Bot. Bull. Acad. Sin. (1997) **38:** 49–56

Revision of the endemic Asian genus *Peracarpa* (Campanulaceae: Campanuloideae) via numerical phenetics

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(Received September 9, 1996; Accepted November 8, 1996)

Abstract. *Peracarpa* (Campanulaceae: Campanuloideae) is a genus of delicate perennial herbs widely distributed in mesic forest habitats of eastern Asia. Previous classifications have recognized a single species, either divided into several varieties or not, or as many as three species. This study utilized the methods of numerical phenetics (cluster analysis and principal components analysis) to assess taxonomic structure within the genus. Analysis of 38 morphological characters extracted from 72 population samples failed to disclose groups of populations that were morphologically distinguishable and geographically coherent. We conclude that the genus comprises a single species, *P. carnosa*, and that this species cannot be divided into intraspecific taxa in any meaningful fashion.

Keywords: Campanulaceae; Cluster analysis; Numerical phenetics; *Peracarpa*; Principal components analysis.

Introduction

Peracarpa (Campanulaceae: Campanuloideae) is a genus of delicate perennial herbs endemic to eastern Asia. Though widely distributed, it has been collected but infrequently. As a result, the genus has escaped detailed synoptic study. The only available accounts are contained in regional floras, and these differ in their treatment of the genus, recognizing either three species, one species with three to five varieties, or a single undivided species.

The purpose of this study was to clarify taxonomic relationships within *Peracarpa* by undertaking a synoptic analysis of all available material from throughout the range of the genus, and to propose a formal classification that would adequately reflect these relationships. Given the broad geographic and elevational range of the genus, we especially sought to determine if there were morphologically distinguishable clusters of populations that were geographically coherent. Questions of this sort are best addressed using the methods of numerical phenetics (Duncan and Baum, 1981; Romesburg, 1984; Abbott et al., 1985).

Taxonomic History

The genus *Peracarpa* was erected by Hooker and Thomson (1858) to accommodate *Campanula carnosa*[3], a species of the Himalayas. This species differed from all other members of *Campanula* L. in its fruit: the capsule has thin membranous walls which rupture irregularly at the base to release 10–16 relatively large seeds. In *Campanula*, the smaller more numerous seeds are dispersed through 3 or 5 pores in the much stouter lateral walls of the capsule.

Feer (1890) added a second species with the transfer of *Campanula circaeoides*. This species of Japan and the Russian Far East greatly resembled *P. carnosa*, with only minor differences in the size and shape of the leaves and flowers. A third species was added by Rolfe (1906), who described *P. luzonica* from the Philippine island of Luzon. Again, the new species was distinguished on the basis of minor quantitative features.

In the only previous treatment to account for *Peracarpa* throughout its range, Hara (1947) treated all known populations as a single species, *P. carnosa*, divided into five varieties: var. *carnosa* ("var. typica Hara") from India, Bhutan, Nepal; var. *circaeoides* from Japan, the Russian Far East, and the Korean island of Cheju Do; var. *kiusiana* and var. *pumila* from the Japanese island of Kyùshù; and var. *formosana* (including *P. luzonica*) from Taiwan and the Philippines. In addition, he distinguished a f. *macrantha* from Honshu under var. *circaeoides*.

Subsequently, Hara (1966, 1971) elaborated on his classification, emphasizing the puzzling patterns of intraspecific variation. He distinguished Himalayan var. *carnosa* and Japanese var. *circaeoides* not only on the basis of morphological data but on cytological grounds as well: the former was said to have a chromosome number of $n = 15$ while the latter had $n = 14$; chromosome counts for other varieties were not available. Though he did not explicitly repudiate var. *kiusiana* and var. *pumila*, his discussion and distribution map suggest that he basically viewed the species as comprising three major geographic entities: var. *carnosa* of the Himalayas, extending eastward into China;

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[3] Author names for all binomials will be found in the Systematic Treatment.

var. *circaeoides* of the Russian Far East, Japan, and Cheju Do, extending westward into China; and var. *formosana* of Taiwan and the Philippines. He did, however, note that plants intermediate between the first two varieties were frequent, not only in China, where both occur, but in Japan and the Himalayas as well.

Most current floras treat *Peracarpa* as unispecific, generally without the recognition of intraspecific taxa (Moeliono and Tuyn, 1960; Kao and DeVol, 1974, 1978; Hong, 1983; Lammers, 1992). The results of the present study support this view. There are exceptions, however. Fedorov (1957) recognized *P. carnosa* and *P. circaeoides* as distinct species. In Nepal, Hara (1982) recognized a single species divided into var. *carnosa* and var. *circaeoides*. Similarly, in Japan, Ohwi (1984) recognized three varieties (these two plus var. *kiusiana*); Shimizu (1993), however, treated var. *kiusiana* as a synonym of var. *circaeoides*. In Korea, Lee (1989) and Yoo (1995) treated the local plants as var. *circaeoides*.

Materials and Methods

Herbarium specimens were the source of morphological data used in this study, serving as operational taxonomic units (OTUs) in the numerical analyses. Because of its inconspicuous nature, *Peracarpa* is rarely collected. The 26 herbaria (see Acknowledgments) that responded to requests for loans contained only about 300 sheets, representing 200 individual collections. From this group an initial representative set of 102 collections, fully half of all available material, was chosen for use in the analyses. These specimens were selected to reflect the full range of morphological, geographic, and elevational variation seen in the genus. Each was assigned a code of two letters indicating the country of origin (BH = Bhutan, BU = Burma, CH = China, IN = India, JA = Japan, KO = Korea, NE = Nepal, NG = Papua New Guinea, PH = Philippines, RU = Russia, TA = Taiwan, TH =Thailand), plus a sequential two-digit number.

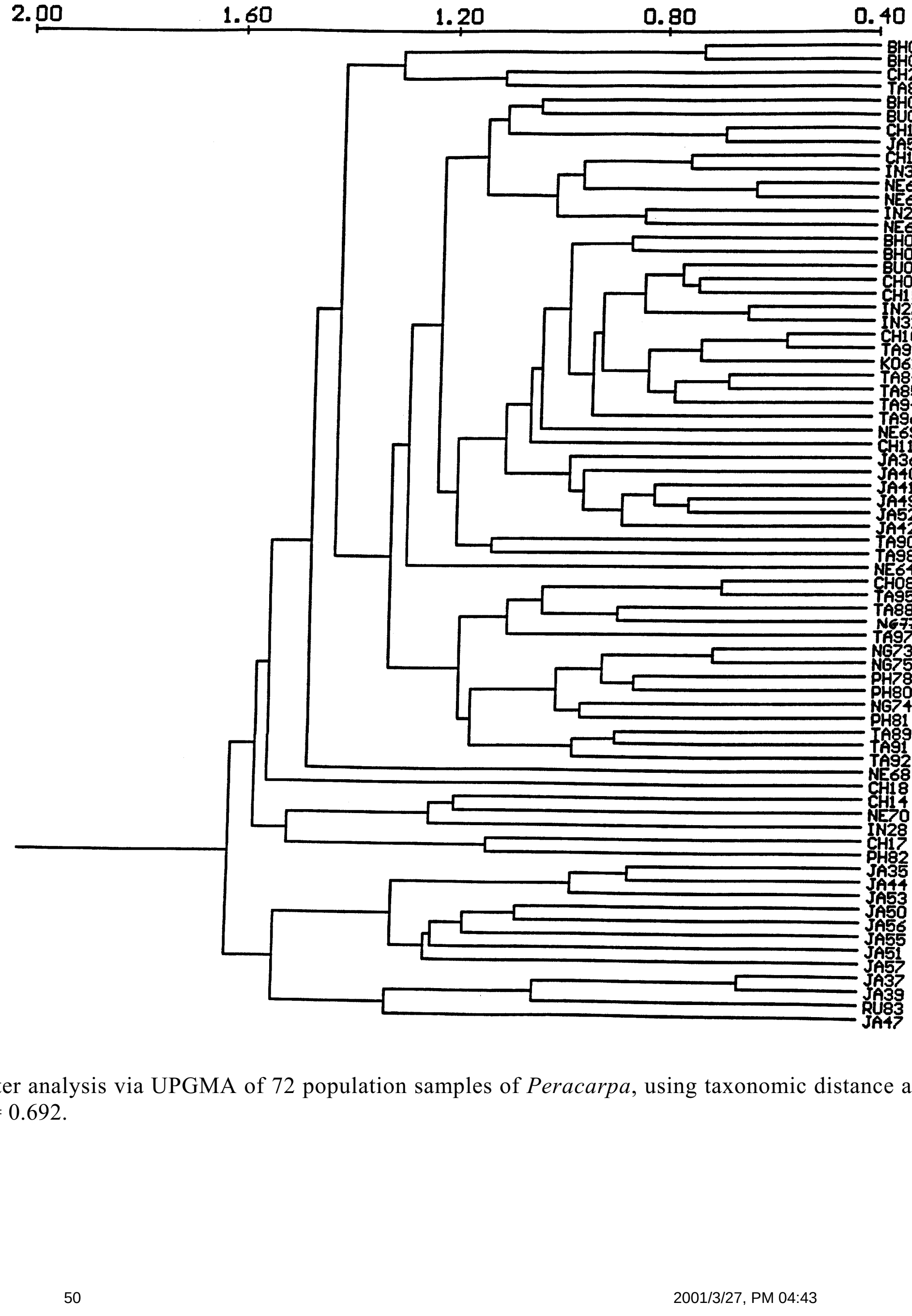

Figure 1. Cluster analysis via UPGMA of 72 population samples of *Peracarpa*, using taxonomic distance as the coefficient of resemblance; $r = 0.692$.

Table 1. Specimens of *Peracarpa* measured for phenetic analyses.

OTU	Locality[a]	Voucher[b]
BH00	Punakha	*Grierson & Long 4686* (E)
BH01	Tobrang	*Ludlow et al. 20224* (BM, E)
BH02	Lami Gompa	*Grierson & Long 1852* (A, E, K)
BH03	Tongsa	*Grierson & Long 1247* (E)
BH04	Dochu La	*Grierson & Long 1055* (E)
BU06	Chawng-maw-tika	*Ward 3194* (E)
BU07	North Triangle	*Ward 20903* (BM)
CH08	Anhui: Jinzhai	*Yao 8941* (A, CAS, K, MO, MU, NY)
CH09	Sichuan: S. Wushan	*Henry 5642* (BM, K)
CH10	Hubei	*Henry 3461* (E, K)
CH11	Guizhou: Mou-Po	*Teng 90172* (A)
CH12	Hubei	*Henry 5656* (GH)
CH14	Yunnan: Meytre	*Henry 9449* (K, NY)
CH15	Yunnan: Tschiangschel	*Handel-Mazzetti 9384* (E)
CH16	Yunnan: Tehching	*Yu 8474* (A, KUN)
CH17	Yunnan: Yangbi Xian	*1984 Sino-American Botanical Expedition 298* (A, CAS)
CH18	"western China"	*Wilson 3981* (P)
CH21	Yunnan: Jingdong	*Peng & Bai 102* (KUN)
IN27	Sikkim	*Clarke 35690* (BM)
IN28	Sikkim	*Herbarium Lacaita, H III 424* (BM)
IN29	"NW Himalaya"	*Duttine 19817* (BM)
IN30	Darjeeling	*Anderson 184* (B)
IN32	Hjimaw Pass	*"RA" 1014* (E)
JA35	Honshu: Kyoto Pref.	*Fukuoka & Fonta 31* (A, C, E, K, L, MAK, NY, P, SING, US)
JA36	Honshu: Shinano Prov.	*Minemura s.n.* (MAK)
JA37	Honshu: Mutsu Prov.	*Sohma 1162* (MO)
JA39	Honshu: Gumma Pref.	*Ono & Kobayashi s.n.* (CAS, L, MAK, US)
JA40	Honshu: Nagasaki Pref.	*Maximowicz s.n.* (GH, K, L, NY)
JA41	Hokkaido: Sapporo	*Sugiyama s.n.* (GH)
JA42	Honshu: Miyagi Pref.	*Ohashi et al. s.n.* (TUS)
JA44	Honshu: Miyagi Pref.	*Ogawa & Sakai 107* (TUS)
JA47	Honshu: NE Jizogahara	*Koyama 7699* (A)
JA49	Honshu: Yamaguchi Pref.	*Charette 1664* (MO, US)
JA50	Honshu: Kanagawa Pref.	*Kobayashi 1875* (CAS)
JA51	Honshu: Akita Pref.	*Hoshi & Ohmiya 3025* (TUS)
JA52	Honshu: Yamagata Pref.	*Tsugaru & Takahashi 6583* (A, NY)
JA53	Honshu: Kyoto Pref.	*Tagawa 7203* (A)
JA54	Honshu: Miyagi Pref.	*Ohashi et al. 8214* (TUS)
JA55	Honshu: Osaka Pref.	*Hiroe 13651* (C)
JA56	Honshu: Shiga Pref.	*Tateishi & Hoshi 13862* (A, TUS)
JA57	Honshu: Kyoto Pref.	*Tsugaru & Takahashi 17856* (A, MO)
KO62	Cheju Do	*Taquet 4642* (E)
NE64	Marsiandi Valley	*Lowndes 904* (BM)
NE65	Beni	*Stainton et al. 211* (BM, E)
NE66	Pokhara	*Stainton et al. 4854* (A, BM, E)
NE67	Ganesh Himal	*Stainton 3661* (BM)
NE68	Siringdham	*Williams 670* (BM)
NE69	Beni	*Stainton et al.* 444 (A, BM, E)
NE70*	No location	*Wallich 1282* (BM, C, E, GH, K, L)
NG73	Morobe Dist.	*Hartley 11141* (A, LAE)
NG74	Goropu Mts.	*Veldkamp & Stevens 5776* (L, LAE)
NG75	West Sepik	*Barker & Umba 67376* (L, LAE)
NG77	West Sepik	*Craig 58* (LAE)
PH78	Luzon: Mountain Prov.	*Sulit 2524* (A)
PH80	Luzon: Benguet	*Merrill 4724* (K, US)
PH81	Luzon: Benguet	*Ramos & Edano 44954* (B, L, NY)
PH82*	Luzon: Benguet	*Loher 3735* (K)
RU83	Far East: Sakhalin	*Ponomarczuk 5492* (A, BM, C, E, MO, NY, US)
TA84	Mt. Ali	*Van Steenis* 20811 (L)
TA85	Hualien Hsien	*Shen 666* (CAS, HAST)
TA86	Hualien Hsien	*Liao 1408* (HAST)
TA88	Kaohsiung Hsien	*Ho 903* (HAST)
TA89	Kaohsiung Hsien	*Wang 1147* (A, CAS, HAST)
TA90	Hsinchu Hsien	*Wang & Hsu 1341* (E, HAST)
TA91	Alishan	*Chen 4606* (RSA)
TA92	Chiayi Hsien	*Bartholomew & Boufford 6146* (CAS)
TA93	Chiayi Hsien	*Chao & Kao 6165* (US)
TA94	Nantou Hsien	*Peng 8028* (HAST)
TA95	Taichung Hsien	*Peng 7932* (HAST)
TA96	Miaoli Hsien	*Peng 8463* (HAST)
TA97	Miaoli Hsien	*Peng 14899* (HAST)
TA98	Arisan	*Gressitt 171* (BM, GH, L, NY)

[a]Country denoted by first two letters of OTU code: BH = Bhutan, BU = Burma, CH = China, IN = India, JA = Japan, KO = Korea, NE = Nepal, NG = New Guinea, PH = Philippines, RU = Russia, TA = Taiwan.
[b]Type specimens are indicated by an asterisk (*).

Table 2. Characters used in the numerical analyses of *Peracarpa*. Codings for states of qualitative characters are given in parentheses, all other characters were quantitative and measured in mm (linear measures) or degrees (angles).

STEMS

1. Length of first internode from apex.
2. Length of second internode from apex.
3. Branching: unbranched *(0)*, branched only from base *(1)*, branched throughout *(2)*.
4. Posture: upright *(0)*, sprawling *(1)*.

LEAVES

5. Margin: serrate *(0)*, serrulate *(1)*, crenate *(2)*.
6. Marginal pubescence: present *(0)*, absent *(1)*.
7. Number of marginal teeth on upper leaf.
8. Number of marginal teeth on median leaf.
9. Length of lamina on upper leaf.
10. Length of lamina on median leaf.
11. Width of lamina on upper leaf.
12. Width of lamina on median leaf.
13. Length/width ratio for upper leaf.
14. Length/width ratio for median leaf.
15. Ratio of length to widest point/total length for upper leaf.
16. Ratio of length to widest point/total length ratio for median leaf.
17. Apical angle for upper leaf.
18. Apical angle for median leaf.
19. Basal angle for apical leaf.
20. Basal angle for median leaf.
21. Overall leafiness: sparse *(0)*, moderate *(1)*, dense *(2)*.

FLOWERS

22. Pedicel length.
23. Hypanthium length.
24. Hypanthium width.
25. Calyx lobe length.
26. Calyx lobe width.
27. Length/width ratio for calyx lobes.
28. Calyx lobe apical angle.
29. Corolla color: white *(0)*, white with purple venation *(1)*.
30. Corolla length.
31. Corolla tube length.
32. Corolla lobe length.
33. Basal corolla tube diameter.
34. Apical corolla tube diameter.
35. Corolla lobe width.
36. Corolla lobe length/width ratio.
37. Position: determinate *(0)*, indeterminate *(1)*.
38. Number of flowers per stem: single *(0)*, 1–4 *(1)*, 4–17 *(2)*.

It soon became apparent that very few specimens of *Peracarpa* bore both flowers and ripe fruit. As a result, it was necessary to divide the OTUs into two subgroups for separate analyses. One subgroup comprised 72 specimens with flowers, and the other 47 collections with fruits. The subsequent analyses of the two subsets yielded essentially identical results. This makes it possible to simplify the discussion and conserve space by only presenting and discussing the data from the subset of flowering specimens (Table 1).

For these specimens, 38 morphological characters were assessed (Table 2): 21 related to vegetative structures, and 17 to floral structures. Thirty of the characters were quantitative, including linear or angular measurements, ratios of linear measurements, or the number of marginal teeth. The remaining eight characters were qualitative, and divided into two or three discrete states. The 72 OTUs with flowers were scored for all these characters to produce a basic data matrix.

Two sorts of analysis were performed using NYSYS-pc, version 1.60 (Rohlf, 1990): cluster analysis and principal components analysis (PCA). Both utilized a standardized data matrix created via linear transformation of the basic data matrix. For the cluster analyses, a pairwise matrix of resemblance values was calculated from the standardized data matrix, using average taxonomic distance, product-moment correlation, and Euclidian distance as the coefficients of resemblance. In each case, a dendrogram was generated by the unweighted pair-group method using arithmetic averages (UPGMA). In order to determine how well the dendrograms represented the underlying matrices of resemblance values, the cophenetic correlation coefficient (r) for each dendrogram was calculated. For the PCA, a matrix of resemblance values among the characters in the standardized data matrix was created. From this, three eigenvectors were extracted, onto which the standardized data were projected, creating a three-dimensional plot of the OTUs.

Results

Overall, resemblance among the OTUs was very high (taxonomic distance ≤ 1.60, Euclidian distance ≤ 10.0, correlation ≥ -0.15). Although there are differences in the exact structure of the three dendrograms, all show the same results and support the same conclusions. Therefore, only the dendrogram with the highest r value, that based on taxonomic distance (r = 0.692), is shown here (Figure 1). This is a rather low cophenetic correlation coefficient, suggesting a highly complex pattern of multiple resemblances for most OTU's, which was difficult for the clustering algorithm to resolve.

The OTU's did fall into two major clusters. One was comprised entirely of plants from Japan and the Russian Far East, while the other included all remaining OTUs, including several more from Japan. This second larger cluster formed a complex series of closely nested clusters.

Though it was expected that geographically proximate OTUs would cluster, this was seldom the case. The clusters that are evident never included all OTUs from a given region and usually included OTUs from disparate regions. For example, the Japanese OTUs fell into two large clusters, with the exception of one stray OTU (JA54) that clustered with a specimen from Hubei (CH12). The majority of specimens from Papua New Guinea and the Philippines clustered, except for NG77, which clustered with plants from Taiwan and Anhui, and PH82 (the type of *P. luzonica*), which clustered with plants of Yunnan, India, and Nepal. Plants from the Himalayas (India, Nepal, Bhutan) were scattered among at least eight different clusters, and plants of Taiwan, among five. The two OTUs from Burma failed to cluster together, and the OTU from Cheju Do (KO62) did not cluster with Japanese OTUs but rather with some of those from Taiwan and Hubei.

These patterns hold on even a finer geographic scale. Not only were the Chinese OTUs scattered throughout the dendrogram, those from Yunnan (CH14–CH17, CH21) fell among at least four different clusters. Likewise, the three OTUs from Miyagi on the Japanese island of Honshu (JA42, JA44, JA54) fell into three disparate clusters.

Output from the PCA (Figure 2) similarly failed to disclose any major gaps in the pattern of morphological variation. Though there is some tendency for OTU's from a geographic region to fall together in a given portion of the three-dimensional factor space (e.g., most of the Japanese OTUs fall on the right side of Figure 2), there is again a great deal of interposition of OTUs from disparate areas.

Discussion

The results of both cluster analysis and PCA can only be interpreted to support recognition of a single species in *Peracarpa*, as originally suggested by Hayata (1908). The degree of morphological similarity among the populations is too high to justify recognition of more than one species, while lack of pronounced gaps in the pattern of variation renders recognition impractical.

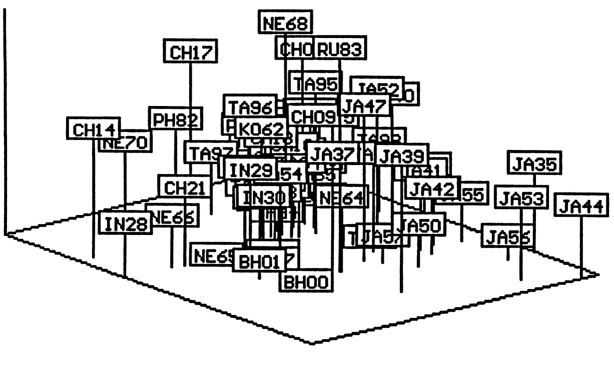

Figure 2. Principal components analysis (PCA) of *Peracarpa*, showing 72 population samples projected onto the first three axes of variation.

Further, our analyses indicate that this species, *P. carnosa*, cannot be subdivided in any meaningful way. This result was rather surprising, in light of the species' highly disjunct distribution. For example, populations in Taiwan lie 460 km from populations in the Philippines, 1,000 km from those in Japan, and 1,000–1,400 km from the nearest populations on the Chinese mainland, while the populations in Papua New Guinea lie nearly 3,000 km from their nearest congeners. One would expect that under such circumstances, a significant degree of morphological diversification would have occurred, making it possible to visually distinguish plants of different regions. Though there are some morphological differences between plants of different regions, as Hara (1971) points out, those differences are too inconsistent and imprecise to allow for the recognition of intraspecific taxa.

Though morphological data do not suggest the existence of more than one taxon within *Peracarpa*, other data might. As noted by Hara (1971), populations examined from Japan and the Russian Far East have 14 pairs of chromosomes (Sokolovskaya, 1960; Hara and Kurosawa, 1965), while those from the Himalayas have 15 pairs (Hara and Kurosawa, 1965; Kurosawa, 1966, 1971). However, with so few counts performed, it is difficult to assess the extent or significance of this variation. Even if more extensive sampling showed that *P. carnosa* comprised two geographically distinct aneuploid races, it would be difficult to employ that characteristic taxonomically in the absence of correlated morphological features. In any case, intraspecific aneuploidy is not rare among Campanuloideae, occurring in species of *Campanula* (Contandriopoulos et al., 1984), *Githopsis* Nutt. (Morin, 1983), *Trachelium* L. (Contandriopoulos et al., 1984), and *Wahlenbergia* Schrad. ex Roth (Smith, 1992), as well as various Lobelioideae (Lammers, 1993).

Systematic Treatment

Peracarpa Hook. f. & Thomson, J. Proc. Linn Soc., Bot. 2: 26. 1858.—TYPE: *Campanula carnosa* Wall.

Unispecific genus, endemic to eastern Asia. Hong (1980) considered it to be most closely related to *Homocodon* Hong of southwestern China and *Heterocodon* Nutt. of the northwestern United States and adjacent Canada, with which it shares the diminutive habit and irregularly dehiscent membranous capsules. Subsequently (Hong, 1995), he assigned all three of these genera to his "Campanula Subgroup," along with *Campanula*, *Adenophora* Fisch., and 13 other genera.

Peracarpa carnosa (Wall.) Hook. f. & Thomson, J. Proc. Linn Soc., Bot. 2: 26. 1858. *Campanula carnosa* Wall. in Roxb., Fl. Ind. 2: 102. 1824.—TYPE: Nepal, 1821, *Wallich 1282* (holotype: K-W; isotypes: BM! C! E[2]! GH[2]! K[2]! L!).

Campanula circaeoides F. Schmidt, Reis. Amur-Land., Bot. 154. 1868. *Peracarpa circaeoides* (F. Schmidt) Feer, Bot. Jahrb. Syst. 12: 621. 1890. *Peracarpa* *carnosa* var. *circaeoides* (F. Schmidt) Makino ex H. Hara, J. Jap. Bot. 21: 20. 1947.—TYPE [designated by Fedorov (1957: 381)]: Russia, Sakhalin, Niburipo between Manue and Mogunkotan, Aug 1860, *Schmidt s.n.* (lectotype: LE).

Peracarpa luzonica Rolfe, Bull. Misc. Inform. 1906: 201. 1906.—TYPE [here designated!]: Philippines, Luzon, Benguet, Data, 2,250 m, Feb 1893, *Loher 3735* (lectotype: K!). Of the two collections cited, this is the more complete.

Peracarpa carnosa var. *formosana* H. Hara, J. Jap. Bot. 21: 19. 1947.—TYPE: Taiwan, Tozan, Mt. Niitaka, Nov 1906, *Nakahara s.n.* (holotype: TI).

Peracarpa carnosa var. *kiusiana* H. Hara, J. Jap. Bot. 21: 20. 1947.—TYPE: Japan, Kyùshù, Prov. Chikugo, Kitayama, 8 May 1927, *Nabeshima s.n.* (holotype: TI).

Peracarpa carnosa f. *macrantha* Nakai ex H. Hara, J. Jap. Bot. 21: 20. 1947.—TYPE: Japan, Honshu, Prov. Sagami, Kawashima, Yokohama, Kitayama, 8 May 1932, *Nakai s.n.* (holotype: TI).

Peracarpa carnosa var. *pumila* H. Hara, J. Jap. Bot. 21: 21. 1947.—TYPE: Japan, Kyùshù, Prov. Hizen, Mt. Unzen, May 1930, *Greatrex 66/30* (holotype: TI).

Delicate perennial herbs, 4–25 cm tall; stolons slender, branched, creeping, 5–15 cm long, often thickened at the nodes; stems erect, reclining, or prostrate, unbranched or rarely few-branched from base, slender, fleshy, sometimes rooting at nodes, glabrous. Leaves alternate, simple, exstipulate, petiolate; lamina ovate, widely ovate, or widely depressed ovate, 3–38 mm long, 3–28 mm wide, fleshy; adaxial surface green, glabrous or pubescent; abaxial surface green, sometimes suffused with purple, glabrous or pubescent; margin flat, serrate, serrulate, or crenulate with 2–10 teeth per side, ciliate or glabrous; apex acute, obtuse, or rounded, often mucronate; base truncate, subcordate, or rarely cordate; petiole 2–17 mm long. Flowers tetracyclic, perfect, actinomorphic, epigynous, protandrous, glabrous, usually terminal or less commonly in the axils of foliage leaves, erect, typically solitary or rarely 2–4(–17) in a fascicle. Pedicels slender, ebracteolate, 2–70 mm long. Hypanthium obconic, 1.1–3.4 mm long, 0.4–2.5 mm wide, glabrous. Calyx synsepalous, the lobes 5, subulate, narrowly triangular, or triangular, erect, 0.5–2.3 mm long, 0.1–1.3 mm wide; margin entire; apex acuminate or acute. Corolla sympetalous, 5-lobed, funnelform, 3–10 mm long, white, sometimes with purple veins or purple shading at tips (rarely pale blue); tube 0.7–4 mm long, 1–3 mm wide at base; lobes elliptic, 1–6 mm long, 0.1–2.3 mm wide, equalling or up to twice as long as the tube, spreading, obtuse or rounded at apex. Stamens 5, antisepalous, free from the corolla; filaments 1.5–3.3 mm long, expanded at base, pubescent or rarely glabrous; anthers lanceolate, 0.7–1.5 mm long; pollen grains 4-6-porate, oblate, 25-40 µm diam., smooth or spinulose. Ovary inferior, (2-)3-loculed, crowned by a hemispherical trisulcate nectar disc; placentation axile, each with 4–5 pairs of ovules; style included, 2.6–6.5 mm long, the upper third densely covered with pollen-collecting hairs; stigmas (2-)3, filiform. Fruit a pendulous capsule, obovoid or broadly obovoid, 2.5–5.5 mm long, 1.5–5 mm diam., crowned by the persistent calyx lobes; pericarp thin, membranous, prominently nerved, distended by the mature seeds, eventually rupturing irregularly, predominately at the base. Seeds oblong, narrowly oblong, ellipsoid, or fusiform, brown, finely striate, 0.7–2.3 mm long, 0.3–1.2 mm diam., 10–16 per capsule. Chromosome number $n = 14$ (Sokolovskaya, 1960 [as *P. circaeoides*]; Hara and Kurosawa, 1965 [as *P. carnosa* var. *circaeoides*]), 15 (Hara and Kurosawa, 1965; Kurosawa, 1966, 1971). Shimizu (1993) reported $n = 27, 36$ for *P. carnosa* var. *circaeoides*, but did not mention $n = 14, 15$; we have not seen original reports for these counts and suspect an error in compilation.

Icones. Schmidt (1868), pl. III, figs. 14–19; Feer (1890), pl. 7b; Terasaki (1933), pl. 777; Hara (1966), pl. 29a–c; Hara (1971), fig. 8a–d; Kao and DeVol (1974), pl. 11; Kao and DeVol (1978), pl. 1190; Hong (1980), fig. 4–6; Lee (1989), pl. 2892; Yoo (1995), fig. 52.

Distribution. On the Pacific rim, from southern Sakhalin south throughout Japan to South Korea (Cheju Do), Taiwan, the Philippines (Luzon), and Papua New Guinea; on the Asian mainland in China (Anhui, Hubei, Sichuan, Guizhou, Yunnan), northern Thailand, northern Burma, and the Himalayas in Bhutan, Nepal, and northern India. Reported in the literature from southern Kamchatka and the Kuriles (Fedorov, 1957) and Panay in the Philippines (Moeliono and Tuyn, 1960), but we have seen no vouchers from these places.

Ecology. Generally found in mesic environments, often along or near streams, from semi-shade to full sun, on forest floor, mossy or grassy banks, and roadsides. In the Russian Far East, Japan, and Cheju Do, it grows at low elevations, from about sea level up to 1,200 m, or occasionally as high as 1,900 m. Farther south on the Pacific rim, it is found only in montane areas: in Taiwan, at 1,200–3,200 m; in the Philippines, 2,300–2,800 m; and in Papua New Guinea, 2,600–3,300 m. On the Asian mainland, it is likewise montane, growing at elevations ranging from 1,300 m in eastern China to 3,800 m in western China and the Himalayas.

Phenology. On the Asian mainland and in Japan, *P. carnosa* flowers from late April to early August. In Taiwan, the season is a bit longer, stretching from March (occasionally late December) to late August. In the Philippines and Papua New Guinea, flowering begins and ends earlier, from late January to late June.

Vernacular Names. In Japan, the plant is known as *tani-gikyò,* with var. *pumila* distinguished as *tsukushi-tani-gikyò* and var. *kiusiana* as *edauchi-tani-gikyò* (Ohwi, 1984).

Representative Specimens Examined. **RUSSIA.** FAR EAST: Sakhalin, *Ponomarczuk 5492* (A, BM, C, E, MO, NY, US). **KOREA.** Quelpaert [Cheju Do], *Taquet 4642* (E). **JAPAN.** HOKKAIDO: Shiribeshi-shicho, *Boufford*

& Kato 22613 (A); Hiyama-shicho, *Boufford & Kato 22646* (BM, GH, MO); Yamaguchi Pref., *Charette 1737* (MO); Kiritachi-toge, *Tsugaru 4912* (A, NY); Ishikari Prov., *Takahashi & Kariya 2467* (RSA); Sapporo, *Faurie 344* (K, MO). HONSHU: Hyogo Pref., *Boufford et al. 19557* (A, CAS, RSA); Kyoto Pref., *Fukuoka & Fonta 31* (A, C, E, K, L, MAK, NY, P, SING, US); Osaka Pref., *Hiroe 13651* (C); Fukoshima Pref., *Ito 415* (MO); Kanagawa Pref., *Kobayashi 1875* (CAS); Gifu Pref., *Kurosaki 12536* (TUS); Nagano Pref., *Murata et al. 30326* (MO); Akita Pref., *Nemoto & Hoshi 4518* (TUS); Tochigi Pref., *Ogawa et al. 227* (TUS); Iwaki-shi, *Ohashi 8521* (A); Gumma Pref., *Ono & Kobayashi 45997* (CAS, L, MAK, US); Mino Prov., *Shiota 3205* (GH); Kaga, *Shiota 3206* (GH); Mutsu Prov., *Sohma 1162* (MO); Niigata Pref., *Togashi 7154* (F); Kyoto Pref., *Togashi 7325* (F); Yamagata Pref., *Tsugaru & Takahashi 6583* (A, NY); Shiga Pref., *Tsugaru et al. 13162* (A, MO); Sagami Prov., *Yamazaki 150* (E). KYUSHU: Nagasaki Pref., *Maximowicz s.n.* (GH, K, L, NY). SHIKOKU: Kochi Pref., *Watanabe s.n.* (GH). **TAIWAN.** CHIAYI HSIEN: *Bartholomew & Boufford 6146* (CAS); Alishan, *Chen 4606* (RSA); Mt. Ali, *Chuang 4488* (US); Arisan, *Faurie 1891* (GH, L); Arisan, *Gressitt 171* (BM, GH, L, NY). KAOHSIUNG HSIEN: *Ho 903* (HAST). HSINCHU HSIEN: *Liu et al. 1407* (HAST). TAICHUNG HSIEN: *Peng 7932* (HAST). NANTON HSIEN: *Peng 8028* (HAST). MIAOLI HSIEN: *Peng 8463* (HAST); Sui Charyo, *Price 35* (K). HUALIEN HSIEN: *Shen 666* (CAS, HAST). **CHINA.** ANHUI: Jinzhai, *Yao 8941* (A, CAS, K, MO, MU, NY). HUBEI: *Henry 5656* (GH). GUIZHOU: MouPo, *Teng 90172* (A). SICHUAN: Tienchuan Hsien, *Chu 2692* (BM); Wushan, *Henry 5642* (BM, K); Omei Hsien, *Sun 339* (A). YUNNAN: Tschiangschel, *Handel-Mazzetti 9384* (E); Meytre, *Henry 9449* (K, NY); Jingdong, *Peng & Bai 102* (KUN); Weixi Hsien, *Wang 64332* (A, KUN); Weixi Hsien, *Wang 64577* (A); Tsang-Yuan, *Wang 73201* (A); Tehchin, *Yu 8474* (A, KUN); Chenkang, *Yu 17017* (A, KUN); Shangchang, *1981 Sino-British Exped. 432* (E); Yangbi Xian, *1984 Sino-Amer. Bot. Exped. 298* (A, CAS). **BHUTAN.** Dochu La, *Grierson & Long 1055* (E); Tongsa, *Grierson & Long 1247* (E); Lami Gompa, *Grierson & Long 1852* (A, E, K); Punakha, *Grierson & Long 4686* (E); Tashiling-Neylong-Charikhachor, *Hara et al. 8296* (E); Ritang-Ratsoo, *Kanai et al. 9986* (BM); Tobrang, *Ludlow et al. 20224* (BM, E); Dobemea Chu, *Lyon 3192* (BM). **NEPAL.** Marsiandi Valley, *Lowndes 904* (BM); Manjet Khola, *Lyon 135* (BM, E); Beni, *Stainton et al. 211* (BM, E); Beni, *Stainton et al. 444* (A, BM, E); Ganesh Himal, *Stainton 3661* (BM); Pokhara, *Stainton et al. 4854* (A, BM, E); Koshi Zone, *Suzuki et al. 88* (BM); Siringdham, *Williams 670* (BM). **INDIA.** Assam, *Chand 7087* (L); Darjeeling, *Clarke 10177* (K); Sikkim, *Clarke 35690* (BM); Tongloo, *Gamble 12* (K); Khasia, *Hooker & Thompson s.n.* (BM, C, GH, L); Kumaon, *Strachey & Winterbottom 5* (K); Manipur, *Watt 7106* (K). **BURMA.** Chawng-maw-tika, *Ward 3194* (E); North Triangle, *Ward 20903* (BM). **THAILAND.** Doi Paham Pols, *Kerr 5201* (K). **PHILIPPINES.** LUZON: Mt. Pulog, *Jacobs 202760* (L); Mountain Prov., *Sulit 2524* (A); Benguet, *Santos 32040* (NY, SING). **PAPUA NEW GUINEA.** West Sepik, *Barker & Umba 67376* (L, LAE); West Sepik, *Craig 58* (LAE); Morobe, *Hartley 11141* (A, LAE); East Highlands, *Stevens & Grubb 54625* (CANB, L, LAE); Milne Bay, *Stevens & Veldkamp 55509* (LAE); Central Prov., *van Royen 10788* (CANB, CBG, L, LAE, MO); Goropu Mts, *Veldkamp & Stevens 5776* (L, LAE); West Sepik, *Veldkamp 6311* (CANB, L, LAE); West Highlands, *Wade & McVean ANU7767* (LAE).

Acknowledgments. This research was carried out while ALB was an undergraduate intern supported by the Office of Academic Affairs of the Field Museum of Natural History. The authors thank the administrators and staffs of the following herbaria for the loan of specimens: A, B, BM, C, CANB, CAS, CBG, E, F, GH, HAST, IBSC, K, KUN, L, LAE, MAK, MO, MU, NY, P, RSA, SING, SNU, TUS, US, and WTU.

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數值表型分類對亞洲固有的山桔梗屬（桔梗科：桔梗亞科）的分類修訂

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山桔梗屬（桔梗科：桔梗亞科）是一群細緻的多年生草本植物，廣泛分佈於東亞森林。前人的分類將此屬分成一個包括零至若干個變種的一個種或至多可分成三個種。本研究應用數值表型分類（群分析及主成份分析）來評估山桔梗屬的分類結構，從 72 個族群樣本中，對 38 個形態特徵進行分析，並未能發現在特定地理區域內有獨特形態特徵的族群。因此，我們認為山桔梗屬應只包括單一種，山桔梗，而不能在種以下再做有意義的種內分類群的劃分。

關鍵詞：桔梗科；群分析；數值表型分類；山桔梗屬；主成份分析。