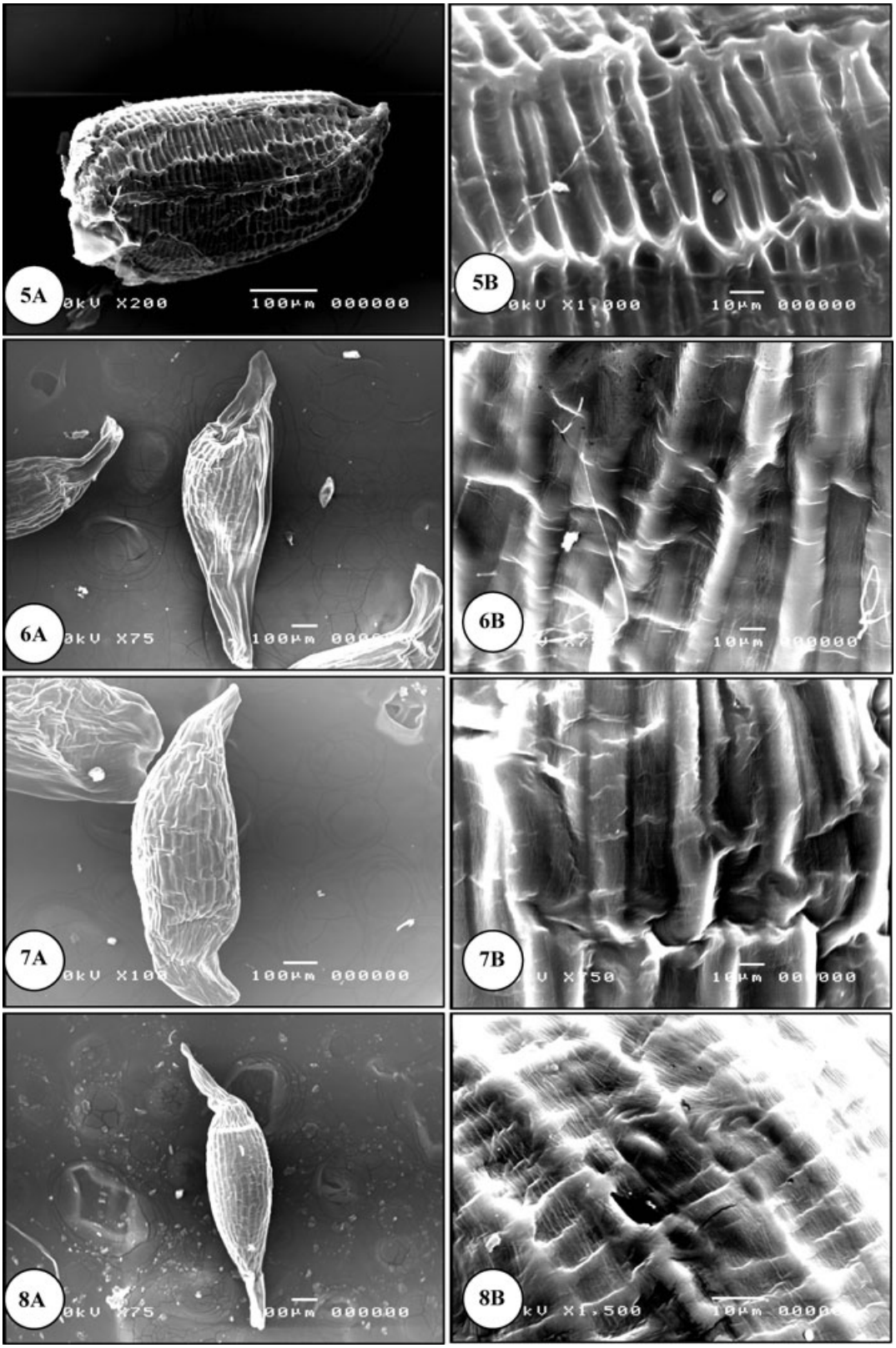
Seed dimensions vary significantly among the examined taxa. The largest obliquely ovoid seeds in *J. acutus* are 1.2–2.0 × 0.3–0.7 mm (Fig. 1), the fusiform seeds in *J. rigidus* are 0.9–2.0 × 0.4–0.6 mm (Fig. 8), and the smallest seeds measure 0.3–0.6 × 0.2–0.3 mm in *J. bufonius, J. fontanesii* subsp. *pyramidatus, J. hybridus*, and *J. inflexus* (Figs. 2–5). The rest of the species has slightly larger seeds, measuring 0.5–0.8 × 0.3–0.5 mm.

Table 2 Seed morphological characteristics in examined *Juncus* species

No	Taxon	Seed shape	Seed size (mm)	Seed color	Seed appendages	Epidermal cell shape	Anticlinal cell wall boundaries	Periclinal cell wall
1	*J. acutus* L.	Obliquely ovoid	1.2–2.0 × 0.3–0.7	Brown	With two caudate appendages (0.2–0.3 mm)	Irregular to elongate in one direction	Raised, straight, smooth to fine folded	Flat to slightly concave; smooth to fine folded
2	*J. bufonius* L.	Ovoid to elliptic	0.3–0.5 × 0.2–0.3	Brown	Without appendages, minutely apiculate at one end	Polygonal to elongate in one direction	Raised, straight to slightly sinuous, smooth to fine folded	Concave; smooth to microreticulate
3	*J. fontanesii* J. Gay subsp. *pyramidatus* (Lah.) Snog.	Ovoid	0.4–0.5 × 0.3–0.4	Pale brown	Without appendages, minutely apiculate at both ends	Irregular to 4–5 gonals	Raised, sinuous, folded	Flat; obscurely striate
4	*J. hybridus* Brot.	Ovoid	0.3–0.4 × 0.2–0.3	Yellowish-brown	Without appendages, minutely apiculate at both ends	Polygonal to elongate in one direction	Raised, straight to sinuous, smooth to fine folded	Flat to concave; smooth to microreticulate
5	*J. inflexus* L.	Ovoid to elliptic	0.4–0.6 × 0.2–0.3	Reddish-brown	Without appendages, minutely apiculate at one end	Elongate in one direction	Raised, straight, smooth	Flat to concave, microreticulate
6	*J. littoralis* C. A. May	Obliquely ovoid	0.6–1.8 × 0.4–0.6	Yellowish-brown	With two appendages (0.2–0.3 mm)	Irregular to elongate in one direction	Raised, straight, smooth to fine folded	Flat to slightly concave; smooth to fine striate
7	*J. punctorius* L.	Obliquly ovoid	0.5–0.7 × 0.3–0.4	Pale brown	With two appendages small (0.1–0.2 mm)	Irregular to elongate in one direction	Raised, straight, fine folded	Flat to slightly concave; smooth to striate
8	*J. rigidus* Desf.	Fusiform	0.9–2.0 × 0.4–0.6	Brown	With two appendages (0.3–0.4 mm)	Polygonal to elongate in one direction	Slightly raised, straight to slightly sinuous, smooth to fine folded	Flat to slightly concave; striate
9	*J. subulatus* Forssk.	Obliquely ovoid	0.5–0.8 × 0.3–0.5	Pale brown	Without appendages	Elongate in one direction	Slightly raised channeled, straight, smooth to fine folded	Flat to slightly concave; reticulate



Figs. 1–4. Scanning electron micrographs of seeds from selected *Juncus* species. **1.** *J. acutus*. **2.** *J. bufonius.* **3.** *J. fontanesii* subsp. *pyramidatus*. **4.** *J. hybridus*. **A,** Entire seed. **B,** Enlargement of seed coat.



Figs. 5–8. Scanning electron micrographs of seeds from selected *Juncus* species. **5.** *J. inflexus*. **6.** *J. littorlis.* **7.** *J. punctorius*. **8.** *J. rigidus.* **A,** Entire seed. **B,** Enlargement of seed coat.

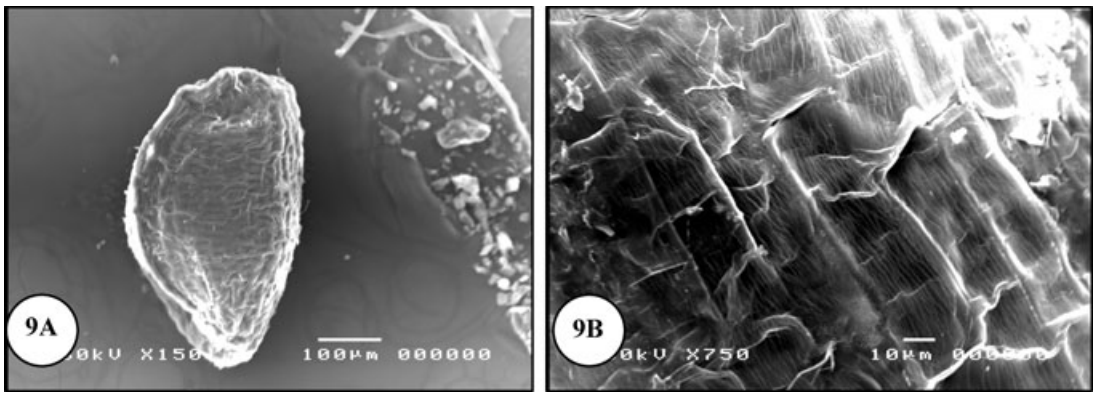


Fig. 9. Scanning electron micrographs of seeds from *Juncus subulatus*. **A,** Entire seed. **B,** Enlargement of seed coat.

2.3 Seed color

The colors of the seeds are of less diagnostic and systematic value among species. The colors vary from reddish-brown in *J. inflexus,* yellowish-brown in *J. hybridus* and *J. littoralis,* brown in *J. acutus*, *J. bufonius*, and *J. rigidus*, to pale brown in *J. fontanesii* subsp. *pyramidatus, J. punctorius*, and *J. subulatus*.

2.4 Seed appendages

Seed appendages show great variation among the studied taxa. They include: seeds with two appendages in *J. acutus, J. littoralis, J. punctorius*, and *J. rigidus* (Figs. 1, 6–8); seeds without appendages in *J. subulatus*; seeds minutely apiculate at one end in *J. bufonius* and *J. inflexus*; and seeds minutely apiculate at both ends in *J. fontanesii* subsp. *pyramidatus* and *J. hybridus*. The length of the appendages can also be useful, varying from short (0.1–0.2 mm) in *J. punctorius* (Fig. 7) to long (0.2–0.4 mm) in *J. rigidus* (Fig. 8).

2.5 Epidermal cell shape

Cellular shapes can be of great diagnostic and systematic value. The cells are: irregular to 4–5 gonals in *J. fontanesii* subsp. *pyramidatus* (Fig. 3); irregular to elongate in one direction in *J. acutus, J. littoralis*, and *J. punctorius* (Figs. 1, 6, 7); elongate in one direction in *J. inflexus* and *J. subulatus* (Figs. 5, 9); and polygonal to elongate in one direction in the rest of the taxa.

2.6 Anticlinal cell wall boundaries

These are generally well developed. There are two types of cell wall boundaries: (i) raised-channeled, straight, smooth to fine folded in *J. subulatus* (Fig. 9); and (ii) raised, straight or sinuous or straight to slightly sinuous, smooth to fine folded in the rest of the taxa.

2.7 Periclinal cell wall

2.7.1 Outer periclinal cell walls The curvature of the outer wall can serve as a good diagnostic character. There are three different shapes for the outer periclinal cell wall: (i) flat in *J. fontanesii* subsp. *pyramidatus* (Fig. 3); (ii) concave in *J. bufonius* (Fig. 2); and (iii) flat to slightly concave in the rest of the taxa.

2.7.2 Secondary cell wall sculpture The surface of the outer cell wall shows great variation among the studied taxa: striate in *J. fontanesii* subsp. *pyramidatus* and *J. rigidus* (Figs. 3, 8); microreticulate in *J. bufonius, J. hybridus*, and *J. inflexus* (Figs. 2, 4, 5); reticulate in *J. subulatus* (Fig. 9); smooth to fine folds in *J. acutus* (Fig. 1); and smooth to fine striate in *J. littoralis* and *J. punctorius* (Figs. 6, 7).

Key to *Juncus* L. species from Egypt, based on seed characters

1a. Seeds with two appendages 2

1b. Seeds without two appendages; minutely apiculate at one or at both ends 5

2a. Seeds fusiform; epidermal cell shape polygonal to elongate in one direction; periclinal cell wall striate; appendage 0.3–0.4 mm long . . . **J. rigidus**

2b. Seeds obliquely ovoid; epidermal cell shape irregular to elongate in one direction; periclinal cell wall smooth to fine folded or fine striate; appendage 0.1–0.3 mm long 3

3a. Seeds pale brown, 0.5–0.7 × 0.3–0.4 mm; anticlinal boundaries fine folded; appendage 0.1–0.2 mm . . . . . **J. punctorius**

3b. Seeds brown or yellowish-brown, 0.6–2 × 0.4–0.7 mm; anticlinal boundaries smooth to fine folded; appendage 0.2–0.3 mm 4

4a. Seeds brown; periclinal cell wall fine folded . . . . . **J. acutus**

4b. Seeds yellowish-brown; periclinal cell wall fine striate . . . . . **J. littoralis**

5a. Epidermal cell shape elongate in one direction . 6

5b. Epidemal cell shape irregular to 4–5 gonals or polygonal to elongate in one direction 7

6a. Seeds pale brown; anticlinal boundaries slightly raised-channeled, smooth to fine folded; without appendages . . . . . **J. subulatus**

6b. Seeds reddish brown; anticlinal boundaries raised, smooth; minutely apeculate at one end . . . . . **J. inflexus**

7a. Epidermal cell shape polygonal to elongate in one direction; periclinal cell wall microreticulate . . . 8

7b. Epidermal cell shape irregular to 4–5 gonals; periclinal cell wall obscurely striate . . . . . **J. fontanesii subsp. pyramidatus**

8a. Seeds ovoid to elliptical; brown; minutely apiculate at one end. . . . . **J. bufonius**

8b. Seeds ovoid; yellowish-brown; minutely apiculate at both ends . . . . . **J. hybridus**

3 Discussion

Several authors have tried to provide a natural system to divide the genus *Juncus* into subgenera, sections, and subsections (Boissier, 1881; Buchenau, 1890, 1906; Kirschner, 2002a, 2002b, 2002c; see Table 1). These studies were based on morphological characters such as life form, stems, leaves, flowers, and fruits. In the present investigation a large number of seed characters were used based on the details of seed coat structure.

Generally, my results show that different patterns of seed morphology are helpful in distinguishing various species (Table 2) and partially confirm the subgenera and sectional classification of the genus *Juncus*.

Boissier (1881) and Buchenau (1890, 1906) classified *Juncus* into five subgenera (sections): (i) *Juncus (Maritimi*); (ii) *Poiophylii (Annui)*; (iii) *Septati (Septati)*; (iv) *Genuini (Communes)*; and (v) *Subulati (Subulati)*. Kirschner (2002a) classified the genus *Juncus* into two subgenera and five sections.

The subgenus *Juncus* was split from the rest of the subgenera on the basis of the species with terete, leafless, pungent, non-septate stems (Boissier, 1881; Buchenau, 1890, 1906). Snogerup (1993) studied the chromosome morphology of the subgenus *Juncus* and he counted that *J. acutus*, *J. littoralis*, and *J. rigidus* have 2n = 48. Moreover Kirschner (2002b) classified the subgenus *Juncus i*nto two sections. He treated *J. acutus*, *J. littoralis*, and *J. rigidus* as members in section *Juncu*s and put *J. punctorius* and *J. fontanesii* as members in section *Ozophyllum*. Furthermore, Drábková et al. (2003) presented a phylogenetic analysis of 58 species from most subgenera and sections of *Luzula* and *Juncus* using the DNA sequence of the chloroplast *rbc*L nucleotide. They indicated that *Luzula* is monophyletic and *Juncus* is non-monophyletic. Within *Juncus,* they show that subgenus *Juncus* clade is well supported (98% support), and the section *Juncus* is well supported (70%). Drábková et al. (2004) undertook a phylogenetic analysis of 55 species from Juncaceae using the DNA sequence of the chloroplast *trn*L–*trn*F intergenic spacer, and they concluded that the duplicated tRNA pseudogene was found in the subgenus *Juncus* species and is amply supported by specific indels. Drábková & Vlček (2009) showed that the general resolution of the main topology of the tree is similar to the separate *rbc*L tree (Drábková et al., 2003). The seed morphology confirms this division, because subgenus *Juncus* (*J. acutus, J. littoralis*, and *J. rigidus*) have seeds with two appendages; irregular to elongate in one direction epidermal cell shape; raised, straight to slightly sinuous, smooth to fine folded anticlinal boundaries and flat to slightly concave periclinal cell wall.

Generally these results are congruent with those of Boissier (1881), Buchenau (1890), Snogerup (1993), Kirschner (2002b), Drábková et al. (2003, 2004), and Drábková & Vlček (2009).

Subgenus *Agathryon* = *Poiophylii* = *Genuini* (*J. hybridus, J. inflexus*, and *J. bufonius*) is characterized by a pair of floral bracteoles, a cymose inflorescence, and flowers borne in single or loose groups. Drábková et al. (2004) showed that the subgenus *Agathryon* species is amply supported by a 4-bp insertion and has an additional 5-bp deletion close to the 3′-end of the intron. Taylor & Mulligan (1968) found that *J. bufonius* has 2n = 34. Cope & Stace (1985) counted that *J. hybridus* has 2n = 34 and *J. bufonius* has 2n = 108 and they concluded that *J. bufonius* constitutes a polyploid. Snogerup (1963) counted that *J. inflexus* has 2n = 40. The seed morphology verifies this division, because subgenus *Agathryon* has ovoid to elliptic seeds, measuring 0.3–0.6 × 0.2–0.3 mm; with minutely apiculate appendages at one or both ends; polygonal to elongate in one direction epidermal cell shape; raised, straight to sinuous, smooth to fine folded anticlinal boundaries and flat to concave, and smooth to microreticulate periclinal cell wall. These data agree with those of Kirschner (2002c)

and Drábková et al. (2004), but disagree with those of Boissier (1881) and Buchenau (1890).

Kirschner (2002b) placed *J. punctorius* and *J. fontanesii* in subgenus *Juncus* section *Ozophyllum*, whereas Buchenau (1890) treated these species as a separate subgenus *Septati*. Boissier (1881) treated *J. punctorius* and *J. fontanesii* as a separate section *Septati*. Furthermore, Snogerup (1985) indicated that *J. punctorius* has 2n = 40 and Zandee (1981) showed that *J. fontanesii* has 2n = 80. Drábková et al. (2004) treated accepted section *Ozophyllum* within the subgenus *Juncus* and they concluded that section *Ozophyllum* contains the 5 acceptor stem, D-domain, and anticodon domain of the tRNA encoding DNA, and that this section is distinguished by E (22 bp).

Seed morphology did not confirm this division, because *J. punctorius* has seeds with two appendages; irregular to elongate in one direction epidermal cell shape; raised, straight, fine folded anticlinal boundaries and flat to slightly concave, smooth to striate periclinal cell wall. *Juncus fontanesii* has seeds that are minutely apeculate at both ends; irregular to 4–5 gonals epidermal cell shape; raised, sinuous, folded anticlinal boundaries; and flat, obscurely striate periclinal cell wall. These results disagree with those of Boissier (1881), Buchenau (1890), Kirschner (2002b) and Drábková et al. (2004), but agree with Snogerup (1985) and Zandee (1981).

Boissier (1881) and Buchenau (1890, 1906) treated *J. subulatus* as a separate subgenus *Subulati* section *Subulati*. However, Nobvikov (1990) treated this species in subgenus *Juncus* section *Subulat*. Furthermore, Kirschner (2002c) placed this species in subgenus *Agathryon* section *Forskalina.* Snogerup (1963) counted that *J. subulatus* has 2n = 42. Seed morphology might be useful in distinguishing *J. subulatus* from the rest of the species by having seeds without appendages; elongate in one direction epidermal cell shape; slightly raised-channeled, straight, smooth to fine folded anticlinal boundaries; and flat to concave, reticulate periclinal cell wall. These data are congruent with those of Boissier (1881), Buchenau (1890), and Snogerup (1963), but disagree with both Nobvikov (1990) and Kirschner (2002c).

The developmental variations of seed morphology are worthy of being taken into account, not only because they give us a better comprehension of sculpture development but also for formulating the taxonomy of *Juncus* on both the subgenera and sectional level and preparing an identification key.

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