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Pachysandra (Buxaceae) Reexamined

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Abstract. Statistical analysis of the taxa of *Pachysandra* with axillary inflorescences shows that differences previously used to separate species and infraspecific taxa are, for the most part, continuous. A revised taxonomy reflecting these observations recognizes three species in the genus, *P. procumbens* Michaux in the United States, *P. terminalis* Sieb. & Zucc. in Japan and China and *P. axillaris* Franchet, with two subspecies, *axillaris* and *stylosa* (Dunn) Boufford & Q. Y. Xiang, stat. nov., in China. A chromosome count of $2n=24$ for *P. procumbens* is the first report for the species. Counts of $2n=24$ for *P. axillaris* subsp. *axillaris* and $2n=48$ for *P. terminalis* were also confirmed.

Key words: Buxaceae; Flora of China; *Pachysandra*; *P. axillaris* subsp. *axillaris*; *P. axillaris* subsp. *stylosa* (Dunn) Boufford & Q. Y. Xiang; Taxonomy.

Introduction

Pachysandra Michaux (Buxaceae), which exhibits the familiar eastern North American - eastern Asian disjunct distribution pattern (see Channel and Wood, 1987), comprises three species, *P. procumbens* Michaux, characterized by a basal inflorescence and endemic to North America, *P. terminalis* Sieb. & Zucc., with a terminal inflorescence and occurring in Japan and eastern China, and *P. axillaris* Franchet, characterized by axillary inflorescences and endemic to China. *Pachysandra procumbens* and *P. terminalis* are well defined and have never been a source of confusion. *Pachysandra axillaris,* on the other hand, is highly polymorphic and has been treated in various ways since it was first described over one hundred years ago.

When Robbins (1968) prepared his treatment of *Pachysandra* the number of specimens available to him from China was severely limited. The insufficient number of specimens resulted in Robbins recognizing two species with axillary inflorescences, *P. stylosa* Dunn with six varieties and the montypic *P. axillaris* Franchet. The six varieties of *P. stylosa* were based on collections from fewer than 20 different locations. Approximately eight localities were represented by the *P. axillaris* collections. Robbins recognized that his treatment of the Chinese species might eventually be revised, but he expressed the opinion that his taxonomy presented a clearer picture of the full extent of variation within the available collections than would a treatment recognizing only two taxa, *P. axillaris* and a highly variable *P. stylosa.*

We have recently had the opportunity to examine a large number of specimens of the axillary flowered species of *Pachysandra* from several Chinese herbaria and compare them with specimens of *Pachysandra* available to Robbins from the Arnold Arboretum (A) and Gray (GH) herbaria. Morphological examination of this new material along with statistical analysis of the characters used by Robbins to delimit taxa provides information that rules against the recognition of *P. axillaris* and *P. stylosa* as distinct species. Furthermore, the characteristics on which the varieties of *P. stylosa* were based also show considerable variation and overlap when sufficient numbers of specimens are examined. We therefore present a revised taxonomy in which we recognize three species of *Pachysandra, P.*

procumbens in the southeastern United states, *P. terminalis* Sieb. & Zucc. in Japan and China, and *P. axillaris*, with two subspecies, restricted to China.

We also present new cytological information for *Pachysandra procumbens* and confirmation of counts for the Asian taxa.

Materials and Methods for Chromosome Observations

Root tips were collected from plants cultivated at the Arnold Arboretum. The root tips were pretreated for up to three hours in a supersaturated paradichlorobenzene (PDB) solution and then fixed in a 3:1 ethanol: acetic acid solution for ca. 18 hours. A 1:1 solution of ethanol: 36% hydrochloric acid was used for hydrolysis. The chromosomes were stained with a 1% aceto-carmine solution and examined using ordinary smear preparations. Voucher specimens (*P. axillaris* subsp. *axillaris* = *Boufford 25704; P. procumbens* = *Boufford 25702; P. terminalis* = *Boufford 25703*) are on deposit in the Arnold Arboretum herbarium (A).

Results

Mitotic root tip cells of *P. terminalis* showed $2n=48$ chromosomes (Fig. 1b) and those of *P. axillaris* subsp. *axillaris* showed $2n=24$. Both of these counts are consistent with reports by Kurosawa (1981). Counts from *P. procumbens* showed it to be $2n=24$ (Fig. 1a). This first report of the chromosome number of *P. procumbens* is of interest since it reveals the species to be a diploid, the same as *P. axillaris* subsp. *axillaris*.

The position of the inflorescence, chromosome numbers and carpel numbers of the three species of *Pachysandra* indicate that the 2-carpellate, tetraploid *P. terminalis* is an advanced species, most likely derived from a 3-carpellate ancestor like *P. axillaris*, a diploid species with axillary inflorescences. The retention of the diploid chromosome number ($n=12$) and 3-carpellate ovaries in *P. procumbens* are of particular interest since they hint at a closer relationship between these two species than between either of them and *P. terminalis*. This situation is analogous to that found in the genus *Diphylleia* Michaux (Berberidaceae) where the American *D. cymosa* Michaux and Chinese *D. sinensis* H. L. Li appear more similar to each other in a number of features than either does to the Japanese/far eastern Russian *D. grayi* F. Schmidt (Ying *et al.*, 1985).

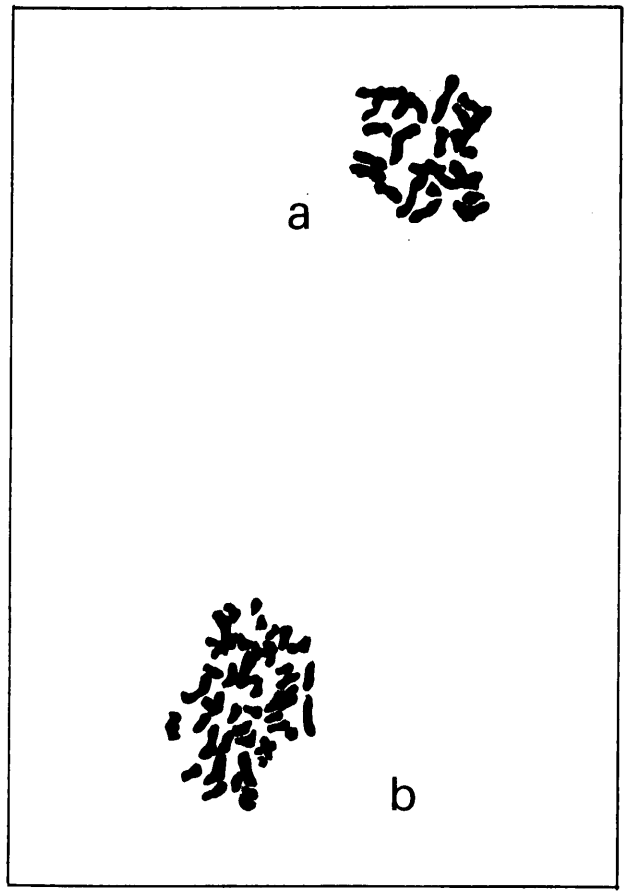

Fig. 1. Camera lucida drawings of chromosomes in somatic cells of *Pachysandra*. a, *P. procumbens*, $2n=24$; b, *P. terminalis*, $2n=48$. (both figures × 780)

Inflorescences within the Buxaceae are most commonly axillary, and on this basis they may arguably be considered the primitive type for the family. It follows, then, that both the terminal inflorescence of *P. terminalis* and the basal inflorescence of *P. procumbens* are derived, although they cannot be considered homologous. On the basis of pollen morphology Gray and Sohma (1964) postulated the genus *Sarcococca* Lindley, which also bears axillary inflorescences, to be the closest relative of *Pachysandra*. Further analysis of the genome of *Pachysandra*, as well as molecular data, such as from enzyme electrophoresis and restriction site analysis of the chloroplast genome, may help to determine more exact relationships of the genus as well as the degree of genetic divergence between the three species.

Statistical Analysis

Considerable variation in leaf morphology exists within the Chinese species *P. axillaris* and has been the basis for recognizing two, more-or-less distinct taxa, *P. axillaris* and *P. stylosa*. A varying number of varieties have been recognized within the latter based on leaf pubescence, leaf shape, and toothing of the leaf margin (Robbins, 1968). The continuous variation of these diagnostic features, however, and the existence of a number of intermediate individuals has made it difficult to consistently distinguish *P. axillaris* and *P. stylosa* and has resulted in confusion because of the inconsistent manner of applying names. Furthermore, it was because of the use of these characters by Robbins to further distinguish six varieties within *P. stylosa* that we decided to perform the statistical analysis.

In our study of the axillary-flowered plants we found leaves with completely eciliate margins, slightly ciliate margins, and conspicuously ciliate margins. We also found leaves with serrate but eciliate margins and leaves ciliate and serrate, but completely glabrous on the lower surface. Variously shaped leaf bases were even seen on a single individual. Except for the presence or absence of cilia along the cartilaginous leaf margin and differences in the size of pollen grains (Gray and Sohma, 1964), we were unable to find any discontinuous characters to conclusively separate the putative varietal taxa. Besides size differences, Gray and Sohma (1964) found varying numbers of pores in pollen taken from specimens of several of the varieties of *P. stylosa* recognized by Robbins (1968), but made no comments on the taxonomic significance at or below the species level.

To obtain a better understanding of the pattern of variation within *Pachysandra axillaris* and to determine a more reasonable taxonomic treatment, we borrowed and examined slightly more than 100 specimens (Appendix 1) of the axillary flowered taxa from Chinese herbaria. These specimens were collected from throughout the range of *P. axillaris*. Statistic analysis of the above leaf characters was carried out. Complete and healthy leaves from each specimen were counted and their character states recorded. The characters used were: lower leaf surface pubescence (LH - long hairs; SH - short hairs; G - glabrous); margin (C - ciliate; EC - eciliate); teeth (MT - more than five teeth; FT - five or fewer teeth); serration (LS - half or less than half serrate; MS - more than half serrate). Specimens exhibiting intermediate states were not included in the analysis. Six hundred leaves in total were used. The results are presented in Table 1 and Figures 2-5.

Figure 2 shows that character states LH and G are closely correlated with character states EC and LS (Fig. 2a, c) and character state SH is closely correlated with C, MT, MS (Fig. 2b). Figure 4a provides evidence that number of teeth is not a good taxonomic character. Figures 3 and 5 show correlations similar to those in Figure 2. These characters can be organized into two related groups, however: C, SH, MS (ciliate, short pubescent on lower leaf surface, more than half the

Table 1. *Frequencies of leaf characters among 600 leaves examined*

	Lower surface			margin		Teeth		serration	
	LH	SH	G	C	EC	MT	FT	LS	MS
LH	111	0	0	0	111	31	80	109	2
SH	0	245	0	245	0	223	22	47	198
G	0	0	244	57	187	139	105	194	50
C	0	245	57	302	0	272	30	63	239
EC	111	0	187	0	298	121	177	287	11
MT	31	223	139	272	121	393	0	149	244
FT	m 80	22	105	30	117	0	207	207	0
LS	109	47	194	63	287	149	207	350	0
MS	2	198	50	239	11	244	0	0	250

LH: Leaves with long hairs on lower surface; SH: Leaves with short hairs on lower surface; G: Leaves glabrous on lower surface; C: Leaves with ciliate margins; EC: Leaves with eciliate margins; MT: Leaves with more than five teeth; FT: Leaves with fewer than five teeth; LS: Leaves serrate half or less their length; MS: Leaves serrate more than half their length.

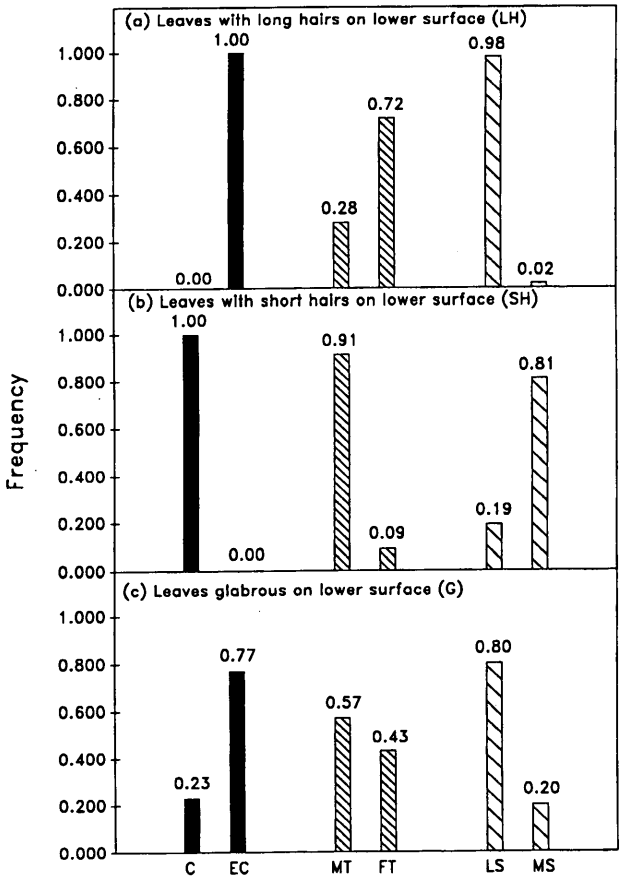

Fig. 2. Frequencies of other characters for leaveswith (a) long hairs on lower surface, (b) leaves with short hairs on lower surface, and (c) leaves glabrous on lower surface. C - ciliate, EC - eciliate, MT - more than five teeth, FT - five teeth or fewer, LS - less than half serrate, MS - more than half serrate.

margin serrate), and EC, LH or G, and LS (eciliate, long hairs of glabrous on lower leaf surface, half or less than half of leaf margin serrate).

Plants with the first combination of characters C, SH and MS, are all from Yunnan Province. Those with the second combination of characters, EC, LH or G, and LS, occur from eastern China to Yunnan, where they show morphological overlap with the former group. Although many intermediates exist where the ranges overlap (Fig. 6), most plants can be separated into one group or the other, particularly by using the presence or absence of cilia on the margins of the leaves as the distinguishing feature.

It therefore appears clear that this group of plants

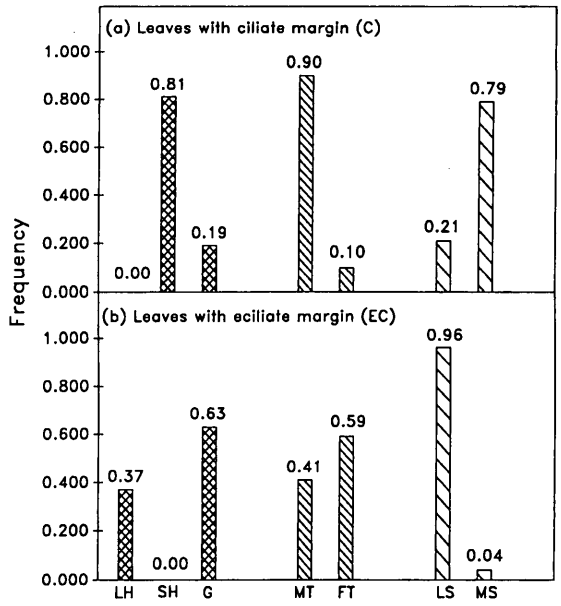

Fig. 3. Frequencies of other characters for leaves with ciliate (a) and eciliate (b) margins. LH - long hairs, SH - short hairs, G - glabrous, MT - more than five teeth, FT - five teeth or fewer, LS - less than half serrate, MS more than half serrate.

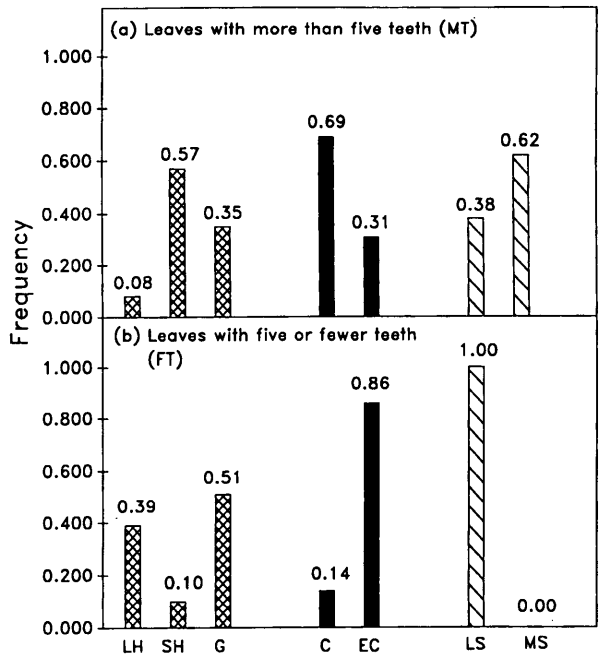

Fig. 4. Frequencies of other characters in relation to (a) leaves with more than five teeth and (b) leaves with five or fewer teeth. LH - long hairs, SH - short hairs, G - glabrous, C - ciliate, EC - eciliate, LS - less than half serrate, MS more than half serrate.

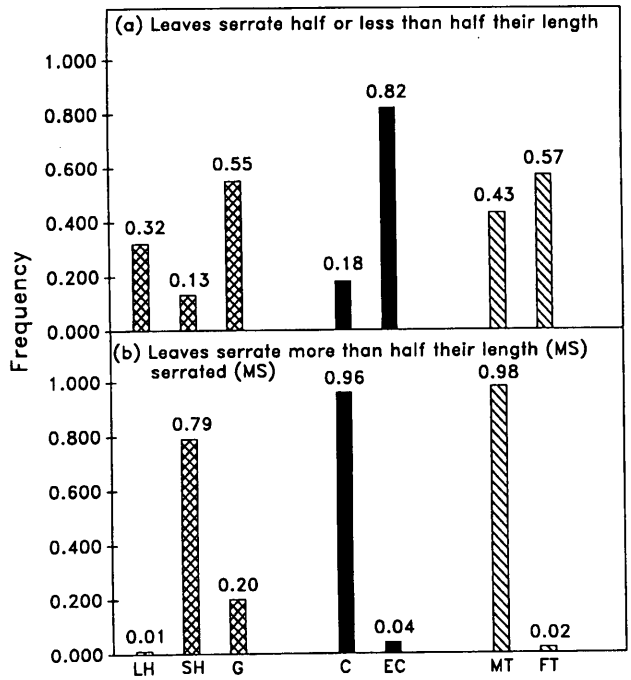

Fig. 5. Frequencies of other characters in relation to (a) leaves serrate half or less than half their length (LS), and (b) leaves serrate more than half their length. LH - long hairs, SH - short hairs, G - glabrous, C - ciliate, EC - eciliate, MT - more than five teeth, FT - five teeth or fewer.

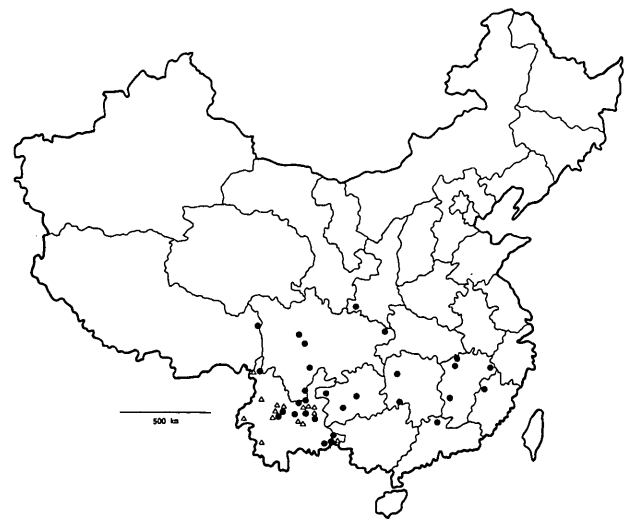

Fig. 6. Distribution of specimens of *Pachysandra axillaris* subsp. *axillaris* (△) and *P. axillaris* subsp. *stylosa* (●) used for leaf character analysis.

with axillary inflorescences belongs to a single variable species, within which can be recognized two weakly separable subspecies. Specimens observed by Franchet and Dunn, who published their observations on *P. axillaris* (Franchet, 1889) and *P. stylosa* (Dunn, 1908) belong, in fact, to the two extremes occurring at the margins of the species' distribution range. Although there are differences between these two extreme types, the differences are obscured by the intermediate plants occurring throughout the entire distribution range, but particularly by those in the parts of Yunnan where the ranges of the two subspecies overlap. Because the extremes are separable, however, and occupy geographically distinct but slightly overlapping ranges, we have decided to recognize this comples as a single widespread species, *P. axillaris,* with two infraspecific taxa. Cheng (1979, 1908) arrived at the same conclusion, although his results were not based on statistical evidence, and he recognized the two taxa at the varietal level. We prefer, however, to recognize these taxa at the rank of subspecies, as subsp. *axillaris* and subsp. *stylosa*. Such treatment of the axillary flowered pachysandras necessitates the following change of taxonomic status.

Pachysandra axillaris Franchet subsp. **stylosa** (Dunn) Boufford & Q. Y. Xiang, stat. nov., based on *P. stylosa* Dunn, J. Bot. 46: 326. 1908, *P. axillaris* var. *stylosa* (Dunn) M. Cheng in M. Cheng & T. L. Ming, Fl. Reipubl. Pop. Sin. 45 (1): 59. 1980.

Synonyms: *P. bodinieri* Léveillé, Repert. Spec. Nov. Regni Veg. 12: 187. May 1913; *P. stylosa* var. *tricarpa* Hayata, Ic. Pl. Formosa. 3: 171. Dec 1913; *P. stylosa* var. *glaberrima* Handel-Mazzetti, Symb. Sin. 7: 236. 1931; *P. axillaris* Franchet var. *kouytchensis* Léveillé, Fl. Kouytchéou 166. 1914; *P. stylosa* var. *reflexa* Robbins, Sida 3: 236. 1968; *P. stylosa* var. *tomentosa* Robbins, Sida 3: 237. 1968; *P. stylosa* var. *kouytchensis* (Léveillé) Robbins, Sida 3: 239. 1968; *P. axillaris* var. *glaberrima* (Handel-Mazzetti) C. Y. Wu, Fl. Yunnan. 1: 154. 1977.

The following key can be used to separate the four taxa of *Pachysandra*.

1. Gynoecium 2-carpellate; inflorescence terminal (although sometimes appearing lateral through extension of lateral branches) . . . . . .

. . . . . 1. *P. terminalis* Sieb. & Zucc.

1. Gynoecium 3-carpellate; inflorescences in leaf axils or near ground level at base of main stem.
   2. Inflorescences in axils of stem leaves. . . . . 2. *P. axillaris* Franchet.
      3. Cartilaginous margin of leaves ciliate (most obvious on lower leaf surface); leaf base truncate to subcordate . . . . . 2a. *P. axillaris* subsp. *axillaris*.
      3. Cartilaginous margin of leaves glabrous; leaf base cuneate to rounded, rarely subtruncate... 2b. *P. axillars* subsp. *stylosa* (Dunn) Boufford & Q. Y. Xiang.
   2. Inflorescences near base of main stem, usually well below lowest leaves . . . . . 3.*P. procumbens* Michaux.

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Appendix 1. Specimens examined

Pachysandra axillaris subsp. *axillaris*

China. Yunnan, Binchuan Xian, 22 Dec 1946, *T. N. Liou 22128* (PE); Dali Xian, 1946, *T. N. Liou 13306* (KUN), *T. N. Liou 13514* (KUN), 8 May 1946, *T. N. Liou 14432* (IBSC, KUN); Fumin Xian, 19 Oct 1964, *B. Y. Qiu 596045* (KUN); near Kunming, Hua-Hong-Dong, 26 Apr 1981, *Sino-Brit. Exped. K 035* (A), 13 Sep 1946, *K. M. Feng 10289* (KUN), 27 Mar 1953, *B. Y. Qiu 50202* (KUN); Luquan Xian, 19 Nov 1952, *P. I. Mao 01824* (KUN); Songming Xian, 10 Oct 1950, *P. I. Mao 115* (KUN, PE), 10 Oct 1953, *B. Y. Qiu 50316* (KUN), 13 Oct 1955, *B. Y. Qiu 51271* (IBSC, KUN, PE), 12 May 1982, *B. Y. Qiu & S. H. Yuan 82007*(A), 23 Oct 1985, *Y. Hu & S. K. Wen 57469* (KUN), 15 Nov 1957, *B. Y. Qiu 55495* (PE; Wuding Xian, *D. D. Tao 840075* (A), 15 Oct 1960, *Z. Ping 60-145* (KUN); Yangbi Xian, 29 Oct 1929, *R. C. Ching 25353* (KUN); Ta-Pin-Tzê, *J. M. Delavay* (A); Ta Long Tan, 10 Oct 1889, *J. M. Delavay* (A), 11 Nov 1887, *J. M. Delavay* (A); Yunnan-Sikang Exped., *M. G. Li 5089* (KUN); "Yunnan," *Bodinier & Ducloux 18* (GH), *J. M. Delavay* (A, GH), *T. N. Liou 13369* (IBSC), *E. E. Maire 10223* (GH, IBSC), *F. T. Wang 838* (KUN), *F. T. Wang 1267* (KUN), *F. T. Wang 1287* (KUN)

Pachysandra axillaris subsp. *stylosa*

China. Fujian, Apr-May 1905, *Dunn 2186* (A), Taining Xian, 5 May 1981, *G. D. Ye 02153* (IBSC).

Guangdong, Ruyuan Xian, 27, Jun 1963, *X. P. Gao 50850* (IBSC), 6 Oct 1963, *X. P. Gao 53336* (KUN), 21 Nov 1957, *C. Wang 44200* (IBSC, KUN).

Guizhou, Guanling (Kwanlin) Xian, Chontan, 17 Nov 1935, *S. W. Teng 1606* (IBSC); Langtai, 5 Nov 1930, *Y. Tsiang 9539* (PE); Weining Xian, 17 Oct 1930, *Y. Tsiang 9174* (A).

Hunan, Xinning Xian, 11 Oct 1962, *L. H. Liu 015103* (IBSC, KUN); Yuanling Xian, 8 Jun 1988, *N. A. Liu et al. 13* (A).

Jiangxi, without further data, 4138 (KUN), *6172* (KUN); Jingan Xian, "Mt. Hangaodsu," Aug 1921. *H. Handel-Mazzetti 491* (A); Jiujiang Xian, Jingang Shan, 20 Oct 1963, *J. S. Yüe 5011* (KUN, NAS); Yushan Xian, 7 Nov 1958, *M. X. Nie 6079* (IBSC, KUN).

Shaanxi, Nanzheng Xian, 10 Oct 1958, *P. Y. Li 463* (KUN).

Sichuan, 1885-88, *A. Henry 7529* (GH), *W. J. Zhen 10229* (KUN); Emei Xian, Mt. Emei, 3 Aug 1952, *W. P. Fang 31900* (PE), 26 Apr 1952, *W. P. Fang 30159* (IBSC), 21 Apr 1932, *T. T. Yü 479* (GH, PE), 21 Apr 1932, *T. T. Yü 481* (GH, PE), *31 Mar 1941, W. P. Fang 15992* (A), 10 May 1941, *W. P. Fang 16542* (A), 20 Apr 1942, *W. P. Fang 18410* (A), *J. H. Xion et al. 31900* (NAS), 14 April 1940, *S. L. Sun 1531* (KUN), 6 May 1940, *S. L. Sun 1859* (A), 3 Nov 1935, *W. K. Hu 8179* (A, IBSC), 21 Aug 1938, *C. Y. Chiao & C. S. Fan 814* (A), 1 May 1940, *H. C. Chow 11594* (A), 19 May 1939, *H. C. Chow 9833* (A), Oct 1937, *Y. S. Liu 1455* (A), Mar 1940, *T. C. Lee 4463* (KUN), 8 May 1957, *G. H. Yang 54423* (KUN), Apr 1939, *Z. S. Zheng 524* (KUN); Guan Xian, 3 May 1930, *F. T. Wang 20729* (KUN), 4 April 1938, *C. S. Fan & Class 137* (A); Hongxi Xian, 18 Jul 1959, Exped. Econ. Pl. Sichuan 1333 (KUN); Huidong Xian, 24 Jun 1959, *S. G. Wu 1552* (KUN), 16 Jun 1957, *S. G. Wu 1045* (KUN).

Yunnan, *Z. X. Zhao 1745* (KUN); between Baoshan and Wayao, 2 Jan 1959, *J. Chen 927* (KUN); La-kou, *E. E. Maire 225* (A), *E. E. Maire 304* (A); Mongdui, 14 Feb 1959, *T. P. Zhu 0644* (KUN); Wayao, *X. Zhou 228E* (KUN); Chuxiong Xian, Sayingpan, *H. F. Handel-Mazzetti 607* (A), 14 Mar 1914, *C. Schneider 396* (A); Dali Xian, 30 Nov 1946, *T. N. Liou 23113* (KUN, PE), 19 Apr 1887, *J. M. Delavay 2607* (A), Jun 1941, *H. C. Wang 822* (KUN, PE), 1 Sep 1963, *Jinshajiang Exped. 63-6707* (KUN); Fumin Xian, 21 May 1964, *B. Y. Qiu 58940* (KUN); Funing Xian, 4 Apr 1940, *C. W. Wang 88218* (KUN, PE), 25 Apr 1940, *C. W. Wang 88836* (KUN); Gongshan Drung-Nu Autonomous Xian, 8 Nov 1959, *K. M. Feng 24441* (KUN), 14 May 1960, *S. G. Wu 8721* (KUN); Guangnan Xian, 6 Mar 1946, *C. W. Wang 87535* (KUN); Lunan Xian, *A. Henry 9959A* (A); Yunnan, Luquan Xian, *Y. B. Chang 480* (IBSC, KUN, PE), 15 May 1952, *P. Y. Mao 772* (KUN), 14 Feb 1957, *W. Q. Yi 0016* (KUN), 18 Jun 1965, *Exped. Woody Oil-contain. Pl. 65-0042* (KUN); Shizong Xian, 26 Apr 1977, *Shizong Brigade 204* (KUN); Wenshan Xian, 12 Aug 1947, *K. M. Feng 11135* (KUN), 24 Apr 1962, *K. M. Feng 22038* (KUN), 22 Jan 1933, *H. T. Tsai 51605* (A, IBSC, KUN), 13 Jan 1933, *H. T. Tsai 51514* (A, IBSC, KUN, PE), 25 Sep 1958, *H. T. Tsai 58-8115* (KUN), 21 Aug 1961, *S. G. Wu 61-3810* (KUN); Yangbi Xian, 11 Apr 1942, *H. C. Wang 1876* (IBSC), 10

Apr 1942, *H. C. Wang 1876E* (PE); SW China Exped., *Y. Tsiang 13152* (KUN).

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板凳果屬(*Pachysandra*，黃楊科)的重新核定

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本文對板凳果屬(*Pachysandra*)具腋生花序的類群進行了統計分析。結果表明，以前作者用于劃分種和種下等級的差異多呈連續變異。根據我們的分析結果，該屬具腋生花序的類群實爲由兩個亞種組成的一個種：*Pachysandra axillaris* Franchet., 爲中國所特有，由亞種ssp. *axillaris*和亞種ssp. *stylosa* (Dunn) Boufford & Q. Y. Xiang, Stat. nov. 組成。加上美國特有的，具基生花序的種 *P. procumbens* Michaux 和分布于中國和日本的，具頂生花序的種 *P. terminalis* Sieb. & Zucc.,全屬共由三個種組成。本文還第一次報導了 *P. procumbens* 的染色體數目爲 $2n=24$；同時重新確定了 *P. axillaris* ssp. *axillaris* 和 *P. terminalis* 的染色體數目分別爲 $2n=24$ 和 $2n=48$。