**PACHYPHRAGMA AND GAGRIA (BRASSICACEAE) REVISITED: MOLECULAR DATA INDICATE CLOSE RELATIONSHIP TO THLASPI S.STR.**

Klaus Mummenhoff¹, Ulrike Coja & Holger Brüggemann

Department of Botany, University of Osnabrück, Barbarastrasse 11, D-49069 Osnabrück, Germany; fax +49 541 969 3171; ¹ Corresponding author, e-mail mummenhoff@biologie.uni-osnabrueck.de

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**Abstract:** The systematic position of *Pachyphragma macrophyllum* (Brassicaceae) is unsettled. This species was either treated as a monotypic section of *Thlaspi* s.l. or was treated as a distinct genus. *Gagria lobata* apparently closely related to *Pachyphragma*, was also given generic rank. To unravel the phylogenetic relationships of *Pachyphragma* and *Gagria*, ITS sequence studies were conducted using as a reference representatives of the main lineages of *Thlaspi* s.l. The molecular data indicate that *Gagria lobata* and *Pachyphragma macrophyllum* are closely related to members of *Thlaspi* s.str., an assemblage of species well separated from the other *Thlaspi* s.l. lineages.

**INTRODUCTION**

The genus *Thlaspi* L. s.l. is the largest genus of subtribe *Thlaspidinae* (tribe Lepidieae) and consists of approximately 75 species (AL-SHEHBAZ 1986). Several controversial classification systems for sections primarily based on fruit characters have been proposed (reviewed in MUMMENHOFF et al. 1997b, Tab. 1). MEYER (1973, 1979) proposed a radical revision of *Thlaspi* s.l. inferred from the analysis of seed coat anatomy. Only six species were retained in *Thlaspi* s.str. whereas the bulk of *Thlaspi* taxa formerly placed within five sections of a single broadly defined genus *Thlaspi* s.l. (SCHULZ 1936) were distributed among eleven segregate genera (see below and MUMMENHOFF et al. 1997b, Tab. 1). Meyer’s treatment contrasts with previous classification schemes (MUMMENHOFF et al. 1997a, b) and has not received support by recent authors (AL-SHEHBAZ 1986, GREUTER et al. 1986). A series of molecular analyses have been conducted in our lab using different markers to test Meyer’s concept: Isoelectric focusing analysis of RUBISCO subunits (MUMMENHOFF & ZUNK 1991, KOCH et al. 1993), cpDNA restriction site analysis (MUMMENHOFF & KOCH 1994, ZUNK et al. 1996, 1999), and sequence analysis of nuclear ribosomal ITS regions (MUMMENHOFF et al. 1997a,b). Lineages detected in these studies correspond to Meyer’s segregates *Thlaspi* s.str., *Thlaspiceras* F.K. MEY., *Noccaea MOENCH* with *Raparia* F.K. MEY. included, *Microthlaspi* F.K. MEY. pro parte, *Vania* F.K. MEY. , and *Neurotropis* (DC.) F.K. MEY. Our molecular analyses also indicate convergence in fruit characters, primarily used for the traditional classification schemes (MUMMENHOFF et al. 1997b). Furthermore, *Thlaspi* s.l. as currently described proved to be paraphyletic because one of its major lineages, i.e. *Thlaspi* s.str. appears to be more closely related to other genera, e.g. *Peltaria* JACQ., *Alliaria SCOP.*, respectively (which were even...
attributed to different tribes in the sense of HAVEK (1911), SCHULZ (1936), JANCHEN (1942)) than to the remaining lineages of Thlaspi s.l. (ZUNK 1994, ZUNK et al. 1996, 1999).

In the earlier classification systems of the genus Thlaspi s.l., Pachyphragma macrophyllum (HOFFM.) BUSH was treated as monotypic section Pachyphragma DC. (CANDOLLE 1821, PRANTL 1891). Later on SCHULZ (1936), BUSH (1939), and HEDGE (1965) treated Pachyphragma as a distinct genus. Apparently, MEYER (1979: 132) agrees with this concept, whereas in the latest edition of Flora europaea, AKEROYD (1993) retained Pachyphragma in Thlaspi, based on a number of shared characters (e.g. inflorescence ebracteate, sepals not saccate, petals clawed, stamens without appendages, fruit an angustiseptate silicula, stigma capitate, radicle accumbent). Chromosome counts of 2n=14 in Pachyphragma (DAVIE & AKEROYD 1983) provide further evidence for a close relationship with Thlaspi s.l., which contains diploids and polyploids based on x=7. However, DAVIE & AKEROYD (1983) did not come to a final decision as to whether Pachyphragma should be included within Thlaspi s.l. The uncertainty in classifying Pachyphragma macrophyllum is also expressed by the fact that AKEROYD (1993: 384) admittedly subsumed this species under Thlaspi s.l., but in a note preceding the species key it was submitted as an unnumbered species T. macrophyllum.

Pachyphragma differs from Thlaspi s.l. by its rhizomatous habit and in fruit morphology, i.e. the septum of the fruit is relatively thick (DAVIE & AKEROYD 1983). Gagria lobata M. KRÁL, a species closely related to Pachyphragma, has recently been described by KRÁL (1981) from the Caucasus. Gagria and Pachyphragma are both characterized by branched rhizomes, simple racemes, six nectaries alternating with six stamens, four-seeded ovules, and a sessile stigma. Following KRÁL (1981) Gagria lobata differs from Pachyphragma in being in all parts smaller and completely glabrous, and in having lobed and crispate basal leaves.

In the present ITS study we have included Gagria lobata and Pachyphragma macrophyllum along with representatives of Thlaspi s.l. lineages, detected in our recent molecular analyses and corresponding to Meyer’s segregates Thlaspi s.str., Neurotropis, Vania, Microthlaspi, Noccaea, Raparia, and Thlaspiceras. The objectives of the current study are (i) to test if Gagria lobata and Pachyphragma macrophyllum are distinct taxa, and (ii) to elucidate the phylogenetic relationships of these two taxa to their supposedly closest relatives, i.e. Thlaspi s.l.

MATERIAL AND METHODS

Plant material

ITS sequences from 20 accessions representing Thlaspi s.l, and related taxa (Pachyphragma, Gagria, Alliaria, Peltaria) were examined. Altogether seven sequences are newly reported, i.e. Gagria, Pachyphragma (2), Alliaria, Peltaria, and outgroups (Tab. 1), and the remaining sequences have been derived from the previous data set of MUMMENHOFF et al. (1997b). Collection data and sources of plant material are given in Tab. 1. Voucher specimens are either deposited in the herbarium of the University of Osnabrück (OSBU) or they are kept at those herbaria / institutions which provided the specimens (see Tab. 1). Species analyzed in this study represent a broad spectrum of the variation in Thlaspi s.l., including representatives of all sections in the sense of SCHULZ (1936) and corresponding to seven out of the 12 segregates defined by MEYER (1973, 1979) (Tab. 1). Systematic evaluation of the classification within Thlaspi s.l. is outside the scope of the present study, but is presented in