

DIE NATÜRLICHEN
PFLANZENFAMILIEN

BAND 17 a IV



DUNCKER & HUMBLLOT / BERLIN

DIE NATÜRLICHEN PFANZENFAMILIEN

Band 17 a IV

DIE NATÜRLICHEN PFLANZENFAMILIEN

NEBST IHREN GATTUNGEN UND WICHTIGSTEN ARTEN,
INSBESONDERE DEN NUTZPFLANZEN

UNTER MITWIRKUNG ZAHLREICHER HERVORRAGENDER FACHGELEHRTER
BEGRÜNDET VON

A. ENGLER UND K. PRANTL

ZWEITE STARK VERMEHRTE UND VERBESSERTE AUFLAGE

HERAUSGEGEBEN VON

A. ENGLER (†), H. HARMS (†), J. MATTFELD (†),
E. WERDERMANN (†), TH. ECKARDT (†), H. MELCHIOR (†)

FORTGEFÜHRT VON

P. HIEPKO

BAND 17 a IV

ANGIOSPERMAE: Ordnung Ranunculales
Fam. Ranunculaceae



DUNCKER & HUMBLLOT / BERLIN

Die Deutschen Bibliothek – CIP-Einheitsaufnahme

Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigsten Arten, insbesondere den Nutzpflanzen / unter Mitw. zahlr. hervorragender Fachgelehrter begr. von A. Engler und K. Prantl. Hrsg. von A. Engler . . . Fortgef. von P. Hiepko. 2., stark verm. und verb. Aufl. – Berlin : Duncker und Humblot. Literaturangaben
NE: Engler, Adolf [Begr.]; Hiepko, Paul [Hrsg.]

Bd. 17 a. 4. Angiospermae. Ordnung Ranunculales. Fam. Ranunculaceae. – 1995
ISBN 3-428-07980-9

Alle Rechte, auch die des auszugsweisen Nachdrucks, der photomechanischen Wiedergabe und der Übersetzung für sämtliche Beiträge vorbehalten

© 1995 Duncker & Humblot GmbH, Berlin

Fremddatenübernahme: Klaus-Dieter Voigt, Berlin
Druck: Berliner Buchdruckerei Union GmbH, Berlin
Printed in Germany

ISBN 3-428-07980-9

Gedruckt auf alterungsbeständigem (säurefreiem) Papier
entsprechend ISO 9706 ∞

PREFACE

The second volume of “Die Natürlichen Pflanzenfamilien” is presented now in the new format: the book is written mainly in English and it contains an extensive General Part including contributions of different authors. The first volume of this kind on the family *Loganiaceae* was published almost 15 years ago.

It is 19 years now that Prof. Michio TAMURA having then some 20 years of experience due to meticulous studies on different aspects of the *Ranunculaceae*, was asked to write a monograph of the family. The completion of this treatment was very time-consuming, especially due to the complicated infrageneric taxonomy in the larger genera of *Ranunculaceae*. Since it took so much time to complete the manuscript it was not possible to use in the text the new standard of “Authors of Plant Names” by R. K. BRUMMITT & C. E. POWELL (1992). In the Index of Plant Names – prepared by the editor as well as the notes on etymology of the generic names – this standard was followed although the citation of authors is therefore often different from that used in the text of the Systematic Part (in the General Part authors of plant names are not cited).

As editor of this volume I would like to thank all authors who made the publication of this book possible; special thanks are due to the main author, Prof. Michio TAMURA, and to the artist Masayoshi UMEBAYASHI for his excellent illustrations. I am particularly grateful to Dr. M. I. HAKKI, who was most helpful in revising the manuscripts.

Finally, I wish to thank the Verlag Duncker & Humblot for the patience in dealing with all problems and the careful and fine production of the volume.

Berlin, March 1995

P. HIEPKO

AUTHORS

Robert HEGNAUER, Cobetstraat 49, 2313 KA Leiden, the Netherlands. Formerly: Laboratorium voor Experimentele Plantensystematiek, University of Leiden.

Joan W. NOWICKE, Botany Department, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Olle PELLMYR, Department of Biology, Vanderbilt University, Nashville, Tennessee 37235, U.S.A.

John J. SKVARLA, Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma 73019, U.S.A.

Michio TAMURA, Faculty of Biotechnology Oriented Science and Technology, Kinki University, Nishimitani, Utita, Nagagun Wakayama 649 - 64, Japan.

Hiroshi TOBE, Department of Biology, College of Liberal Arts and Sciences, Kyoto University, Kyoto 606, Japan.

ILLUSTRATIONS

(all originals if not otherwise stated)

Masayoshi UMEBAYASHI, Department of Biology, Faculty of Science, Kanazawa University, Kanazawa 920 - 11, Japan.

CONTENTS

Introduction (by M. TAMURA)	XI
I. General Part (1. - 6. by M. TAMURA)	
1. History of the family	3
2. Habit and outer morphology of the vegetative organs	6
2.1. Aerial shoot	6
2.2. Geophilous organs	7
2.3. Phyllotaxy	11
2.4. Leaf	14
2.5. Ontogenetic development of leaves	21
3. Anatomy of the vegetative organs	26
3.1. General anatomical features	26
3.2. Anatomy of the stem	27
3.3. Anatomy of the root	33
3.4. Petiole anatomy	36
4. Reproductive structures	41
4.1. Inflorescence	41
4.2. Receptacle	47
4.3. General composition of the flower	49
4.4. Calyx	52
4.5. Corolla	53
4.6. Androecium	61
4.7. Gynoecium	61
4.8. Fruit	66
4.9. Germination	69
5. Karyology	77
5.1. Subdivision of the family by the chromosome type	77
5.2. Chromosome number	83
5.3. Karyotype	85
6. Geographical distribution	89
6.1. Geographical characteristics of the family	89
6.2. Distribution in the northern extratropical zone	92
6.3. Distribution in tropical and southern extratropical zones	94
References to chapters 1 - 6	97
7. Embryology (by H. TOBE)	106
7.1. Introduction	106
7.2. Anther-wall formation, microsporogenesis and microgametogenesis	106
7.3. Development of integuments and ovular orientation	108
7.4. Obturator	110
7.5. Development of nucellus and megagametophyte	110
7.6. Antipodal cells	112

7.7. Fertilization, and development of embryo and endosperm	113
7.8. Development of seed and seed coat	115
7.9. Ultrastructure	116
7.10. Discussion	116
7.11. Appendix: Genera investigated and selected references	121
7.12. References	121
8. Pollen morphology (by JOAN W. NOWICKE & J. J. SKVARLA)	129
8.1. Introduction and pollen literature review	129
8.2. Descriptions of pollen in the tribes	138
8.3. Discussion	156
8.4. References	157
9. Pollination biology (by O. PELLMYR)	160
9.1. Introduction	160
9.2. Pollinators rewards	162
9.3. Pollinator attractants	164
9.4. Review of case histories by genus	165
9.5. References	179
10. Vergleichende Phytochemie und Chemotaxonomie (von R. HEGNAUER)	185
10.1. Alkaloide	185
10.2. Ranunculin und verwandte Glucoside	190
10.3. Triterpene und Triterpenglykoside (Saponine)	193
10.4. Verschiedene Steroide	195
10.5. Zimtsäuren und flavonoide Verbindungen	195
10.6. Rein acetogene Phenole	198
10.7. Cyanhydrine, Cyanide, Nitroverbindungen und Amide	198
10.8. Organische Säuren	201
10.9. Reservestoffe	202
10.10. Chemotaxonomie	203
10.11. Literatur	206
11. Nutzpflanzen (von R. HEGNAUER)	211
11.1. Zierpflanzen	211
11.2. Giftpflanzen	211
11.3. Arzneipflanzen	212
11.4. Nahrungspflanzen	214
11.5. Farbstoffpflanzen	215
11.6. Literatur	215
II. Systematic part (by M. TAMURA)	
<i>Ranunculaceae</i>	223
System of the <i>Ranunculaceae</i>	225
Key to the genera	228
Subfam. I. Helleboroideae	231
Trib. 1. <i>Helleboreae</i>	232
Subtrib. 1a. <i>Calthinae</i>	232
1. <i>Caltha</i>	233
2. <i>Calathodes</i>	236
3. <i>Trollius</i>	238
4. <i>Megaleranthis</i>	244
Subtrib. 1b. <i>Beesia</i>	246
5. <i>Beesia</i>	246

Subtrib. 1c. <i>Helleborinae</i>	248
6. <i>Helleborus</i>	248
7. <i>Eranthis</i>	253
Trib. 2. <i>Cimicifugeae</i>	256
8. <i>Anemonopsis</i>	257
9. <i>Souliea</i>	257
10. <i>Cimicifuga</i>	259
11. <i>Actaea</i>	264
Trib. 3. <i>Nigelleae</i>	266
12. <i>Komaroffia</i>	267
13. <i>Nigella</i>	267
14. <i>Garidella</i>	272
Trib. 4. <i>Delphinieae</i>	272
15. <i>Aconitum</i>	274
16. <i>Delphinium</i>	291
17. <i>Consolida</i>	307
Subfam. II. <i>Ranunculoideae</i>	312
Trib. 5. <i>Adonideae</i>	314
18. <i>Callianthemum</i>	314
19. <i>Adonis</i>	316
Trib. 6. <i>Anemoneae</i>	320
Subtrib. 6a. <i>Kingdoniinae</i>	320
20. <i>Kingdonia</i>	321
Subtrib. 6b. <i>Anemoninae</i>	323
21. <i>Anemone</i>	324
22. <i>Hepatica</i>	349
23. <i>Metanemone</i>	351
24. <i>Barneoudia</i>	351
25. <i>Oreithales</i>	352
26. <i>Knowltonia</i>	354
27. <i>Pulsatilla</i>	356
Subtrib. 6c. <i>Clematidinae</i>	365
28. <i>Archiclematis</i>	366
29. <i>Clematis</i>	368
30. <i>Naravelia</i>	387
Trib. 7. <i>Ranunculeae</i>	389
Subtrib. 7a. <i>Trautvetteriinae</i>	390
31. <i>Trautvetteria</i>	390
Subtrib. 7b. <i>Myosurinae</i>	391
32. <i>Myosurus</i>	393
Subtrib. 7c. <i>Ranunculinae</i>	395
33. <i>Kumlienina</i>	397
34. <i>Arcteranthis</i>	398
35. <i>Halerpestes</i>	400
36. <i>Oxygraphis</i>	402
37. <i>Peltocalathos</i>	403
38. <i>Callianthemoides</i>	405
39. <i>Cyrtorhyncha</i>	405
40. <i>Paroxygraphis</i>	408
41. <i>Hamadryas</i>	410
42. <i>Aphanostemma</i>	410
43. <i>Ranunculus</i>	412

44. <i>Ceratocephala</i>	435
45. <i>Krapfia</i>	436
46. <i>Laccopetalum</i>	439
Subfam. III. Isopyroideae	441
Trib. 8. <i>Coptideae</i>	442
Subtrib. 8a. <i>Asteropyrinae</i>	443
47. <i>Asteropyrum</i>	443
Subtrib. 8b. <i>Coptidinae</i>	444
48. <i>Coptis</i>	444
49. <i>Xanthorhiza</i>	449
Trib. 9. <i>Isopyreae</i>	451
Subtrib. 9a. <i>Isopyrinae</i>	452
50. <i>Enemion</i>	452
51. <i>Isopyrum</i>	454
52. <i>Leptopyrum</i>	459
53. <i>Paraquilegia</i>	459
Subtrib. 9b. <i>Aquilegiinae</i>	460
54. <i>Semiaquilegia</i>	462
55. <i>Urophysa</i>	464
56. <i>Aquilegia</i>	464
Subtrib. 9c. <i>Dichocarpinae</i>	466
57. <i>Dichocarpum</i>	468
Subfam. IV. Thalicthroideae	473
Trib. 10. <i>Thalictreae</i>	473
58. <i>Thalictrum</i>	474
Subfam. V. Hydrastidoideae	495
Trib. 11. <i>Hydrastideae</i>	495
59. <i>Hydrastis</i>	496
References	498
Index of plant names	520
Index of plant constituents	551

INTRODUCTION

By M. TAMURA

The *Ranunculaceae* is a moderately large family with 59 genera and ca. 2500 species. Many species have beautiful flowers or substances with strong physiological activity. They are used as ornamental or medicinal plants. This family shows great diversity in both vegetative and reproductive structures as well as in ecology. It retains many primitive characters and is regarded as one of the most primitive angiospermous families, but on the other hand it often presents quite specialized or advanced features. Therefore the family has attracted attention of many botanists from various points of view, and its members have been studied not only taxonomically, but also morphologically, anatomically, embryologically, palynologically, cytologically, phytochemically, serologically, and so on. The *Ranunculaceae* are indeed an intensively studied family.

I have been studying the *Ranunculaceae* taxonomically for more than 40 years. When I started the study of the family in 1949, Prof. S. KITAMURA suggested to me that at the beginning I should read the treatment on the *Ranunculaceae* in "Die natürlichen Pflanzenfamilien". In 1975 at the XII International Botanical Congress in Leningrad (now St. Petersburg) I was asked to write the treatment of *Ranunculaceae* for the second edition of this famous work. Soon after the Congress, Prof. TH. ECKARDT, the former editor of the publication, passed away. Since then more than 19 years elapsed too quickly. Still I don't feel that my work has been completed. New papers, some of which are quite important, appear one after another. I considered only a few papers published very recently, because publication of this book is already overdue.

In the history of the taxonomic studies of the *Ranunculaceae*, there were three monumental works. The first is that of A. P. DE CANDOLLE. In the first volume of his "Systema Naturale" (1817) the family has been monographed at the species level for the first time. His work was excellent and gave a sound base to the taxonomy of the family and influenced the subsequent work for a long time. The second monograph at the generic level is that of K. PRANTL (1888) which appeared in "Die natürlichen Pflanzenfamilien". This author used anatomical and embryological characters, in addition to traditional morphological ones for the classification of the family, and tried to make a phylogenetic system. The third work is of O. F. I. LANGELET (1932) based on caryology. He noticed the importance of karyological features in the taxonomy of the *Ranunculaceae* and defined the phyletic groups mainly by such characters. His work is one of the most successful examples of cytotaxonomy established in those days. My classification presented here is an extension of the work of these three. Although my work is far from being com-

plete, I believe that it is still the most comprehensive and the most detailed one until now.

Throughout my studies of the *Ranunculaceae* I have felt the deficiency of the knowledge on the species of the southern hemisphere. The classifications of the family presented previously were mostly based on the northern species. The present classification is also insufficient in this point. In future more intensive studies on the southern species will be necessary.

Recently molecular phylogenetic studies have become more popular and common, and some reports on the *Ranunculaceae* have already been published. Their results are not included in this book, because the molecular methods cannot be considered to be fully established as reliable methods for the taxonomy at least in the *Ranunculaceae*. In future these methods will be important for a phylogenetic review of the family.

During preparation of the manuscript I have been helped by many botanists. Especially Prof. Dr. P. HIEPKO has given all facilities and advice for my studies; without his help and encouragement I would not have been able to finish this work. Dr. M. HAKKI has also given me valuable comments on the manuscript. I would like to express my cordial thanks to them. I also would like to thank the directors, curators and other staff members of the following herbaria for the research facilities: A, ABD, B, BK, BKF, BM, BO, BRI, CANB, CDBI, E, G, HBG, K, KANA, KUN, KYO, L, LAE, LE, MAK, MO, NOU, NSW, NY, P, PDA, PE, RYU, SAN, SAPA, SING, SUVA, TAI, TI, TNS, UC, W, WTU, WU, etc.

I. GENERAL PART

1. HISTORY OF THE FAMILY

By M. TAMURA

All ranunculaceous genera, except *Hydrastis*, were grouped into *Multisiliquae* by LINNAEUS (1764), though this group included some improper genera, such as *Dic-tamnus*, *Ruta* and *Peganum*. ADANSON (1763) also recognized that ranunculaceous genera formed a natural family, *Ranunculi*. But *Nigella* and *Garidella* were excluded from this family, and on the other hand, the improper genera, *Damasonium* (= *Limnocharis* L.), *Sagitta* (= *Sagittaria* L.) and *Alisma* were included in it. JUSSIEU (1789) greatly improved the delimitation of the family by including all ranunculaceous genera known at that time. The only improper genus included by him was *Podophyllum*, and he adopted the name *Ranunculaceae* for the group. DE CANDOLLE (1817) excluded *Podophyllum* and the *Ranunculaceae* defined by him had been believed for a long time to be one of the typical natural families, mainly owing to the similarity in the floral constitution of all members.

Ranunculaceae were first divided by DE CANDOLLE (1817) into 5 tribes, *Clematideae*, *Anemoneae*, *Ranunculeae*, *Helleboreae* and trib. *Paeoniaceae* including *Actaea*, *Xanthorhiza* and *Paeonia*. HOOKER & THOMSON (1855) improved this system in delimiting the *Paeoniaceae* as a monotypic tribe of *Paeonia*, and BENTHAM (1862) followed their treatment.

PRANTL (1887, 1888) recognized the peculiarities of *Paeonia*, *Glaucidium* and *Hydrastis* and classified them in the tribe *Paeoniaceae*. He characterized his *Paeoniaceae* by the feature that the outer integument is longer than the inner one, and considered that the *Paeoniaceae* were the direct offspring of the ancestor from which *Berberidaceae* and *Ranunculaceae* were derived and argued that the *Paeoniaceae* might be placed at the beginning of the *Berberidaceae*. Since then, the systematic positions of these genera have been often discussed. Also heterogeneity of the *Ranunculaceae* became a problem with the introduction of new characters from different fields of biology, e.g. morphology, cytology, embryology, phytochemistry and serology.

Among the genera of the classical *Ranunculaceae* defined by PRANTL (1887, 1888), *Paeonia* and *Glaucidium* were excluded from the family, and separate families were created *Paeoniaceae* (RUDOLPHI 1830, WORSDELL 1908a, 1908b, HEINTZE 1927, KUMAZAWA 1935, 1938b, EAMES 1961, TAMURA 1963a, CRONQUIST 1981) and *Glaucidiaceae* (TAMURA 1963a, 1972), respectively. *Circaeaster* had often been classified in the *Ranunculaceae*, but now the *Circaeasteraceae* (HUTCHINSON 1926, TAMURA 1963a), is generally accepted as a monotypic family.

Hydrastis has sometimes been considered to be the representative of a distinct family, *Hydrastidaceae* (LEMESLE 1948, 1955, EAMES 1961, TOBE & KEATING 1985).