

Packera insulae-regalis (Asteraceae, Senecioneae), a new species endemic to Isle Royale, Michigan, U.S.A.

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Abstract. *Packera insulae-regalis* (Asteraceae, Senecioneae) is a new species that is only known from one population occurring near the summit of Mount Franklin on Isle Royale, Michigan, U.S.A. It resembles both *P. paupercula* and *P. indecora* but is hexaploid, whereas the former has diploid and tetraploid populations and the latter is octoploid around the western Great Lakes. Whereas most species of *Packera* are self-incompatible (as is *P. paupercula*) and a few are self-compatible (as is *P. indecora*), *P. insulae-regalis* is unique in the genus in being partially self-compatible, as far as is known. Its origin post-glacially by hybridization between these two species is hypothesized.

Key Words: Asteraceae, endemic, hexaploid, Isle Royale, *Packera*, Senecioneae.

The genus *Packera* Á. Löve & D. Löve (Asteraceae, Senecioneae) contains at least 64 species, occurring largely in North America (Trock, 2006), from Oaxaca, Mexico (Freeman & Barkley, 1995) to Banks Island in the Northwest Territories, Canada (Porsild & Cody, 1980), with two Arctic-alpine species also extending into Siberia, one of which reaches the Ural Mountains and, disjunctly, alpine central Asia (Sokolovskaja & Strelkova, 1938; Korobkov & Jurtzev, 1987). Many populations of *Packera* do not quite fit within the morphological and ecological circumscriptions of the traditionally recognized species (Barkley, 1978, 1988; Trock, 2006). Racial variation adapting a widespread species to different climates and habitats is common, and the more well-marked races are formally recognized as varieties (Barkley, 1962; Trock, 2006; Mahoney & Kowal, 2008). A number of diploid species contain tetraploid races, one species contains a hexaploid race (Kowal, 1975; Morton, 1981; Bain, 1985; Freeman, 1985; Kowal, unpubl. data), and an octoploid species contains hexaploid populations (Morton, 1981). Apparent F₁ individuals are common where disturbance

brings two species together, and hybrid swarms sometimes occur (Barkley, 1962; Kowal, 1975; Uttal, 1982; Trock, 2006). In two cases a polyploid clone (one a tetraploid, the other an approximate pentaploid) has apparently resulted from the crossing of two diploid species (Kowal, unpubl. data). Thus, *Packera* is cytologically complex. It contains numerous polyploid races, some of which merit recognition as new species. One such is described here.

On Isle Royale, Mount Franklin is the northeasternmost summit on the Greenstone Ridge, which forms the spine of the island. About 25 m southwest of the summit, along the Greenstone Ridge Trail, is an isolated population of *Packera*. Although initially identified as *P. indecora* (Greene) Á. Löve & D. Löve and somewhat resembling *P. paupercula* (Michaux) Á. Löve & D. Löve, its morphology, modes of sexual and asexual reproduction, and chromosome number require treating it as a new species.

Materials and methods

Only two previous collections are known to the authors, the first collected in 1868 from

“Isle Royale” (*University Party s. n.*, MICH) and the second collected in 1930 from a “rock opening, top of Mt. Franklin” on Isle Royale (*McFarlin 2181*, MICH); both were filed under *Packera paupercula*. None other were found by the senior author at the University of Michigan (MICH), the Claude Garton Herbarium of Lakehead University (LKHD), Herbarium of the Natural Heritage Information Centre, Ontario Ministry of Natural Resources (NHIC, mjo), and the W. P. Fraser Herbarium, University of Saskatchewan (SASK) or by Judziewicz at the herbaria of Isle Royale National Park (IRP) and of Michigan Technological University (MCT, now at MSC).

On July 16, 1972, Michael Nee noticed this unusual population of *Packera* and collected a living plant for the senior author. Two replicates of this individual (Individual 1A [1972]) were grown in each of two standard-environment transplant gardens of *Packera* species at the University of Wisconsin-Arboretum from 1974 through 1982 (Test Garden 2) and from 1978 through 1983 (Test Garden 3).

Judziewicz visited the population on August 7, 1993, July 26, 1994, June 5, 1997, August 25, 1998, and June 20 & 27 & July 6, 2003, (with Fern Daniels) and made observations of its extent, size, and associated species (Judziewicz, 2004; Table 1). Eight achenes collected in 1993 produced three seedlings, but all died within two years.

On June 24–26, 1998, the senior author visited Isle Royale. The only new population of *Packera* seen was one of *P. indecora* along the lake-side trail east of Starvation Point. A search of the Greenstone Ridge trail and northwards in open woodland and on rock ledges on Mt. Franklin and Mt. Ojibway (the next summit to the southwest) uncovered no new populations. Observations were made on the original population, and three living individuals (Individuals 1, 2 & 3 [1998]) were collected from the two ends and the middle of the segment of trail that *P. insular-regalis* occupies, replicates of which were grown both in the greenhouse (Birge Hall, University of Wisconsin-Madison) and in a standard-environment transplant garden behind the senior author’s house in Madison (Test Garden 5) from 1999 through 2001, when the last replicate died.

The design of the standard-environment transplant gardens and protocol for collecting data were comparable to those described in Kowal (1975), as was the procedure for making artificial crosses. Each field-collected individual was represented by two replicates, insofar as possible, and replicates were randomly positioned within each garden. Inflorescences of test garden replicates in 1999 were covered with cheese-cloth to exclude contaminant pollen. “Crossed” heads were brushed with pollen from a head taken from another individual and then bagged in lens-paper until mature. “Selfed” heads were simply bagged. An attempt in 2001 to test whether brushing with pollen from the same plant might itself increase achene set failed, but the plant provided heads that developed past anthesis under cheese-cloth and that were bagged subsequently. These are equivalent to “selfed” heads.

A new character, not measured in Kowal (1975), provides an index of the relative showiness of an inflorescence, an attribute that is of greater concern to self-incompatible species, which must attract pollinators, than to self-compatible species, which need not be visited to form fruit. One way of increasing the showiness of an inflorescence is to have the heads mature at more nearly the same time, so that their rays cumulatively present a larger pollinator target than any one head individually. Having more of the lateral heads starting anthesis when the terminal one is in full anthesis contributes to this objective. During the flowering season, each test garden was scanned every day, and the day on which the terminal head of the tallest flowering stalk of a replicate had its last (center-most) floret come into anthesis (defined as pushing its pollen out of its anther-tube) was used as “the flowering date” for that replicate. At this time, the number of lateral heads that had at least one disk floret in anthesis was counted. This number serves as an index of the degree of synchronization: LHA-N = “Lateral Head Anthesis-Number”. The higher this number, the more showy the inflorescence becomes and, presumably, the more attractive it is to pollinators, with LHA-N = 0 corresponding to the least showy inflorescence (Fig. 1D, F).

Most of the descriptive data are from cultivated plants, which grow much more

TABLE I
 SIZE OF THE MT. FRANKLIN POPULATION OF PACKERA *INSULAE-REGALIS* FROM 1993 TO 2010.

Year	Number of flowering stalks	Total number of heads	Number of vegetative rosettes	Observer
1993	±24	—	—	E. J. Judziewicz
1994	3	—	±200	E. J. Judziewicz
1997	—	—	440	E. J. Judziewicz
1998	6	—	—	R. R. Kowal
1999	6	—	—	J. Edwards
2000	17	78	—	J. Edwards
2001	24	—	—	J. Edwards
2003	2	7	777	E. J. Judziewicz & S. Daniels
2004	8	29	—	J. Edwards
2005	31	126	—	J. Edwards
2006	16	43	—	V. Hofman & J. Edwards
2007	5	17	—	J. Edwards
2008	—	—	±500	V. Hofman
2009	13	55	—	J. Edwards
2010	4	14	—	J. Edwards

luxuriantly than the same individuals in the thrifty and competitive wild; for example, plants are taller, cauline leaves are better developed, and number of heads per inflorescence is greater. The advantage of seeing an individual under cultivation is that, in general, the potential of its genotype expresses itself in more detail in the phenotype: traits not expressed in a runt become evident. However, for the diagnosis of the species, field-collected specimens and plants grown in pots in the greenhouse, which approximate plants found in the field, were used.

Results and discussion

Packera insulae-regalis R. R. Kowal, **sp. nov.**

Type: United States. Michigan: Keweenaw Co., Isle Royale National Park, Mount Franklin, 22–28 m by trail SW of Mt. Franklin overlook, just beyond first grove of spruce and fir, along ca. 6 m of Greenstone Ridge Trail, 48°07'35"N, 88°34'01"W (T66N, R34W, Sec. 12, NW ¼ of SW ¼), 1080 ft (329 m), 24 Jun 1998, R. R. Kowal 3127 (holotype: WIS). (Figs. 1, 2, 3)

Species nova foliis imis et caulinis *Packerae indecorae* similis, sed juventute pubescentia arachnoidea exili differt, autem capitulis radiatis similibus *Packerae pauperulae*; reproductio vegetativa in radicibus per rosulas adventitias minutas. Chromosomatum numerus $2n = ca. 66 + 66 = ca. 6x$.

Herbaceous perennials (hemicryptophytes), reproducing abundantly by adventitious shoots on roots, producing at most very short ascending rhizomes. *Stems* 16.5–31.2 cm long. *Rosette leaves* medium to dark green, sometimes splotchily purple-tinged abaxially, sparsely pubescent on both surfaces, often becoming glabrate; petioles 0.5–5(–8) cm long; blades broadly elliptic to ovate or nearly orbicular, bases truncate to obtuse, apices rounded, margins with (3–)6–14(–24) crenate-serrate teeth per side (doubly crenate-serrate on larger blades), 1.4–4.4(–5) × 0.8–2.8 cm. *Cauline* leaves progressively reduced up the stem; proximal leaves similar to rosette leaves; middle leaves sessile, narrowly oblong, lobed proximally, 1.4–3.4 × 0.45–1.1 cm (narrowly ovate and deeply pinnatifid, to 10 × 5.1 cm in garden); distal leaves reduced to bracts in the inflorescence. *Inflorescence* a subumbellate cyme with 1–7 heads (more highly branched and up to 88 heads in garden). *Involucre*s 7–8.6(–10.1) mm long, with mostly 21 phyllaries, 5.5–7.3(–8.2) × 0.6–1 mm. *Florets* (*ray and disk*) 66–101, ray florets mostly (10–)13(–14), rays medium yellow, 5.1–8.9 × 1.3–2.8 mm. *Achenes* (2 observed) glabrous, 2.3–2.9 mm long. $2n = ca. 132 = ca. 6x$.

Distribution and ecology.—Known only from the type locality, just southwest of the summit of Mount Franklin on Isle Royale. *Packera insulae-regalis* is restricted to the

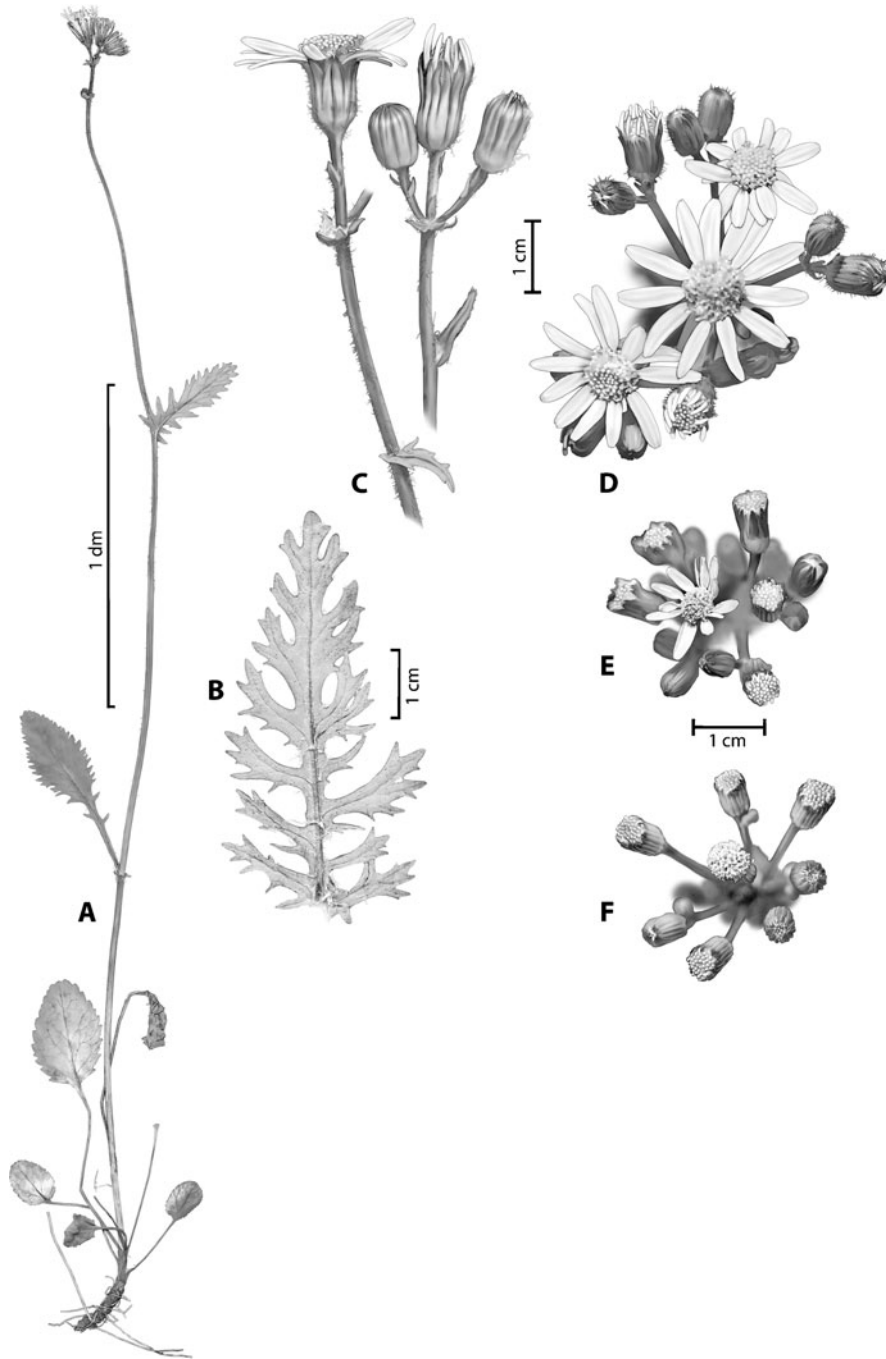


FIG. 1. *Packera insulae-regalis* (A–D) and *P. indecora* (E–F). **A.** Habit. **B.** Mid-cauline leaf of garden-grown plant. **C.** Capitulescences with heads in lateral view. **D.** Capitulescence of garden-grown plant seen from above on day terminal head reaches full anthesis. **E.** Capitulescence of garden-grown plant of radiate *P. indecora* seen from above on day terminal head reaches full anthesis. **F.** Capitulescence of garden-grown plant of discoid *P. indecora* seen from above on day terminal head reaches full anthesis. (A drawn from holotype; B from *Kowal 3290*, WIS; C from photograph, type locality, 26 Jun 1998; D from photograph, type locality, Individual 2A [1998] grown in Test Garden 5, position D20, 2 Jun 1999; E from photograph, U. S.A., Wisconsin, Ashland Co., North Twin Island, Individual 2, grown in Test Garden 3, position M35, 21 Jun 1978; F from photograph, Canada, Quebec, Val-Jalbert, Individual 3, grown in Test Garden 2, position C24, 19 Jun 1974.).

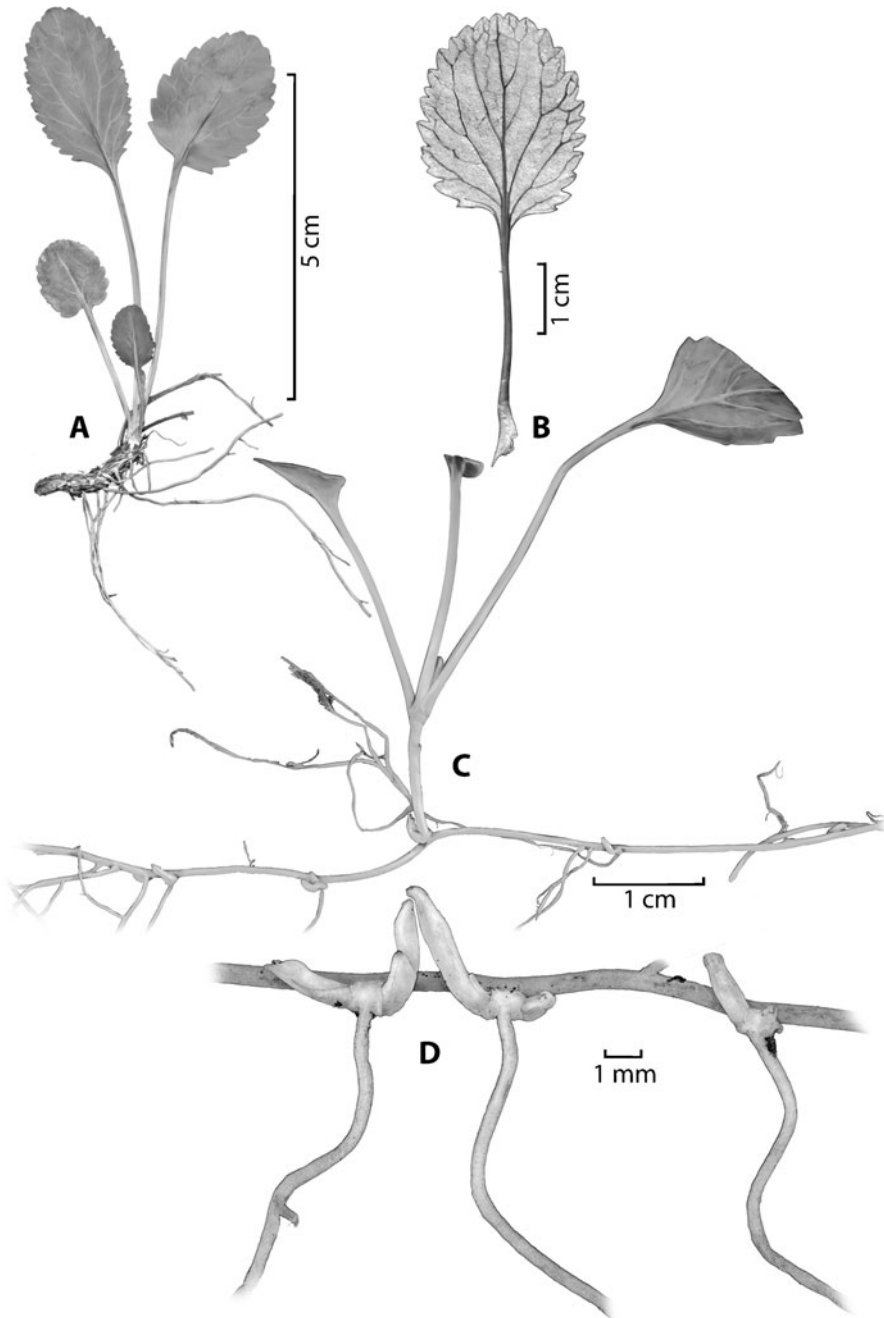


FIG. 2. *Packera insulae-regalis*. **A.** Vegetative rosette. **B.** Leaf of vegetative rosette, abaxial view. **C.** Young vegetative rosette arising adventitiously from a root and very young shoots differentiating from callus tissue along the root. **D.** Close-up of three very young shoots differentiating from callus tissue along a root. (A drawn from holotype; B from photograph, type locality, Individual 2BC [1998], grown in greenhouse, 28 Feb 2001; C, D from fresh material of selfed seedling of Individual 2BC [1998], grown in greenhouse.).

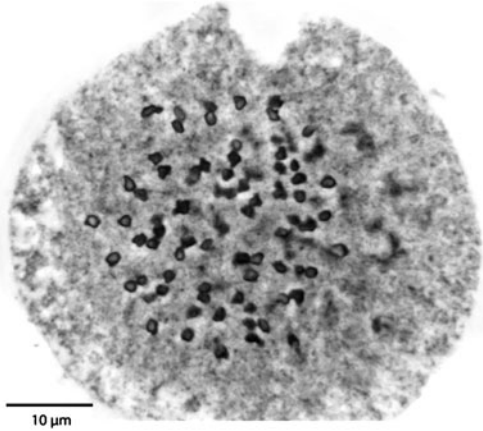


FIG. 3. Cell of *Packera insulae-regalis* in anaphase I of meiosis, giving $2n = \text{ca. } 66 + 66 = \text{ca. } 6x$ with through-focusing.

border of the trail in a level, lightly shaded opening in the forest of *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., and *Populus tremuloides* Michx., where it gets about a half day of full sun. It grows with *Pteridium aquilinum* (L.) Kuhn, *Aralia nudicaulis* L., *Diervilla lonicera* Mill., *Amelanchier* Medik. sp., *Anemone americana* (DC.) H. Hara, *Apocynum androsaemifolium* L., *Campylopus rotundifolius* L., *Castilleja septentrionalis* Lindl., *Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult., *Cypripedium arietinum* R. Br., *Eurybia macrophylla* (L.) Cass., *Fragaria virginiana* Duchesne, *Halenia deflexa* (Sm.) Griseb., *Hepatica americana* (DC.) Ker Gawl., *Hieracium kalmii* L., *H. piloselloides* Vill., *Lonicera dioica* L., *Maianthemum canadense* Desf., *Melampyrum lineare* Desr., *Orthilia secunda* (L.) House, *Oryzopsis asperifolia* Michx., *Poa compressa* L., *Rubus parviflorus* Nutt., and *Symphytotrichum ciliolatum* (Lindl.) Á. Löve & D. Löve. The population occurs along ca. 6 m of the trail, largely on its southeast edge, mostly within 0.5 m of the trail (extending at most 1 m into the forest). The hundreds of vegetative rosettes (Table I), rooted in brown humus, are largely produced asexually by the formation of shoots adventitiously on roots (Fig. 2C, D); rhizomes are absent. The thin soil is underlain by greenstone, a metamorphosed basalt (Huber, 1975) rich in calcium that tends to make the overlying soils basic (Birkeland, 1999).

The size of the population is summarized in Table I. After Judziewicz cleared competing herbaceous vegetation from part of the site in 2003, the number of flowering stalks increased from two during that year to 31 in 2005 and then decreased during succeeding years. Thus periodic removal of competing herbaceous vegetation, perhaps every second or third year, would probably benefit the species' long-term survival.

Phenology.—Flowering in late June and early July in the field. In three test gardens in Madison, Wisconsin, *Packera insulae-regalis* flowers with the late-flowering taxa like *P. anonyma* (Wood) W. A. Weber & Á. Löve, *P. paupercula* var. *paupercula* (both diploid and tetraploid populations), and *P. indecora*, typically during the first half of June. This is in contrast to such earlier flowering taxa as *P. aurea* (L.) Á. Löve & D. Löve, *P. obovata* (Muehl. ex Willd.) W. A. Weber & Á. Löve, *P. paupercula* var. *pseudotomentosa* (Mack. & Bush) R. R. Kowal & var. *savannarum* R. R. Kowal, *P. plattensis* W. A. Weber & Á. Löve, and *P. pseudoaurea* (Rydb.) W. A. Weber & Á. Löve var. *flavula* (Greene) W. A. Weber & Á. Löve & var. *semicordata* (Mack. & Bush) T. M. Barkley & D. K. Trock, which typically flower during May.

Etymology.—The specific epithet of *Packera insulae-regalis*, “the *Packera* of Isle Royale,” refers to the island to which it is endemic.

Cytology.—The species is hexaploid with $2n = \text{ca. } 66 + 66$ (based on one meiotic cell in anaphase I; voucher: Kowal 3287 (WIS); Fig. 3).

Conservation status.—*Packera insulae-regalis* is assessed as Critically Endangered because its EOO (extent of occupancy) is, as far as is known, less than 100 km², and it is only known to occur at a single location; thus, criterion CR B1a of the IUCN (2001) applies.

Additional specimens examined. UNITED STATES.

Michigan: Keweenaw Co., Isle Royale, 1868, *University Party s. n.* (MICH); Isle Royale, top of Mt. Franklin, rock opening, 1930 Jul 15, *McFarlin 2181* (MICH); Isle Royale National Park, Mount Franklin, along both sides of Greenstone Ridge Trail, ca. 30 m SW of flat, naked summit, just beyond first grove of spruce and fir, T66N, R34W, Sec. 12, NW¼ of SW¼, 1080 ft. (329 m), Individual 1A [1972] (originally collected by Michael Nee, 1972 Jul 16), grown in Test Garden 2, position A18

(TG2-A18), 1975 Jun 10, *Kowal 3286* (MO); ib., TG2-J34, 1975 Jun 11, *Kowal 3287* (WIS); ib., TG2-J34, 1977 May 24, *Kowal 3288* (WIS); ib., TG2-A18, 1977 May 26, *Kowal 3289* (US); ib., TG3-B9, 1979 Jun 11, *Kowal 3290* (WIS); ib., Individual 3A [1998], one of three originally collected by R. R. Kowal, 1998 Jun 24, TG5-F21, 2000 Jun 9, *Kowal 3164* (WIS); 1999 cross 12 (Individual 2 [1998] × Individual 3 [1998]), seedling 3. Cult. l.c., 2002 Jun 5, *Kowal 3198* (NY); ib., Individual 1 [1998]. Grown in greenhouse, Birge Hall, Dept. of Botany, Univ. of Wisconsin-Madison, 2002 Jul 2, *Kowal 3213* (WIS); 1999 cross 28 (Individual 3 [1998] selfed), seedling 1. Cult. l.c., 2002 Jul 2, *Kowal 3210* (MICH); 1999 cross 12 (Individual 2 [1998] × Individual 3 [1998]), seedling 2. Cult. l.c., 2002 Jul 2, *Kowal 3211* (F); 1999 cross 13 (Individual 2 [1998] selfed), seedling 2. Cult. l.c., 2002 Jul 2, *Kowal 3212* (CAN); 1999 cross 9 (Individual 2 [1998] selfed), seedling 1. Cult. l.c., 2002 Jul 11, *Kowal 3214* (GH); Isle Royale National Park, trailside glade in boreal forest, 22–28 meters SW of Mt. Franklin on trail to Mt. Ojibway, 6 Jul 2003, *Judziewicz 15045* (UWSP).

The senior author initially identified Individual 1A [1972] as a radiate form of *Packera indecora*, because it is virtually identical vegetatively to that octoploid species. Its leaves are very lightly arachnoid pubescent rather than glabrous, but this is an extremely slight and unremarkable difference. However, its reproduction, both asexual and sexual, separates it decisively from *P. indecora*. Asexually, adventitious shoots on roots are the main mode of reproduction in the field (Fig. 2C, D); these are absent in the field in *P. indecora* (although they can occur very rarely under cultivation; Kowal, 1975). Sexually, it has the morphology of a self-incompatible species, with an attractive inflorescence bearing heads that have normal-sized, showy rays (Kowal, 1975; Fig. 1D vs. 1E, F). The two self-compatible species of *Packera*, *P. pauciflora* and *P. indecora*, typically lack rays (Fig. 1F), although the latter frequently is radiate, but with rays shorter (commonly 6 mm or less long) than those of the other *Packera* species (Fig. 1E). Also, as in the self-incompatible species, heads within an inflorescence of *Packera insulae-regalis* tend to come into anthesis in quick succession so that the rays of a number of heads together create a prominent attractive display. One evidence of this greater synchronization in the maturation of heads within an inflorescence is that the number of lateral heads beginning anthesis on the day that the terminal head reaches full anthesis (LHA-N)

is greater than that in the self-compatible *P. indecora*, whose heads produce abundant fruit even when not out-crossed (Kowal, 1975, unpubl. data). In the latter species, typically no lateral head is in anthesis when the terminal one reaches full anthesis (Fig. 1E, F), i.e., LHA-N is usually 0. In contrast, the self-incompatible species typically have 1 or more lateral heads in anthesis at this stage. Replicates of the tetraploid populations of *P. paupercula*, which are morphologically similar to the new species, have a median LHA-N around 4, and so do replicates of *P. insulae-regalis* (Fig. 4).

Crosses confirm that *Packera insulae-regalis* is, indeed, at least largely self-incompatible. The median percentage achene sets of crossed and selfed heads from 1999 are 16.1 and 3.4%, respectively, a difference that only approaches statistical significance in a Wilcoxon Rank Sum Test (Wilcoxon & Wilcox, 1964), but adding the selfed heads from 2001, which have a median percentage achene set of 2.6%, to the test gives a highly significant result (Table II). That the selfed heads still produce a fair number of achenes, with a mean and median percentage of 5.6 and 3.0%, respectively (Table II), is unique in *Packera*, as far as is known. Selfed heads in four self incompatible diploid species had, on average, only 0.0, 0.2, 0.4 and 2% achene set, compared to 75 and 90% in the two octoploid, self-compatible species (Kowal, 1975), and unpublished crosses made from 1971 through 2003 confirm this relatively clear-cut distinction. In 1976 fruiting data were systematically collected from Test Garden 2, and both replicates of Individual 1A [1972] produced frequent achenes.

Because of the prodigious asexual reproduction of *P. insulae-regalis* and the sward of rosettes formed in the field, the idea that the population consists of only a single clone must be considered. The crossing data indicate that this is not so. Although the one cross between Individuals 1 [1998] and 2 [1998] gave an achene set of only 2.9% and so could be equivalent to “selfing”, the five crosses of Individual 3 [1998] with the other two individuals had a mean achene set of 19.4% (7.6–33.7%), indicating that at least this individual is genetically different from the other two (Table II).

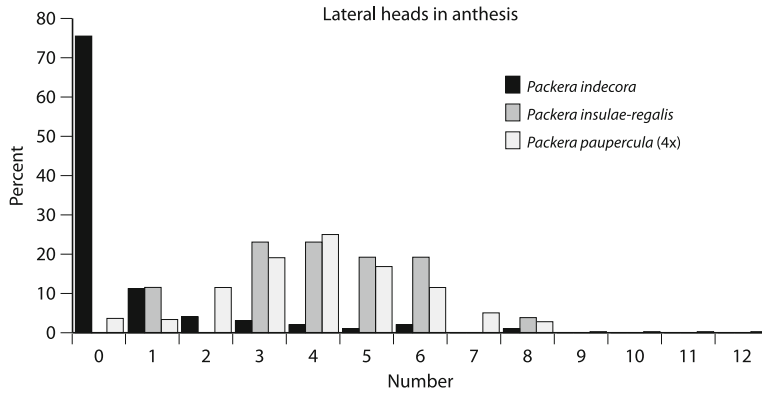


FIG. 4. Percentages of the number of lateral heads beginning anthesis when the terminal head is in full anthesis in an inflorescence for *Packera indecora*, *P. insulae-regalis*, and tetraploid populations of *P. paupercula*, based on 98, 26, and 356 replicates, respectively, cultivated in Test Gardens 2 and 3 from 1974 to 1983.

Cytologically *Packera insulae-regalis* is unusual within *Packera* in being hexaploid: $2n = ca. 66+66$ (based on one meiotic cell in anaphase I; Fig. 3). Most species in the genus are diploid with $2n = 23 II$ or $22 II$, although tetraploids are common (Kowal, 1975; Morton, 1981; Kowal, unpubl. data). A hexaploid taxon related to *P. aurea* occurs on the Gaspé Peninsula (Kowal, 1975). Typically *P. indecora* is octoploid with $2n = 88 II$ or roughly that, certainly so around Lake Superior (l.c.). Hexaploid populations do exist: $2n = ca. 130$ in the Yukon (published as “*S. pauciflorus* Pursh”) and $2n = ca. 126$ in Alberta (Morton, 1981). However, the two respective vouchers are discoid, morphologically typical *P. indecora* (Kowal, pers. obs.), so the Mt. Franklin taxon is clearly not that species. Significantly, *P. indecora*, itself, does occur on Isle Royale (Slavick & Janke, 1993), but in a very different habitat: at lake level, often among mossy rocks along the shore,

within reach of storm waves (Judziewicz & Kowal, per. obs.).

Packera insulae-regalis bears some resemblance to the *P. paupercula* complex, in particular the tetraploid populations with $2n = 44 II$ that occur in the region of the western Great Lakes (Kowal, 1975; Morton, 1981; Kowal, unpubl. data). They both have relatively large heads and share the typical inflorescence morphology of the self-incompatible species: large, showy rays and heads that are synchronized in their anthesis (Fig. 1C, D). However, *P. insulae-regalis* differs in small but clear-cut ways. The blades of its rosette leaves are relatively broader and more abrupt at the base (ovate-elliptic to elliptic and truncate to obtuse rather than narrowly elliptic to oblanceolate and cuneate to tapering; Fig. 2A, B). In well-developed, garden-grown plants, its pinnatifid cauline leaves, which are much larger and relatively wider than in the field, have lobes that commonly have one or two teeth running

TABLE II

SELF- AND CROSSPOLLINATIONS WITHIN *PACKERA INSULAE-REGALIS*: ACHENE SET PER HEAD AND WILCOXON'S TWO SAMPLE TESTS.

Treatment	Number of heads	Mean floret number	Mean achene number	Percent achene set:		
				Mean	Median	Range
Selfed (1999)	7	86.1	5.9	6.9	3.4	0.0–28.6
Selfed (2001)	13	84.2	4.2	4.9	2.6	0.0–11.1
Selfed (1999 & 2001)	20	84.9	4.8	5.6	3.0	0.0–28.6
Crossed (1999)	6	85.8	15.3	16.6	16.1	2.9–33.7

Selfed (1999) vs. selfed (2001): $P (T=72) \gg 0.10$

Selfed (1999) vs. crossed (1999): $P (T=29) < 0.10$

Selfed (1999 & 2001) vs. crossed (1999): $P (T=39) < 0.01^{**}$

down the proximal side and even onto the winged midrib (Fig. 1B), a condition characteristic of well-developed *P. indecora* but occurring only rarely in tetraploid *P. paupercula*. Both tetraploid *P. paupercula* and *P. insulae-regalis* reproduce asexually by adventitious shoots on roots. However, whereas the tetraploids, like many *Packera* species, produce rhizomes or branched rootstocks, the new species does not (although a rosette that produces a flowering stalk usually survives into the following year by producing rosettes at its base); it relies solely on adventitious shoot production like *P. pseudaurea* var. *semicordata* and *P. paupercula* var. *savannarum* (Mahoney & Kowal, 2008; Kowal, pers. obs.). Finally, the two differ decisively cytologically and are sexually isolated thereby.

Thus, considering the data on morphology, habitat, chromosome number, and modes of asexual and sexual reproduction together, the population near the top of Mt. Franklin on Isle Royale differs in one way or another from all recognized species of *Packera* and, in particular, from the two that are morphologically and ecologically most similar to it, *P. indecora* and *P. paupercula*. It is a new species under any version of the Biological Species Concept, e.g., the Ecogenetic Species Concept of Levin (2000), and, as such, it is scientifically important that it be recognized. In addition, because an unnamed species goes unnoticed and unprotected and because this species is known from a single small population along the edge of a trail that is being overgrown, naming it is critical to its preservation.

The origin of *Packera insulae-regalis* is probably relatively recent. Isle Royale was beneath ice through the Marquette Phase of the Wisconsin Glaciation and only emerged about 11,200 calendar years ago (Hough, 1963; Teller, 2001; Lee Clayton, pers. com.; Dyke, 2004; Timothy G. Fisher, pers. com.). A further ca. 45-meter rapid lake-level fall 9300 years ago exposed more of the island for colonization (Yu et al., 2010). One possible scenario is that it formed locally as the island was colonized, through hybridization between octaploid *P. indecora* and a member of the northern tetraploid complex of *P. paupercula*. The simple crossing of the latter ($n=44$; self-incompatible) with *P. indecora* ($n=88$; self-compatible) would give a

hexaploid, in one step. Its genomic constitution would then be $P_1P_2I_1I_2I_3I_4$, where “P” and “I” each correspond to a set of 22 chromosomes of *P. paupercula* and *P. indecora*, respectively, with the tetraploid and the octaploid having two and four such sets, respectively, in their gametophytic (haploid) genomes. If the P_1 / P_2 genomes were reasonably homologous and the $I_1 / I_2 / I_3 / I_4$ genomes were reasonably homologous as well, the F_1 might well be slightly self-compatible with morphological characters of both parents but resembling *P. indecora* more, due to its contributing four of the six genomes. Both *P. paupercula* and *P. indecora* occur on Isle Royale (Slavick & Janke, 1993), and, although the *P. paupercula* populations look to be diploid, the tetraploid race is frequent around the northern Great Lakes, and ecologically there is no reason for its not occurring there in times past.

Recreating such a hybrid and showing that the species had the chloroplast haplotype of the female parent would provide evidence for this hypothesis, although the latter line of evidence is complicated by many *Packera* species having diverse and shared chloroplast haplotypes (Bain & Jansen, 1995; Bain & Golden, 2000). Artificial crosses relevant to this hypothesis do not support the hypothesis: tetraploid *P. paupercula* \times *P. indecora* (1978 crosses 102 & 103) and the reciprocal cross using only the pistillate ray florets of *P. indecora* (1978 cross 106) produced no fruit, although poor technique could well be the cause. Although crosses of *P. insulae-regalis* with tetraploid *P. paupercula* as the male parent produced fruit sets no greater than those consistent with that expected due to the partial self-compatibility of the former species (1999 crosses 17, 29 & 35, with 0–3.6% fruit set), the reciprocal crosses were quite fertile (1975 cross 60 and 1999 cross 18, with ca. 62% and 7.5% fruit set, respectively), as was a cross of *P. insulae-regalis* with *P. indecora* as the male parent (1975 cross 71, with 43.5% fruit set). Although time constraints did not permit attempts to germinate the resultant achenes, the results at least indicate that *P. insulae-regalis* is related to the two putative parents.

Packera insulae-regalis is the only known endemic vascular plant species on Isle Royale (Slavick & Janke, 1993). Its occurrence here

can be viewed as part of a pattern of such polyploids of putative hybrid origin and with restricted distributions produced in the wake of the last glaciation. Another Great Lakes endemic is *Solidago houghtonii* Torr. & A. Gray of the northern shores of Lakes Michigan and Huron; a hexaploid, like *Packera insulae-regalis*, it is thought to have arisen postglacially by hybridization between *S. asteroides* Semple (*S. ptarmicoides* Torr. & Gray) and either *S. ohioensis* Riddell or *S. riddellii* Frank (Morton, 1979; Voss, 1996; Semple et al., 1999). Farther east, in the region of the Gulf of St. Lawrence, is the disjunctly distributed *Symphyotrichum anticostense* (Fernald) G. L. Nesom, a decaploid derivative of *S. boreale* (Torr. & Gray) Á. Löve & D. Löve and *S. novi-belgii* (L.) G. L. Nesom (Labrecque & Brouillet 1990, 1996; Brouillet et al., 2006). On the Gaspé Peninsula there is an unnamed hexaploid race resembling *Packera aurea* (Kowal, 1975). Because it produces adventitious shoots on roots extremely vigorously, *P. pseudoaurea* var. *semicordata*, a species of the upper Midwest that does the same, is suspected of being involved in its origin. The taxon may have a wider distribution: specimens from Cochrane County, Ontario, north of Lake Superior (*Oldham & Sutherland 25823*, WIS, MICH, mjo; *Oldham 36354*, TRT, NHIC, WIS; *Oldham 36458*, WIS, NHIC; *Oldham 36491*, WIS, mjo; *Oldham 36192*, WIS, mjo) may well represent this hexaploid. Finally, an unnamed hexaploid taxon occurs in the sandy flood plain of the Mississippi River at Perrot State Park in Trempealeau Co., Wisconsin (Kowal, unpubl. data; *Nee 14918*, Kowal & Mahoney 3124, Kowal 3199, WIS). It resembles both *P. plattensis* and *P. paupercula* var. *savannarum* and is suspected to be a hybrid derivative of these two taxa, tetraploid and diploid, respectively, both of which occur nearby.

The recognition of *Packera insulae-regalis* as a species is a small contribution to the biosystematics of *Packera*. Its chromosome number almost surely largely isolates it from

related taxa. However, as with many closely related species of the genus (Barkley, 1962; Kowal, 1975; Uttal, 1982; Trock, 2006; Kowal, unpubl. data), hybridization and its resultant potential for genetic exchange is certainly possible, and the crosses reported here indicate such a potential; only future molecular work can verify such a possibility. In any case, our concept of a biological definition of species is not rigid or simplistic; like Barkley's concept (1988), it embraces the possibility of limited gene exchange, leaving the preponderance of the genes that give a species its morphological and ecological identity largely intact.

Again, this contribution addresses only the hexaploid population on Isle Royale. Even in the limited region of Lake Superior there is the additional problem of the existence of diploid and tetraploid populations currently subsumed under *Packera paupercula* var. *paupercula* (Kowal, 1975; Morton, 1981; Kowal, unpubl. data). Judd et al. (2007) provide cogent arguments for recognizing diploid and tetraploid races of *Tolmiea menziesii* (Saxifragaceae) as separate species, and Soltis et al. (2007) encourage the naming of autopolyploids and presumed autopolyploids when they are at least somewhat morphologically, ecologically, and geographically different from the diploids because they represent distinct evolutionary lineages. The tetraploids of *P. paupercula* var. *paupercula* in the vicinity of the western Great Lakes are more robust and tend to have somewhat larger heads than the diploids. Otherwise, too little is known, including whether or not they have multiple origins, to warrant more than the mentioning of their presence.

The following is a key to the taxa immediately related to *Packera insulae-regalis* that occur in the vicinity of Lake Superior. Mahoney & Kowal (2008) provide a key to the broader *P. paupercula* complex in eastern North America. The symbols "s" and "x" refer to the sporophytic (diploid) and base chromosome numbers, respectively.

**Key to *Packera insulae-regalis*,
P. paupercula, and *P. indecora***

1. Basal leaves subcordate or abruptly contracted to the petiole; asexual reproduction either absent (except for new rosettes forming at the base of a flowering stalk) or only by adventitious shoots on roots, commonly resulting in a rosette terminating a simple, short, erect rootstock (a "nubbin"); leaves glabrous or sparingly

- arachnoid pubescent.
2. Rays inconspicuous, shorter than 6 (-7) mm or absent; vegetative reproduction absent; rosette leaf blades glabrous; self-compatible, achenes abundant in all heads; at low elevations, frequently within the splash zone around the Northern Great Lakes (s=8x; x=22?) *P. indecora* – northern squaw-weed, rayless ragwort
 2. Rays prominent, longer than 6 mm; vegetative rosettes abundantly produced adventitiously from roots; rosette leaf blades sparsely arachnoid pubescent; partially self-incompatible, achene production sporadic; endemic to the summit of Mount Franklin on Isle Royale (s=6x; x=22?) *P. insulae-regalis* – Isle Royale ragwort
1. Basal leaves tapering to the petiole; asexual reproduction by rhizomes, sometimes with adventitious shoots on roots in addition; leaves glabrous to heavily pubescent *P. paupercula* (s.l.) – northern ragwort
 3. Plants glabrous or pubescent and gracile; heads smaller; wet or moist habitats around the Great Lakes and in calcareous fens inland (s=2x; x=22). var. *paupercula* – diploid race
 3. Plants usually more or less pubescent and coarser; heads larger; moist to mesic habitats, mostly in the northern Midwest (s=4x; x=22) var. *paupercula* – northern tetraploid complex

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