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Taxonomic Implications of Seed Coat in the Subtribe Calthinae (Ranunculaceae)

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Anatomical features of seed coat were examined on *Trollius*, *Calathodes*, and *Caltha* of Ranunculaceae to evaluate the taxonomic circumscription of *Megaleranthis saniculifolia*, which is monotypic and endemic in Korea. *Megaleranthis saniculifolia* showed the exotestal type of seed coat exhibiting a well-developed palisade structure in exotesta and its external surface of exotesta cells was concave. On the other hand, the shape of exotesta cells in *Caltha* was cuboidal and the outer surface was smooth. The exotesta of *Calathodes* seeds was formed of the palisade structure like *M. saniculifolia*, but the outer surface of exotesta cells was smooth. The palisade structure was much better developed in the exotesta of *Calathodes* as well as *Megaleranthis* seeds than in the exotesta of *Trollius* seeds. The outer surface of exotesta cells in *Trollius* was either convex or concave according to the species examined. Since the genera of the subtribe Calthinae of the family display differences in seed sculpturing and the anaotmy of seed coat, these characteristics are useful to access taxonomic relationships among them. The morphological and anatomical features of seed coat suggest that *Megaleranthis* be possibly allied with *Trollius* rather than *Caltha* or *Calathodes*. Concave surface of seed coat cells and well-developed palisade structure of exotesta are shared by *M. saniculifolia* and some species of *Trollius* in common.

Key words: Calthinae, endemic species, *Megaleranthis*, Ranunculaceae, seed coat

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Megaleranthis Ohwi is a monotypic genus, of which a sole member, *M. saniculifolia*, is endemic in Korea (Lee, 1969). The genus is characterized by a perennial herb with a single basal leaf and a single terminal apocarpous flower of five sepals and five white petals. Basal leaf is distinctively tripartite with each segment deeply 2-3 incised-dentate, and cauline leaf is similar to the basal beneath the flower. Vessels are well-distributed and pollen grains are tri-aperture (Ohwi, 1935). It was collected at Mt. Jiri and established as a new genus by Ohwi (1935). Its taxonomic treatment has been still in dispute since the taxonomic position was changed as *Trollius chosenensis* with a brief description without any explanations on his taxonomic treatment (Ohwi, 1937).

The earlier palynological study demonstrated that the pollen morphology of *M. saniculifolia* is very similar to *Trollius* in having striate surface (Kim and Lee, 1987). Later, Lee (1990) has also claimed that *Megaleranthis* should be included in *Trollius* based on pollen morphology and other morphological characters. The phylogenetic analysis of 26S ribosomal DNA sequences indicated that *Megaleranthis* might be congeneric with *Trollius* (Ro *et al.*, 1999). Recently, Jang and Heo (2005) suggested that *Megaleranthis* may be very closely related to *Trollius* and that even the former possibly be placed in the latter because the comparative study on reproductive morphology did not yield any significant differences between *Megaleranthis* and *Trollius*.

Tobe (1995) reviewed on the morphology of seeds and seed coats for the family Ranunculaceae by literature survey. In review, he insisted that more intensive studies on the exotesta would be necessary in particular because exotesta could serve well as a taxonomic tool for the family. In this study, anatomical features of seed coat were examined for the genera of the subtribe Calthinae *sensu* Tamura (1995) to test the taxonomic circumscription of *Megaleranthis* within the subtribe.

Materials and Methods

An anatomical examination was carried out for *Megaleranthis saniculifolia*, twenty-one species of *Trollius*, one species of *Caltha*, and one species of *Calathodes* within subtribe Calthinae *sensu* Tamura (1995, Table 1). For the observation of ovule development and young seed coat structure, several ovules and young seeds of *Trollius japonicus* were soaked in F.A.A. After dehydration through t-butyl alcohol series, materials were embedded in paraplast with a melting point at 56℃. They were sectioned by 8 μm thickness with a rotary microtome. The sections were stained with Heidenhain's hematoxylin, Safranin O, and fast green FCF, and then mounted with Entellan.

The morphology of mature seeds was observed with a scanning electron microscope. Mature seeds were dehydrated through a series of ethanol, and then dried with CO_2 critical point dryer. After being coated with gold, the prepared seeds were observed with a Hitachi S3500 scanning electron microscope at 15kV. The terminology of seed coat and sculpturing of seed surface follows Corner (1976) and Schmid (1986).

Results

Megaleranthis saniculifolia

The gynoecium is apocarpous of several carpels. Each carpel contains six to eight ovules arranged in two rows along the ventral suture showing a typical marginal placentation. At maturity, the surface of seed coat cells is more or less uneven and concave (Fig. 1f), although it looks smooth when observed by naked eyes (Fig. 1e). After the complete maturation, the seed coat is made up of a palisadal exotesta, of which thickness is 35 to 40 μm with collapsed mesotesta and endotesta of a few cell layers (Fig. 1g; Table 2). Except for the above description, other seed coat information such as seed shape, seed size, seed color, and seed coat type has already published in the previous article by the first author (Jang and Heo, 2005).

Caltha palustris

The gynoecium is apocarpous of six to fifteen carpels arranged in a whorl. Each carpel contains six to twelve anatropous and bitegmic ovules, which are borne in two rows on the marginal placentation. Mature seeds are black to brown in color and ellipsoidal in shape (Fig. 1h). The size of mature seeds ranges from 2.2 to 2.3 mm in length and 1.0 to 1.1 mm in width from raphe to antiraphe side (Fig. 1h). The surface of seed coat cells is smooth and the shape is long-cubic (Fig. 1i). *Caltha* differs from *Megaleranthis*, *Calathodes*, and *Trollius* in point of seed coat cells of hexagonal shape.

In young ovules, the inner integument always appears to be two cell layers thick while the outer integument is composed of four to five cell layers. After fertilization, the tegmen is crushed. In mature seeds, endotesta and mesotesta become collapsed eventually, while the cells of exotesta are developed as cuboidal cells with a thick cuticle layer. Cuboidal cells are about 25 to 30 μm in thickness and filled with tannin substances (Fig. 1j). Therefore, the seed coat type of *Caltha palustris* is an exotestal type although it differs from exotesta structure in comparison with other genera examined in the subtribe.

Table 1. Collection data and voucher number of materials used in this study

Taxa	Collection data
Calathodes polycarpa Ohwi	Taiwan. Mt. Nengkao, 1964 August 12, M. Tamura & H. Koyama 23333 (TI)
Caltha palustris L.	Korea. Gangwon Province, Mt. Taegi, alt. 1100m., 1999 May 20, K. Heo 330 (KWNU)
Megaleranthis saniculifolia Ohwi	Korea. Gangwon Province, Mt. Taegi, alt. 1100m., 1999 May 20, K. Heo 333 (KWNU)
Trollius acaulis Lindl.	India. Rupan pass, Bushahr, Simla, 1934 September 2, N. Parmanand 1191 (TI)
T. albiflorus (A. Gray) Rydb.	U.S.A. Herbarium of North Western College, 1903 August 31, L. Umbach 811 (MO)
T. asiaticus L.	Russia. Central Siberia, from Irkutsk to Kultuh, 1975 July 13, H. Hara *s.n.* (TI)
T. chinensis Bunge	China. Hopei 1962 June 21 (PE 653661)
T. dschungaricus Regel	China. Xinjang, Uygurs autonomous region 1958 August 3, Junatov & Juan-fen *s.n.* (MO)
T. europaeus L.	France. Commercial seed stock, B & T World seeds company 2002 November 15 (KWNU)
T. farreri Stapf	China. Mt. Nangqen just west of Jiangxi forest station, alt. 3600m, 1996 August 27, M. Gilbert *et al.* 2433 (MO)
T. hondoensis Nakai	Korea. Cultivated at Pyongchang Botanical Garden 2004 May 22, K. Heo *s.n.* (KWNU)
T. hondoensis Nakai	Japan. Shinano, Kirigamine, North of Suwa 1956 August 11, G. Murata 9944 (KYO)
T. japonicus Miq.	Japan. Hokkaido, Mt. Daisetsu 1928 August, T. Nakai *s.n.* (TI)
T. japonicus Miq.	Korea. Cultivated at Kangwon National University 2002 June 11, W. K. Lee *s.n.* (KWNU)
T. laxus Salisb.	U.S.A. Southeastern Pennsylvania, Bucks Co., 1923 June 9, Bayard Long 27310 (MAK)
T. ledebourii Rchb.	China. Heilongjiang Province, 1943 September, S. Nakao *s.n.* (KYO)
T. ledebourii var. *polysepalus* Regel	Japan. Hokkaido, Wakanai Co., 2004 August 3, K. Heo *s.n.* KWNU)
T. macropetalus F. Schmidt	Korea. Hamkyong-namdo, Gema plateau, 1932 August 22, S. Kitamura *s.n.* (KYO)
T. patulus Salisb.	Caucasus. Cane region, (MO 3725931)
T. pumilus D. Don	Nepal. Chaurapani Bajhang District, 1976 August 1, H. Tabata 8946 (KYO)
T. ranunculinus (Smith) Stearn	Georgia. Kazbegi village, alt. 1760m 1975 July 14, T. Tsuyama *s.n.* (TI)
T. ranunculoides Hemsl.	China. Wang wen-tsai, Zheguwan, alt. 3500m 1989 July 28, Zhao Qing-Sheng 0055 (PE)
T. riederianus Fisch. & C. A. Mey.	Japan. Hokkaido, Shiretoko, Mt. Rausu, alt. 1400m, 1984 August 26, T. Yamazaki *s.n.* (TI)
T. riederianus Fisch. & C. A. Mey.	Japan. Hokkaido, Kitami Monbetsu Co., upper Hirayama, alt. 1700m, 1963 August 26, S. Okamoto *s.n.* (KYO)
T. riederianus var. *japonicus* Ohwi	Japan. Nagano Nagatani cho, Senbetake, 1954 September 4, M. Mizushima *s.n.* (MAK)
T. sp.	Russia. Sakhalin, near Sokol field stadium, alt. 200m along side of river, 2002 July 29, N. Fuji 00983 (MAK)
T. taihasenzanensis Masam.	Taiwan. Mt. Nengkao, alt. 2800m, 1964 August 11, M. Tamura & H. Koyama 23289 (KYO)

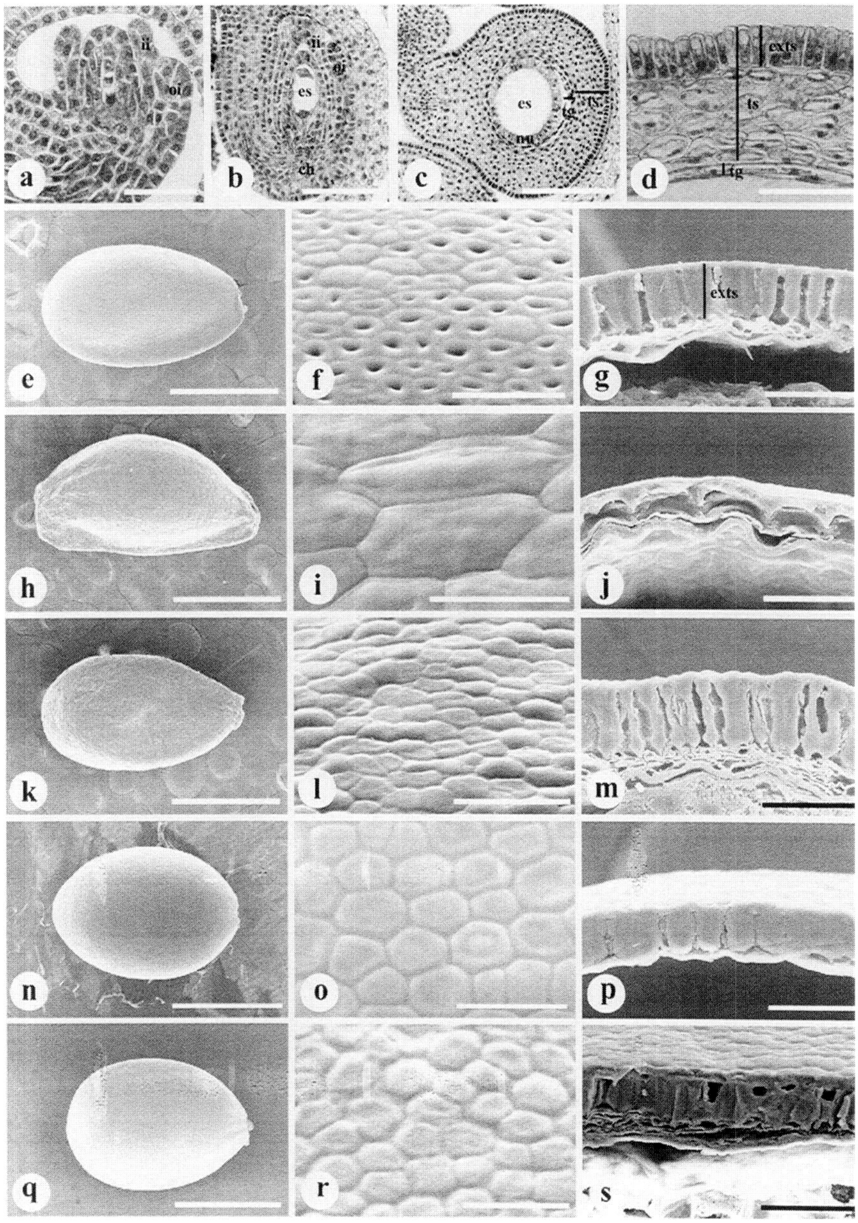

Fig. 1. Development of integuments (a-c), exotesta (d), shape of mature seed, seed surface sculpture, and mature seed coat structure of *Caltha*, *Calathodes*, *Megaleranthis*, and *Trollius*. a-d, *T. japonicus*; e-g, *M. saniculifolia*; h-j, *Caltha palustris*; k-m, *Calathodes polycarpa*; n-p, *Trollius acaulis*; q-s, *T. albiflorus*. Abbreviations: ch, chalaza; es, embryo sac; exts, exotesta; ii, inner integument; nu, nucellus; oi, outer integument; tg, tegmen; ts, testa. Scale bars: 10 μm for a-d; 1 mm for e, h, k, n and q; 50 μm for f, g, i, j, l, m, o, p, r and s.

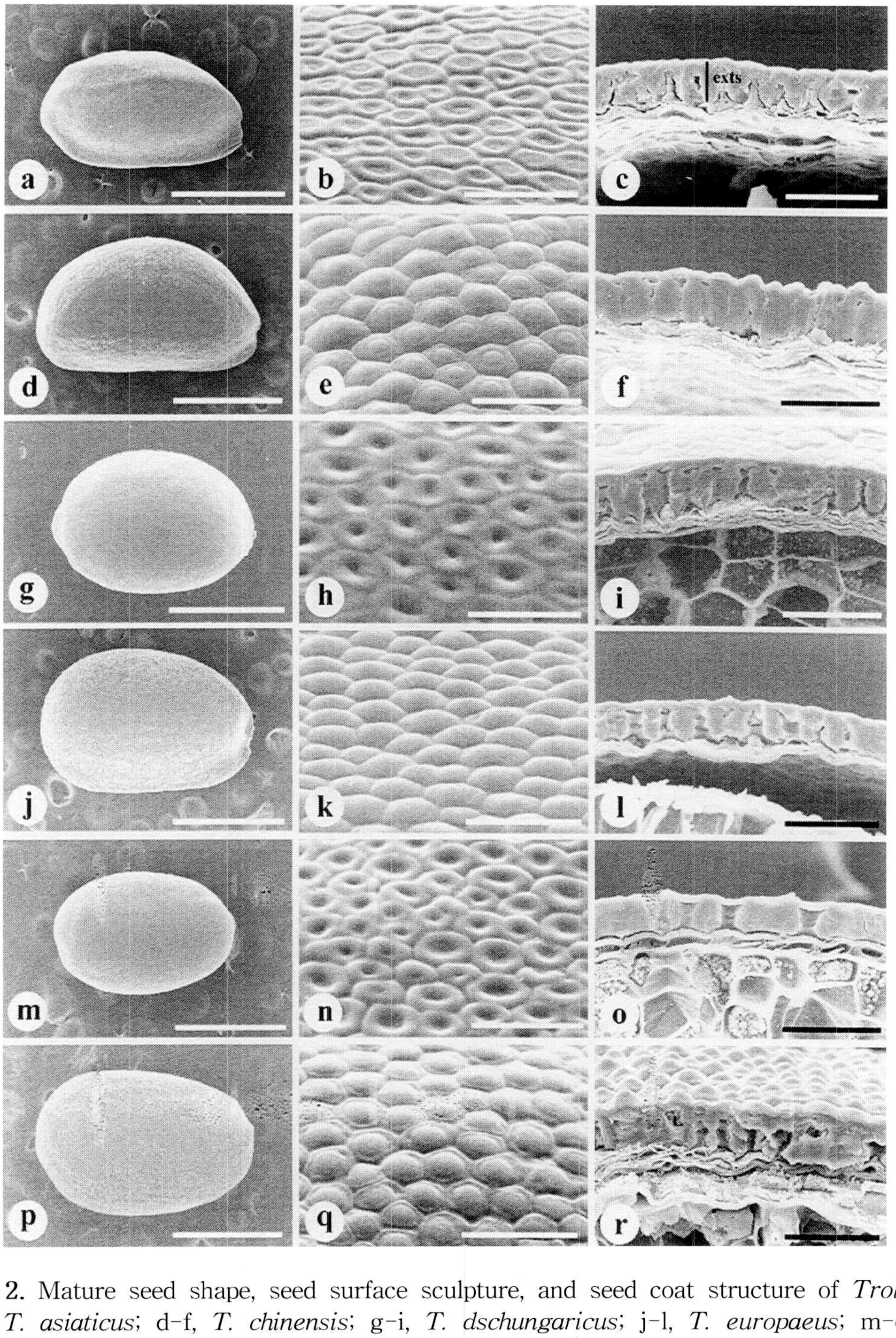

Fig. 2. Mature seed shape, seed surface sculpture, and seed coat structure of *Trollius*. a–c, *T. asiaticus*; d–f, *T. chinensis*; g–i, *T. dschungaricus*; j–l, *T. europaeus*; m–o *T. farreri*; and p–r, *T. hondoensis* (KWNU). Scale bars: 1 mm for a, d, g, j, m and p; 50 µm for b, c, e, f, h, i, k, l, n, o, q and r.

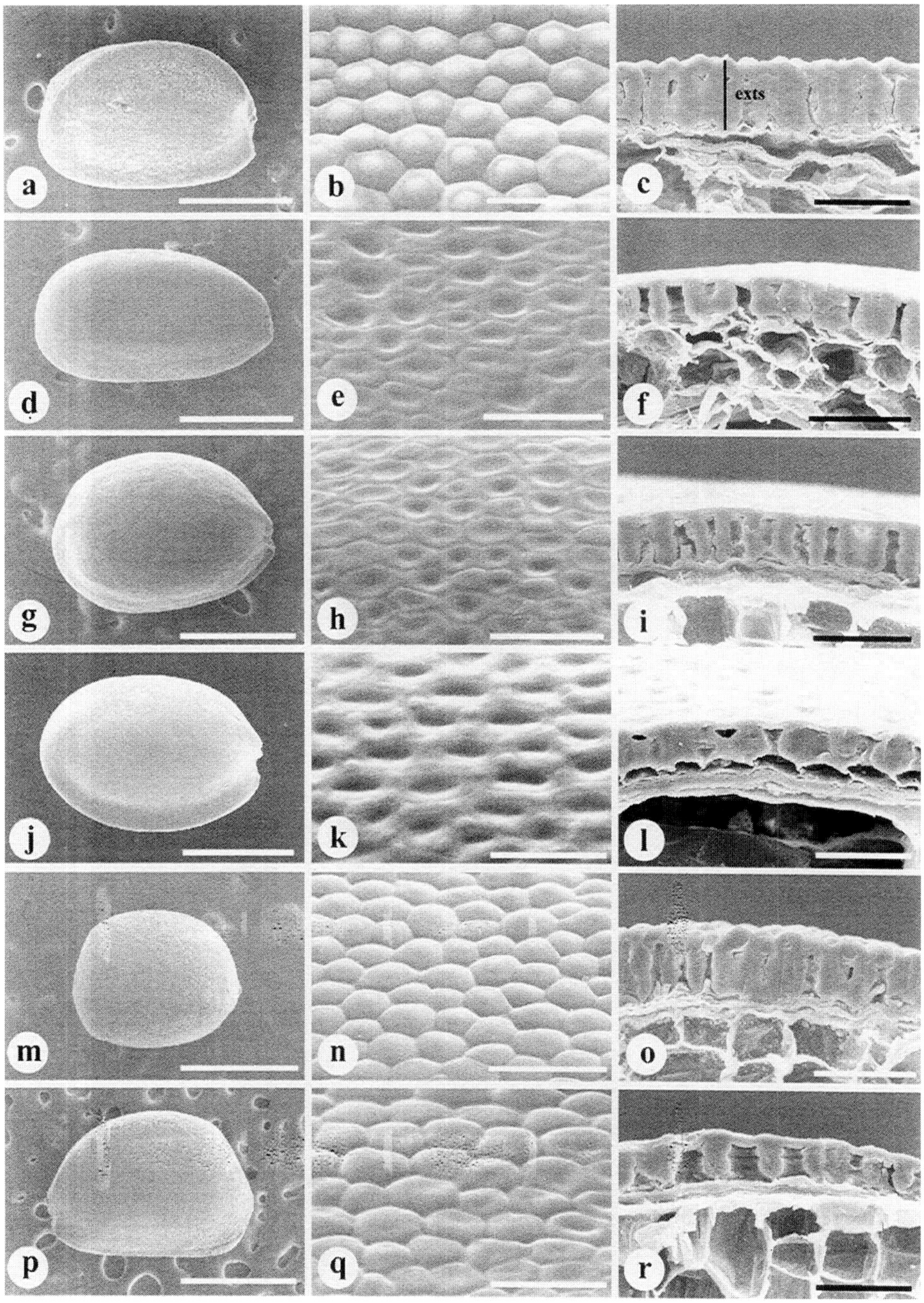

Fig. 3. Mature seed shape, seed surface sculpture, and seed coat structure of *Trollius*. a–c, *T. hondoensis* (KYO); d–f, *T. japonicus* (TI); g–i, *T. japonicus* (KWNU); j–l, *T. laxus*; m–o, *T. ledebourii*; p–r, *T. ledebourii* var. *polysepalus*. Scale bars: 1 mm for a, d, g, j, m and p; 50 μm for b, c, e, f, h, i, k, l, n, o, q and r.

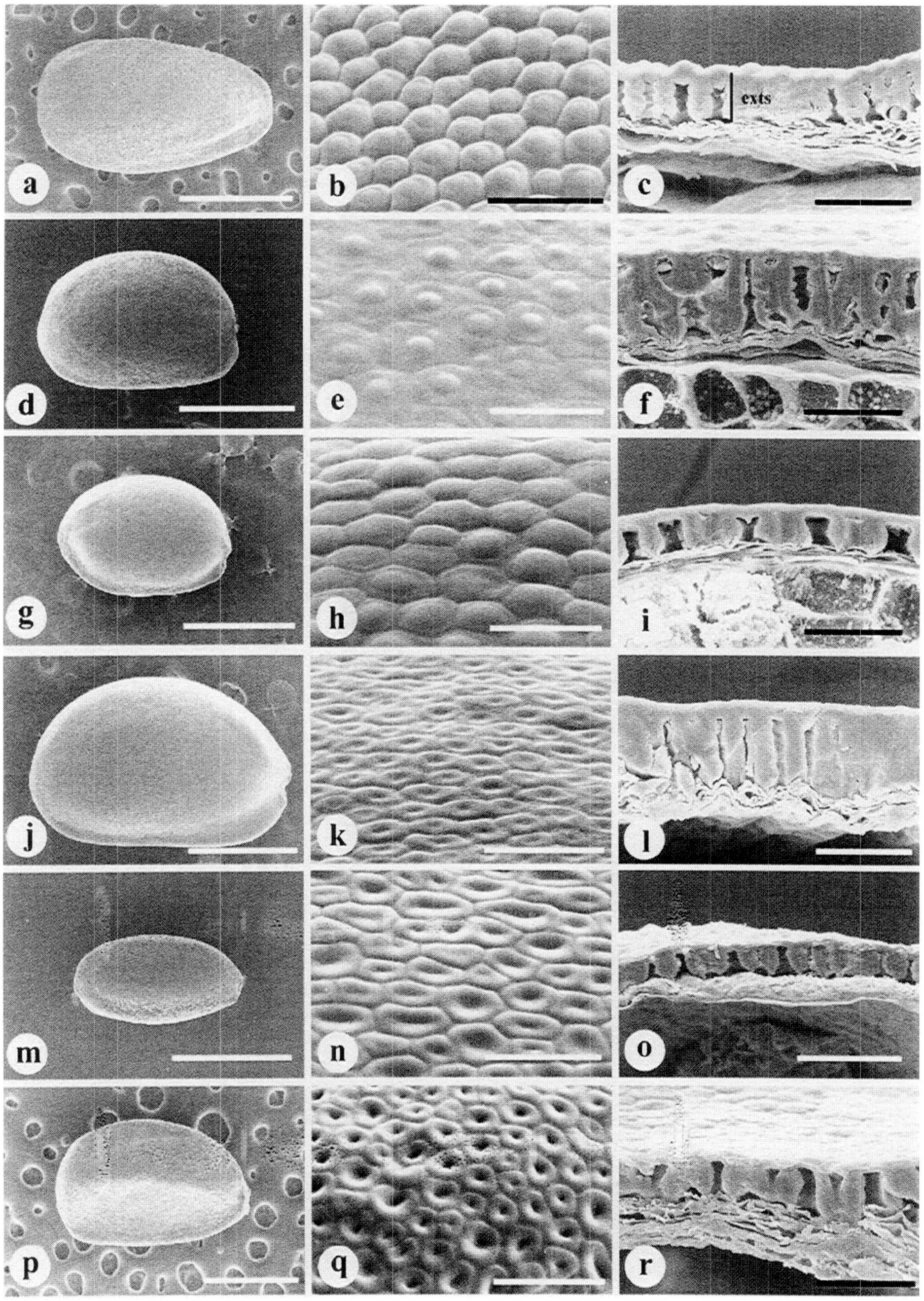

Fig. 4. Mature seed shape, seed surface sculpture, and seed coat structure of *Trollius*. a-c, *T. macropetalus*; d-f, *T. patulus*; g-i, *T. pumilus*; j-l, *T. ranunculinus*; m-o, *T. ranunculoides*; p-r, *T. riederianus* (TI). Scale bars: 1 mm for a, d, g, j, m and p; 50 μm for b, c, e, f, h, i, k, l, n, o, q and r.

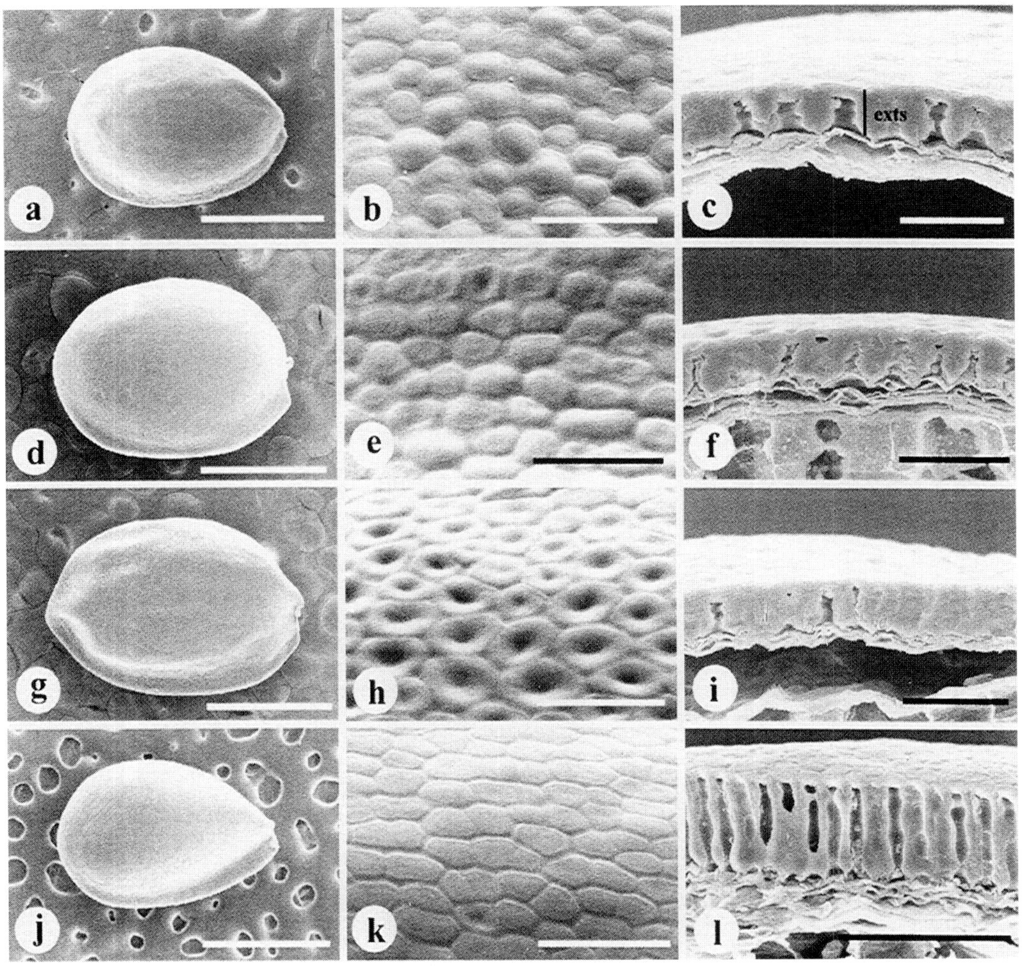

Fig. 5. Mature seed shape, seed surface sculpture, and seed coat structure of *Trollius*. a-c, *T. riederianus* (KYO); d-f, *T. riederianus* var. *japonicus*; g-i, *Trollius* sp.; j-l, *T. taihasenzanensis*. Scale bars: 1 mm for a, d, g and j; 50 μm for b, c, e, f, h, I, k and l.

Calathodes polycarpa

Calathodes has eight to 30 apocarpous carpels (sometimes over 30) in a flower. Ovules are positioned below the middle of each carpel. A follicle has several exarillate seeds, which are black and ellipsoid at maturity (Fig. 1k). Seeds range from 1.8 to 2.0 mm in length and from 1.0 to 1.2 mm in width from raphe to antiraphe bundle side (Table 2). They are also dark-color and albuminous. The surface of seed coat cells is not even and more or less convex in sculpture (Fig. 1l). After seeds are completely matured, the seed coat is composed of a palisadal exotesta, which is well-developed to the thickness of 40 to 45 μm. Mesotesta and endotesta with a few cell layers are collapsed. Tegmen is completely crushed at the end (Fig. 1m). Tegmen structure of *C. polycarpa* is very similar to that of *Megaleranthis*, and it implies that the seed coat type of *C. polycarpa* is also exotestal (Fig. 1m; Table 2).

Trollius

Since *Trollius* has several apocarpous carpels in a flower, there are several follicles, which bear several seeds in two rows on marginal placentation.

At a young stage, ovule has bitegmic (Fig. 1a). The inner integument is always two to three cells thick, whereas the outer integument is initially two to three cells thick (Fig. 1b). At a mature stage, the outer integument (testa) is multiplicative in cell thickness (Fig. 1c). Especially, exotesta develops as palisade tissue (Fig. 1d).

Mature seeds are ellipsoidal to ovoid in shape, and black to brown in color. The surface of seed coat is smooth and even glossy in naked eyes. Seeds range from 1.3 mm to 2.3mm in length and from 0.6 to 1.5mm in width (Table 2). Seeds are exarillate and albuminous, and have a minute embryo.

Within the genus, the structure of mature seed coat shows some differences especially in the thickness of exotesta and the sculpturing of seed surface (Table 2). The exotestas of *Calathodes polycarpa* and *T. taihasenzanensis* are thickest among species examined in this study (Figs. 1m, 5l). On the other hand, the exotesta of *T. farreri* is thinnest (Fig. 2o). For the sculpturing of seed surface, seed surface shows more or less different structure by scanning electron microscope although it appears smooth when examined with naked eyes. Two types of seed surface sculpturing are observed in the species of *Trollius*, i.e., convex and concave types. In convex type, the outer surface of seed coat cells is convex, which is shown in *T. acaulis* (Fig. 1o), *T. albiflorus* (Fig. 1r), *T. chinensis* (Fig. 2e), *T. europaeus* (Fig. 2k), *T. hondoensis* (Figs. 2q, 3b), *T. ledebourii* (Fig. 3n), *T. ledebourii* var. *polysepalus* (Fig. 3q), *T. macropetalus* (Fig. 4b), *T. patulus* (Fig. 4e), *T. pumilus* (Fig. 4h), *T. riederianus* (Fig. 5b), and *T. riederianus* var. *japonicus* (Fig. 5e). On the other hand, the outer surface of seed coat cells is concave type in remaining species (Figs. 2b, h, n, 3e, h, k, 4k, n, q and 5h). However, the seed surface sculpturing of *T. taihasenzanensis*, which is distributed in Taiwan, is not concave or convex but smooth (Fig. 5k; Table 2).

In the genus *Trollius*, ovule is anatropous and bitegmic, which is comprised of inner and outer integuments. The inner integument is initially two to three (micropyle part) cell layers, but does not become multiplicative in further developing stages. On the other hand, the outer integument is formed of four cell layers for most part, comprised of an outer epidermis, two middle layers and an inner epidermis. During the development of

Table 2. Comparison of seed and seed coat characteristics in the subtribe Calthinae of Ranunculaceae

Taxa	Length	Seed size (mm)*		Seed surface	Exotesta		Seed coat
		Width (R-A)	Width (L-L)	sculpture	Shapes	Thickness (μm)	types
Calathodes polycarpa	1.8~2.0	1.0~1.2	0.8~1.0	convex	palisade	40~45	exotestal
Caltha palustris	2.2~2.3	1.0~1.1	0.9~1.0	smooth	cuboid	25~30	exotestal
Megaleranthis saniculifolia	1.6~2.0	1.1~1.2	0.9~1.1	concave	palisade	35~40	exotestal
Trollius acaulis	1.6~1.8	1.1~1.3	1.1~1.3	convex	palisade	30~35	exotestal
T. albiflorus	1.6~1.8	1.1~1.2	1.0~1.2	smooth	palisade	25~30	exotestal
T. asiaticus	1.7~1.9	1.0~1.2	0.9~1.1	concave	palisade	23~28	exotestal
T. chinensis	1.8~2.0	1.1~1.3	0.8~1.0	convex	palisade	25~30	exotestal
T. dschungaricus	1.7~1.8	1.1~1.2	0.8~1.0	concave	palisade	20~25	exotestal
T. europaeus	1.8~2.0	1.2~1.4	1.0~1.2	convex	palisade	20~25	exotestal
T. farreri	1.6~1.7	1.0~1.1	0.8~0.9	concave	palisade	18~23	exotestal
T. hondoensis (KWNU)	1.8~2.0	1.0~1.2	1.0~1.2	convex	palisade	23~28	exotestal
T. hondoensis (KYO)	1.7~2.0	1.0~1.4	1.0~1.3	convex	palisade	25~30	exotestal
T. japonicus (TI)	1.8~2.2	1.0~1.1	0.9~1.1	concave	palisade	25~30	exotestal
T. japonicus (KWNU)	1.8~2.0	1.1~1.4	1.0~1.2	concave	palisade	25~30	exotestal
T. laxus	1.8~2.0	1.2~1.3	0.9~1.1	concave	palisade	25~30	exotestal
T. ledebourii	1.4~1.5	1.1~1.2	0.8~0.9	convex	palisade	25~30	exotestal
T. ledebourii var. *polysepalus*	1.7~1.8	1.2~1.4	1.0~1.1	convex	palisade	23~28	exotestal
T. macropetalus	1.9~2.1	1.1~1.2	0.8~0.9	convex	palisade	25~30	exotestal
T. patulus	1.7~2.0	1.2~1.4	1.1~1.2	convex	palisade	35~40	exotestal
T. pumilus	1.4~1.6	1.0~1.1	0.8~1.0	convex	palisade	23~28	exotestal
T. ranunculinus	2.1~2.3	1.4~1.5	1.2~1.3	concave	palisade	35~40	exotestal
T. ranunculoides	1.3~1.5	0.6~0.8	0.5~0.6	concave	palisade	23~28	exotestal
T. riederianus (TI)	1.8~2.0	1.2~1.4	1.0~1.2	concave	palisade	25~30	exotestal
T. riederianus (KYO)	1.6~1.8	1.0~1.2	0.9~1.0	convex	palisade	25~30	exotestal
T. riederianus var. *japonicus*	1.7~1.9	1.2~1.3	1.0~1.1	convex	palisade	23~28	exotestal
T. sp.	2.0~2.2	1.3~1.4	1.0~1.2	concave	palisade	20~25	exotestal
T. taihasenzanensis	1.7~1.9	1.1~1.2	0.9~1.0	smooth	palisade	40~45	exotestal

* Seed sizes were made by measurement five seeds at least. R and A means the width between raphe and antiraphe. L and L means that between lateral and lateral.

ovule, the outer epidermis is developed by more or less palisade-like radially elongated cells, and the middle layers are multiplicative. In result, the outer integument becomes eight to nine cell layers thick in a mature embryo sac. At maturity, the exotesta is well-developed as a palisade cell in seeds. The mesotesta and endotesta become crushed in mature seeds (Figs. 1p, s). Cells of tegmen become also crushed and more or less flattened (Figs. 1p, s), which is considered as the exotestal seed coat type.

Discussion

Anatropous and bitegmic ovules and exotestal seed coats in *Caltha*, *Calathodes*, and *Trollius* were confirmed in this study (Kapil, 1962; Kapil and Jalan, 1962; Tamura, 1993, 1995). Ovules are anatropous and bitegmic and seed coats are exotestal also in the genus *Megaleranthis*. Even though the exotestal seed coat is exhibited for all taxa of the subtribe Calthinae examined in this study, there is a clear variation in the sculpture of seed surface, the structure of seed coat and the thickness of exotesta, which provides an important taxonomic implication for *Megaleranthis* in the subtribe (Table 2).

Although the seed coat of *Caltha palustris* is exotestal, it differs from exotesta structure of other genera examined in the subtribe (Kapil and Jalan, 1962). *Caltha* is different from *Megaleranthis* by cuboidal structure of exotesta and smooth seed surface sculpture. Even though *Calathodes* shows a very similar structure of seed coat to *Megaleranthis*, they show some differences in the sculpture of seed surface. *Megaleranthis* has concave surface sculpturing while *Calathodes* has smooth surface sculpturing. When compared to *Trollius*, *Megaleranthis* is very similar to *Trollius* in the morphology of exotestal seed coat, which exhibits virtually no differences within the genus. Since *Trollius* contains both concave and convex types in seed surface feature, *Megaleranthis* showing the concave shape could be included in *Trollius* category.

In previous cytological studies (Lee and Yeau, 1985; Tamura, 1995), *Megaleranthis* has the chromosome number 2n = 16 (X = 8) and R-type, which is considered to be primitive in the family. *Trollius* has also the same basic chromosome number (X = 8) consistently within the genus (Tamura, 1995). In addition, palynology presented that *Megaleranthis* has a striate type in pollen surface architecture as of *Trollius*, which also supports that *Megaleranthis* is closely related with *Trollius* (Kim and Lee, 1987). Accordingly, Lee (1990) has strongly claimed that *Megaleranthis* should be renamed as *Trollius chosenensis* as a legitimate name.

In the external morphology, its sepal color is white as shown in *T. afghnicus*, *T. albiflorus*, and sometimes in *T. laxus* (Tamura, 1995; Kadota, 1996). Both *Megaleranthis* and *Trollius* have petals, but *Caltha* and *Calathodes* are apetalous in the subtribe Calthinae (Tamura, 1995). Especially, a distinct feature of *Megaleranthis* is the presence of a single cauline leaf, which is sessile and located close at the flower (Tamura, 1995). However, Yoo *et al.* (1999) recognized a branched cauline leaf in some populations of *Megaleranthis*, which is also observed in *Calathodes*, *Caltha*, and *Trollius*. Despres *et al.* (2003) published that *Adonis* is a sister group to *Trollius* on the basis of AFLP data. However, they had not included *Megaleranthis* in experiments. Ro *et al.* (1997) suggested that *Trollius* is very close to *Adonis* in their 26S rDNA data without *Megaleranthis*. Nevertheless, they differ from fruit type. *Trollius* has follicle whereas *Adonis* has achene type. After this, Ro *et al.* (1999) suggested that *Megaleranthis* has to be integrated in *Trollius* based on 26S rDNA sequence data, although they included only one species of *Trollius*, *Megaleranthis* and *Caltha* excluding *Calathodes*. Recently, Jang and Heo (2005) proposed that *Megaleranthis* should be included in *Trollius* on the basis of reproductive morphology, although they could not include embryological materials of *Calathodes* and *Caltha*.

Anatomical features of seed coat support that *Megaleranthis* is much more closely related to *Trollius* than to *Calathodes* and *Caltha*. The structure of seed coat and the sculpture of seed surface are well congruent with the previous claims on the taxonomic inclusion of *Megaleranthis* into *Trollius* by reproductive morphology (Jang and Heo, 2005), palynology (Kim and Lee, 1987), cytology (Lee and Yeau, 1985; Tamura, 1995), and DNA sequences data (Ro *et al.*, 1997, 1999).

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미나리아재비과 동의나물아족의 종피형태와 분류학적 검토

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한국 고유종인 모데미풀의 분류학적 검토를 위하여 모데미풀과 근연분류군의 종피 형태를 관찰하였다. 모데미풀의 종피 형태는 외종피 세포가 책상조직모양의 후벽세포로 발달하는 외종피외층형으로 나타났고, 종피의 표면은 오목형 구조를 보였다. 근연분류군인 동의나물의 외종피 외층은 입방형(cuboid)이며, 표면구조는 매끄러워서 모데미풀속과는 쉽게 구별되었다. 그러나 *Calathodes*속이나 금매화속은 외종피 외층이 모데미풀과 같은 책상조직 형태의 후벽세포로 잘 발달하였으며, 종피 표면 구조는 오목형과 볼록형이 연속적으로 나타났다. 이것은 모데미풀속의 종피구조가 금매화속의 종피구조 범위내에 포함됨을 암시하고 있다. 따라서 동의나물 아족에서는 종피의 해부형태와 표면구조가 아족내에서 분류학적 평가에 유용하게 사용될 수 있었다. 결론적으로, 종피의 표면구조와 해부형태 특징은 고유종인 모데미풀이 동의나물속이나 *Calathodes*속보다는 금매화속에 보다 가깝다는 것을 나타내었다. 종피의 오목형 표면구조와 잘 발달된 외종피 외층형 종피유형은 모데미풀과 금매화속이 함께 공유하는 형질이었다.

주요어: 동의나물아족, 고유종, 모데미풀, 미나리아재비과, 종피

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