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HISTORY OF THE CLASSIFICATION OF THE GENUS *CAREX*

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Summary

The history of the classification of the genus *Carex* from 370 B.C.–1955 A.D., including a synopsis of the etymology of the generic name *Carex*, is reviewed. The refinement of descriptive terminology during the Middle Ages, caricology during the Renaissance period and the concepts of classification systems for *Carex* are also discussed.

Introduction

> Crescit profecto apud me certe tractatu ipso admiratio antiquitatis, quantoque maior copia herbarum dicenda restat, tanto magis adorare priscorum in inveniendo curam, in tradendo benignitatem subit.[2]
>
> [*Pliny the Elder. Naturalis Historia XXVII.* I. 1.]

Caricology (the study of the genus *Carex*) has a long history and it would be erroneous to assume that the herb gatherers, or Rhizotomoi, of antiquity did not possess a wide acquaintance of these plants. Indeed, the scholars of agriculturally oriented cultures of ancient civilizations of Egypt, Assyria, and China undoubtedly possessed a wide knowledge of sedges with reputed medicinal and forage value. The information, however, was fragmentary and of an inaccessible form, for little was preserved on parchment and most was passed on by the spoken word as folklore attended by the usual superstition. Nevertheless, it is with the civilization of ancient Greece, and later Rome, that we will begin our history of caricology, since among these peoples numerous written records have survived. From thence one can trace the origin and development of our modern classification of the genus *Carex*.

370 B.C.–1500 A.D.

Theophrastus of Eresus (370–c285 B.C.) was a pupil of Plato and Aristotle. He inherited the botanic garden at Athens which Aristotle had founded. It was here that he gathered together much of the information from the Rhizotomoi and from observations on plants which he had cultivated in the botanic garden. In his *Enquiry Into Plants*, comprising nine books, he engaged in a classification and description of plants and defined the basic concepts of plant morphology which stood essentially

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[2] "The mere treatment of this subject undoubtedly increases the admiration that I at least have for the men of old; the greater the number of plants waiting to be described, the more one is led to revere the careful research of the ancients and their kindness in passing on the results." (Translation by H. Rackman and W. H. S. Jones.)

unchanged and scarcely enlarged for nineteen centuries until the development of lenses and microscopes revealed the function and structure of the flower.

Theophrastus described about 500 species of plants which he classified into four groups: trees, shrubs, undershrubs and herbs. He called *Carex* "boutonou" and provided descriptions of the morphology and growth habits of the Greater Pond Sedge (*Carex riparia* Curtis).

It is claimed by some that the earliest encounter of *Carex* by name is in a poem by the Roman poet Catullus (c84–c54 B.C.). In this poem *Carex*, along with *Juncus*, is mentioned as being used to thatch a poor cottage: (Poem 19.2)

> Hunc ego juvenes locum, villulanque palustrem,
> Tectam vimine *junceo, caricique* maniplis,
> Quercus arida, rustica conformata securi,
> Nutrivi.

But this poem was erroneously attributed to Catullus and was written at a much later date in the fourth century A.D. by an unknown author; that is why it is not included in modern translations of Catullus' works (for example, Zukofsky, 1969).

Virgil published his *Georgics* in 30 B.C. In *Georgics III* he mentions the name *Carex* in its ablative singular form:

> ". . . et inter dura iacet pernox instrato saxa cubili frondibus hirsutus et *carice* pastus acuta." [. . . and nightlong makes his bed on bare rough stones, with prickly leaf and pointed sedge for food.] [231–232].

In this instance Virgil was emphasizing the worst kind of fodder. He mentions *Carex* only once more when he accuses Tityrus of hiding behind the sedge thickets: "Tu post *carecta* latebas." [*Eclogue III.* 20]. The word *Carice*, as used by Virgil, is one of the earliest written examples of descriptive terminology. It is a derivative of ancient Greek words *charaktos*, meaning notched or toothed, *karcharos*, meaning jagged from sharp teeth along the edges and midveins of the leaves, and *keirin*, meaning to cut. The origin of the word *sedge* also has its roots in Virgil, i.e., *sege*; although in his sense it meant a sharp weapon (Georgics II. 142, Aeneid VII. 526 and XII. 664). The analogy between these Greek words, especially *karcharos* and *sege* is quite close and it is precisely from their meanings that the colloquial German words sege (a saw) and segge (a cutter) were applied to *Carex* in the 16th century. For example, Turner (1551) writes: "Carex is called in English a sege, it groweth in fennes and watery places, it is called in Northumberland sheargrasse because it cutteth mennes handes that touch it."

Columella (c60 A.D.), a Spaniard from Gadez, refers to the culinary aspects of *Carex* along with ferns, and also suggest the best time for harvesting it:

> ". . . filix quoque aut *Carex* ubicunque nascitur, Augusto mense recte extirpatur, melius tamen circa idus Julias ante Caniculae exortum." [It is also right to uproot ferns and sedges, wherever they grow, during the monfh of August, it had better, however, be done about mid-July before the rising dogstar.] [*De Re Rustica XI. II.* 62].

Many commentators imply that, to the ancients, particularly Virgil, *Carecta* and *Carice* meant a species of *Juncus*. But Servius (c300–400 A.D.) describes Virgil's *Carex acuta* as a "very rough grass": "Carica acuta, herba durissima, asparago simili." [Servius. 84a]. This is certainly an apt, if crude, description of the genus *Carex*, particularly *Carex acuta* L., which is very common throughout Europe. Isidorus (560–636 A.D.), on the other hand, is a little more explicit about Virgil's *carice:*

"Carex herba acuta and durissima sparto similis. De qua Virgilius . . . Spartus frutex vir-

gosus sine foliis ab asperitate vocatus volumina enim funium que ex eo fiunt aspera sunt." [*Etymologarium XVII.* Ch. 9].

Thus, according to Isidorus, Virgil's *Carex acuta* is similar in appearance to *Spartina junceum*, the Spanish broom. Martyn (1811) citing Anguillara, says that in the vicinity of Padua and Vincensa they refer to a rush by the name of *Careze* which appears to be a modernization of the ancient word *Carex*. "*Carex*. Ancora hoggi sul Padouano, and Vicentino que sta pianta si dimanda *Careze* è specie di Giunco, che nasce in luoghi palustri." [*Anguillara.* 210]. Martyn refers to this as a rush but his interpretation is somewhat ambiguous because Anguillara's description could easily apply to sedges (*Carex*) rather than rushes (*Juncus*). If Virgil meant a rush rather than a sedge, he would have said so by using the word *iunco*. Certainly, his contemporaries did, for example Ovid (43 B.C.–18 A.D.). Ovid twice distinguished the difference between *Juncus* and sedge-grass: "cum . . . iuncus gratamque paludibus ulvam . . ." [. . . with fine rushes and sedge-grass of the marsh] [*Metamorphosis VI.* 345] and ". . . ulvaeque leves iuncique palustres . . ." [. . . sedge-grass and rushes of the marsh . . .] [*Metamorphosis VIII.* 336]. The fact that Virgil also mentions *ulva* in two passages shows a preoccupation with something very different from *Juncus*: "Propter aquae rivum viridi procumbit in ulva." [Wearily sinks down on the green sedge beside a stream] [*Eclogues VIII.* 87] and ". . . interea pubi indomitae non gramina tantum nec vesca salicum frondes ulvamque palustrem." [. . .meanwhile feed not unbroken youth on grass alone nor meagre willow leaves and marshland sedges.] [*Georgics III.* 174–175].

The analogy that the ancients drew between the families Juncaceae and Cyperaceae seems to have been quite close but, nevertheless, distinct. Pliny (23–79 A.D.) described galingale (*Cyperus longus* L.) as a kind of rush with a triangular stem, white rhizomes, and a dark fleshy inflorescence: "Cyperos iuncus est, qualiter diximus, angulosus, iuxta terram candidus, cacumine niger pinguisque." [*Naturalis Historia XXI. LXX.* 117]. Apparently, Pliny recognized four groups of grass-like plants: iuncus (*Juncus*), cyperos (*Cyperus*), herbam (*Graminea*) and ulva (*Carex*). Referring to soft ties for vines, he defines three groups of plants: "Graecia vero universa iunco, cypero, ulva." [Throughout Greece they use *Juncus, Cyperus* and *Carex*.] [*Naturalis Historia XVII. XXXV.* 213–214].

A contemporary of Pliny who was frequently cited by Renaissance botanists was Dioscorides (c1–100). Dioscorides was a military physician under Nero. His *Materia Medica* was the main source of economic botany during the early Roman empire. Like Pliny his perspective of plants had a marked economic bias in which medicinal plants were given precedence. Nevertheless, his treatment of plant anatomy, along with Pliny's, forms the roots of our modern botanical terminology. Thus, when caricologists speak of culm, mucronate, tenuis, cespitose, scabrous, diffuse, and costa, for example, he uses words of early herbalist jargon which Dioscorides and Pliny had inherited from ancient Rome and Greece and which have been passed on to us with little or no change in original meaning.

Until the Middle Ages, following the decline of the Greek and Roman domination, insignificant progress was made apart from that of Isidorus, previously mentioned, and Albert of Bollstadt (1193–1280), more commonly styled Albertus Magnus, Bishop of Regensburg. The best known works of Isidorus was *Etymologiarum* in twenty books, an etymological glossary covering all branches of human knowledge. Here again we see Latin words common to caricologists such as arista, cespites, culmus and spica. Albertus Magnus was a prolific writer whose general philosophy was based on the teachings of Aristotle and whose botanical concepts were inherited from Theophrastus. For example, in his *De Vegetabilibus* his description of species was derived from Theophrastus through Palladius (c350) and other sources. He divided the plants into respective woody and herbaceous species and arranged them in alphabetical order. His concept of the plant world was permeated with the 'doctrine of signatures' in which he often conceived the plants as being zoomorphic and en-

deavoured to describe them by making false analogies drawn from the animal world. Albertus apparently recognized the transmutation of species by concluding that wheat became rye according to the nature of the soil. Obviously, he did not recognize the existence of sexual processes in plants, but concluded that male and female were combined in one plant.

1500–1800

At the close of the Middle Ages, the scholars of western Europe were reawakened by the rediscovery of classical civilizations and, as they absorbed the philosophies of ancient Greek and Roman thought, they tended to harmonize their own situation with it. Science, particularly botanical science, has as good a claim as the arts to regard the 16th century as the period of its own renaissance. Although the ancient writings of Greece and Rome were limited, their effect, nevertheless, stimulated and reformed the scientific investigation of the plant kingdom. This renewed vigour in botanical studies was greatly assisted by the young art of printing, in which woodcuts were employed with a remarkable degree of dexterity and fidelity to express scientific thought. Among those in the Renaissance period to apply Greek and Latin names to plants in their own region were the 'German fathers of botany' which included Tabermontanus (1625), Otho Brunfels (1530–36), Leonard Fuchs (1542), Tragus (1552), and Valerius Cordus (1561). With them, as with plants in general, began the scientific examination of *Carex*. Tragus, also known as Hieronymus Bock, applied polynomial Latin names to species of *Carex* under the names of *Graminis* . . . and *Calamagrostis* . . . . His contemporary, Turner (1551), as previously quoted, described *Carex* as a sedge and these he was careful to separate from the closely related genus *Cyperus* which he called 'Englyshe Galangale' (*Cyperus longus* L.). Later Lobelius (1576) described several *Carex* species under various Latin polynomials such as *Gramen cyperoides* . . . , *Gramen junceum* . . . , and *Juncus maritimus* . . . . Other notables during that era were Dodoens (1578), Joachim Camerarius (1588), Thalius (1588) and, finally, Gerard (1597). Because Gerard drew freely on the works of his contemporaries and earlier writers, his 'Herbal' (1597), especially his second edition (1633), was a true reflection of the art of botany in that period. Although no phylogenetic classification system was devised until much later, Gerard achieved a rudimentary classification by grouping plants in a more complex way than had his predecessors. Although he included most of the members of the Cyperaceae family under *Gramen*, this is not to say that he considered them as graminoids in the modern sense of *Gramineae*. He knew well enough to treat *Cyperus* in the classical sense as distinct from grasses and, although he included *Carex* in *Cyperus* . . . as well as *Gramen* . . . , nevertheless he described *Carex* as grass-like plants as distinct from grasses. In Gerard's *Herbal* binomial nomenclature was used extensively. But, he did not use binomials exclusively and it must be stressed that these were actually diagnostic binomials consisting of two terms only because no more were necessary. Among the *Carex* described and illustrated by Gerard are: *C. diandra* Schrank (*Gramen cyperoides parvum*), *C. flava* L. (*Gramen palustre echinatum*), *C. hirta* L. (*Gramen exile hirsutum*), *C. leporina* L. (*Gramen sylvaticum minus*), *C. nigra* (L.) Reichard (*Gramen cyperoides angustifolium majus*), *C. pallescens* L. (*Gramen cyperinum nemorosum*), *C. paniculata* L. (*Gramen palustris cyperoides*) and *C. rostrata* Stokes (*Gramen cyperoides*).

In Gerard's second edition (1633), considerably enlarged by Thomas Johnson, numerous references are made to Kaspar Bauhin's *Prodromus Theatri Botanici* (1620). Bauhin was a pupil of Fuchs and, like the 'German fathers of botany', his plants were described and discussed just as they were found with only occasional attempts to group them in a systematic order. In its day, Bauhin's *Phytopinax* (1596) was considered the best method for indexing plants, which included etymology of the plant name in Greek and Latin, its author, and synonymy of each plant name. In

Prodromus Theatri Botanici (1620) and *Pinax Theatri Botanici*, Ed. 1 (1623), Bauhin, like Gerard, also used binomials but these too are, strictly speaking, polynomials. There are two plants which he calls *Carex* by name, viz., *Carex minus* and *Carex tragi*. *Carex minus* was first described by Adamus Lonicerus in *Naturalis historia opis novum*, Vol. 2 (1551–55); and *Carex tragi* was described in *Historia Lugdunensis* which was begun by Dalechamps (1586) and completed posthumously by John Molineaus in 1587. In the second edition of *Prodromus Theatri Botanici* (1671), Bauhin considered *Carex minus* to be a synonym of *Gramen junceum spicatum seu triglochin*. Although this appears to be *Triglochin maritima* L., it is still not clear whether this was the species Dalechamps had in mind. He could have, perhaps, been referring to *Carex salina*. Dalechamps' *Carex tragi* is, indeed, a true *Carex* and was described by Bauhin as a synonym of *Gramen cyperoides latifolium spica rufa; five caule triangulo (Carex rostrata)*. Although Bauhin's treatment of *Carex* was much more extensive than Gerards', he was not quite so methodical in his classification or so clear-cut in distinguishing between grasses and grass-like plants, with the exception of the section *Gramen Cyperoides*. For instance, he includes *Scirpus*, *Carex* and *Juncus* in his groups *Gramen arundinaceum*, *Gramen nemorosum* and *Gramen echinatum*. Most are easily recognizable, particularly *C. vesicaria* L. (*Gramen cyperoides angustifolia spicis longis erectis*), *C. pseudo-cyperus* L. (*Gramen cyperoides spica pendula breviore*), *C. flava* (*Gramen palustre aculeatum germanicum vel minus*).

Besides the general pursuit of a classification of the vegetable kingdom, serious attention was given to a precise interpretation of botanical terminology. Thus, a very timely publication on botanical terminology was written by Joachim Jung, a German philosopher and mathematician whose *Isagogue Phytoscopia* was published posthumously in 1678 by one of his students Johannes Vagetius. Jung is considered to be the 'father of terminology'. His concepts were molded by Theophrastus and Albertus Magnus. Being a mathematician, imbued with Aristotelian philosophy, he introduced a precision of observation and logic which enabled him to define more accurate descriptions of plant morphology than his predecessors. Indeed, although Jung did not understand the precise functions of the *stamen* and *style*, it was he who defined them as they are understood today. Jung's work was particularly important to early caricologists because he clarified and enlarged upon the terminology of his predecessors. To historical botanists, he is the bridge between early writers, particularly Isidorus and Albertus Magnus, and his successors in the 18th century who are acknowledged as the forerunners of modern systematic botany.

Towards the close of the 17th century the monumental works of Morrison (1680), Plukenett (1691), Ray (1686–88 and 1704) and Tournefort (1684 and 1700) were published. Of these, Ray provides the most significant advance in the study of *Carex*. Although Ray maintained the traditional groupings of trees, shrubs and herbs, he classified these into monocotyledons and dicotyledons which he further subdivided on the basis of leaf and floral characteristics. In *Historia Plantarum*, V. 2, Book XXII, Ray groups 32 species of *Carex* under the section *'De gramine cyperoides and cypero'*. Thus, we see the first major attempt to isolate *Carex* from grasses even though, perhaps erroneously rather than purposefully, he included some *Carex* species in other sections of *'De Graminibus'*. Another significant feature of Ray's classification is the division of *Carex* into two groups, viz.: (1) Gramen cyperoides polystachyon. [With many spikes.], and (2) Gramen cyperoides cum spicis aut paniculis in summitate caulis. [Spikes paniculate at the summit of the culm.] In group 1 there are 15 species of *Carex* and in group 2 there are 17 species.

Tournefort's *Institutiones Rei Herbariae* (1684), followed by a Latin version in 1700, is significant in that the concept of genera was introduced. He included 698 genera, some 10,000 'types', and numerous varieties. Most of the *Carex* were treated under the genus *Cyperoides* (Class XV, Sect. V, Gen. 1, p. 529–530). Essentially, he treated each *Cyperoides* with descriptive polynomials in much the same way as did his predecessors. Bachman (1690) also adopted the generic principle and declared

that the binary nomenclatural system was the most suitable for the designation of plants. For some peculiar reason, he did not adopt the system exclusively and so, in many respects, his treatment is similar to that of Gerard. Bachman rejected the ancient division of plants into trees, shrubs, and herbs, deciding that no such distinction occurs in nature. He proposed, instead, an artificial classification based on the form of the corolla. Tournefort, conversely, strove to devise a classification based on a natural system, giving precedence to the entire structure of the flower and including vegetative parts where necessary. Despite this, and his immense influence in botany, Tournefort refused to accept the reality of sexuality in plants which had been so effectively demonstrated by his contemporary Rudolph Camerarius (1694).

The Renaissance influence culminated in the works of Barrelier (1714), Ruppius (1726), Vailliant (1727), Micheli (1729), Dillenio (1732), Haller (1742), and Gmelin (1747). By then the concept of genera became widely accepted and refined. Ruppius (1726) and Micheli (1729) both applied the ancient name *Carex* in the true sense of genus. But here they did not apply it in the broad sense of *Carex* in general, referring it mainly to distigmatic *Carex*. Haller (1742), on the other hand, applied a name of equal vintage, *Ulva*, to *Carex* in general but this was never widely accepted. Although *Ulva* is etymologically related to *Carex*, it was later adopted by Linnaeus for a generic name of algae.

The binomial system to designate genus and species in the modern sense was defined by Linnaeus in his *Fundamenta Botanica* (1736) and introduced in the first edition of his *Species Plantarum* (1753). The principle of his sexual system of classification gave caricologists the only manageable means for classifying the complex and numerous species of *Carex*. In the first edition of *Species Plantarum* (1753) he enumerated twenty-nine species of *Carex*, and in the second edition the number of *Carex* species was increased to thirty-seven. The *Carex* were divided into five sections, i.e.:

(1) Spicis unica simplici [Single-spiked]

(2) Spicis androgynis [Androgynous-spiked]

(3) Spicis sexu distinctis: femineis sessilibus [Spikes wholly pistillate or staminate: pistillate spikes sessile]

(4) spicis sexu distinctis: femineis pedunculatis [Spikes wholly pistillate or staminate: pistillate spikes peduncled]

(5) Spicis sexu distinctis: masculis pluribus [Spikes wholly pistillate or staminate: staminate spikes several]

In later systematic treatments, (1) would be equivalent to Monostachyae, (2) to Homostachyae and (3) to (5) to Heterostachyae. So Linnaeus, in his characteristic fashion, established the foundation of a modern systematic classification of *Carex*. The Linnaean era coincided with the golden age of botanical exploration in the New World and with it the introduction of many new plants from North America, many of which Linnaeus himself described from collections sent to him by his students, such as Peter Kalm (1753) and Daniel Solander who visited Newfoundland and Labrador with Joseph Banks in 1766. Kalm's collection formed a conspicuous part of the material that aided Linnaeus' understanding of American plants. Evidently, the first two American *Carex* to be described were *C. squarrosa* L. and *C. folliculata* L. (Linnaeus, 1753), both collected by Peter Kalm during his visit to North America in 1749. Solander was one of Linnaeus's star pupils, who at one time was considered to be his successor. Solander was given the task of enumerating the collections brought back from Newfoundland and Labrador, as well as those plants in the rich and prestigious herbaria that Banks acquired which included the valuable Gronovius herbarium. While many of these early specimens have been lost, there still remain 17 *Carex* species from the Newfoundland and Labrador collections in the British Museum (Lysaght, 1971).

Walter (1788) gave a short but imperfect description of 11 *Carex* from North Carolina and Lamarck (1789) enumerated 62 *Carex* which included five new species

from North America. Michaux (1803) travelled extensively throughout northeastern America and described 22 *Carex*, 17 of them considered to be new to North America.

1800–1955

By the turn of the 19th century, the systematic foundation for *Carex* was well established. Jussieu (1789) had designated the sedge family as Cyperaceae and the number of *Carex* species began to increase rapidly. Wahlenberg (1803) described 142 species. A year prior to this, Schkuhr published Part 1 of *Beschreibung der Riedgräser* (1801) which included 105 *Carex* but contained few of the North American species. This deficiency he later corrected in Volume IV of Willdenow's *Species Plantarum* (1805) which included 42 *Carex* sent to him by Dr. Muhlenberg of Pennsylvania. Part II of Schkuhr's *Beschreibung der Riedgräser* (1806) in which 220 species are described is one of the great botanical classics, highlighted by 93 beautiful colored plates of exceptional quality, even by today's standards. Agardh (1823) described 328 species, Sprengel (1826) 267, Kunth (1837) 440, Steudel (1840) 524, and Boott (1840–56) 550. Kunth, in a general classification, designated *Carex* as Tribe VI: Caricineae within the family Cyperaceae which was fully accepted. In their classification, Schweinitz and Torrey (1825) accepted Beauvois' segregation of *Carex* species into *Vignea* (distigmatic) and *Carex* (tristigmatic). Each subgenus was divided into (1) single spikes and (2) two or more spikes. Within each division, the species were grouped in analytical subdivisions based on the sex of the spike, particularly their terminal spike. The earlier works of Goodenough (1794) and Dewey (1823–35) also deserve mention here because of their influence on Schweinitz and Torrey, although neither seriously attempted a revised classification. Kunth (1837) took much the same approach by grouping the species into thirteen sections under *Vignea* and twenty sections under *Carex*. In essence, their classifications were more or less a refinement of Linnaeus' classification. During that era the work of Hoppe (1826), Gay (1827), Fries (1835), Koch (1837), Kunze (1840), and Nees ab Esenbeck (1843) also added much to the science of caricology. The genus had become a very complex one due to the extreme diversity and large number of species. Even Fries was exasperated by the multiplicity of species. Each in his own way wrestled with the problem and attempted to devise their own manageable classifications, with little success. For instance, Rafinesque (1840 a and b) and Heuffel (1844) divided *Carex* into several subgenera; eighteen were proposed by Rafinesque and seven by Heuffel, but none of these were accepted.

Tuckerman (1843) proposed a natural classification of *Carex* that differed significantly from the Linnaean system. Rather than two subgenera, he proposed five sections: I. Psyllophorae, II. Vignea, III. Vigneastrea, IV. Leptantherae, and V. Legitimae. Under sections II, IV, and V, he found it necessary to have subsections. Species were grouped in subanalytical categories, such as *Dioeceae, Nardinae, Pauciflorae*, etc. This was a revolutionary approach and, although none of his sections were retained, nearly all of his categories were accepted and are still in use as sections in modern systematics.

Drejer (1844), whose work was published posthumously by Vahl, devised a natural classification system along somewhat the same principle as Tuckerman's. Like Tuckerman, Drejer felt that monostachyous species did not warrant a section of their own. His *Vignea* and *Caricis Genuinae* were not considered in the traditional distigmatic and tristigmatic sense, respectively. Rather, homostachyous species with both androgynous and gynaecandrous spikes represented *Vignea*, while *Caricis Genuinae* comprised distigmatic and tristigmatic heterostachyous species. Under these two subgenera, there were to be 'greges' but, unfortunately, his work was unfinished and he describes only ten 'greges', all of them under *Caricis Genuinae*. Holm (1903), working on Drejer's principle, increased the number of 'greges' to thirty-nine. Despite earlier attempts to supplement the missing 'greges' by Bailey (1886) with those

of Kunth, Fries, Tuckerman, Carey (1847), and others, Drejer's principle was overshadowed by Tuckerman's system. Another unique feature of Drejer's work is his discussion on the interrelationship of the various 'greges' and species which were amply illustrated in three charts. Drejer's concept of natural affinities between groups of *Carex* was, in effect, a study in evolution greatly influenced by Lamarckian thought and, in some ways, his classification was superior to that of Tuckerman's. Evidently, many 19th century caricologists never fully understood Drejer's principle; had they done so, perhaps Drejer would be more widely recognized as an evolutionary theorist, for it was he who first proposed that monostachyous species are reduced from heterostachyous species.

By the mid 19th century, an increasing attention was focused on systematic studies in Asia by Miquel (1865–66), Maximowicz (1886), Franchet (1884–88, 1895, 1897–98), Hance (1871), and Leveille and Vanoit (1901–1904). Although the valuable works of Boott (1858–67) and Böckeler (1875–76) dealt with species on a world-wide basis, the systematic classification of *Carex* was derived mainly from European and North American species. Pax (1887), recognizing this deficiency, based his classification on species from all major continents. In doing so, he reinstated the Linnaean principle of three major groups, i.e., *Monostachyae, Homostachyae* and *Heterostachyae*, which were subdivided into sections not unlike those of Tuckerman's (1843). But it was Kükenthal (1892–1922) who made the greatest impact in the history of modern caricography. His *Cyperaceae-Caricoideae* in Engler's *Pflanzenreich* (1909) is a classic which has never quite been equaled and, although systematic botany has advanced considerably since then, his classification with minor revisions is still in use. Kükenthal's classification is composed of a mixture of views of earlier caricographers and his own opinions. He divided the *Carex* into four subgenera: I. *Primocarex*, II. *Vignea*, III. *Indocarex*, and IV. *Eucarex*. Each of these was divided into sections with occasional subsections, many of which were adopted from Tuckerman (1843). Kükenthal's subgenera are defined as follows:

A. Spikes solitary, terminal .....Subgenus I. *Primocarex*
B. Spikes two or more
Spikes sessile, bisexual, rarely with bracts, stigmas two or rarely 3 ..... Subgenus II. *Vignea*
Some spikes bisexual, the terminal spike staminate, growing from perigynium-shaped bractlet, stigmas three .....Subgenus III. *Indocarex*
Spikes unisexual, rarely bisexual, pedunculate or solitary, bracts sheathing stipule, stigmas two or three .....Subgenus IV. *Eucarex*

Kükenthal considered that the genus *Uncinia* and subgenus *Primocarex* were derived from the genus *Schoenoxiphium* through the intermediate genus *Kobresia* by reduction of the rachilla. The remaining subgenera, *Vignea, Indocarex,* and *Eucarex,* which lack a rachilla, were assumed to have descended from *Primocarex*. Kreczetowicz (1932, 1936, 1941, and 1952), on the other hand, considered the more complex species of *Carex*, i.e., those with many spikes, to be more primitive, having arisen by digressive reduction during the periglacial and postglacial migrations. The single-spiked *Primocarex* were not prototypic but naturally arose through the normal course of reduction. The *Indocarex* were considered transmutational reduction types arising from climatic changes resulting from regression of the equator to southern latitudes during the late tertiary and early quaternary periods. Consequently, he placed most of the species of *Primocarex* in *Eucarex* and the remainder in *Vignea* and created a new subgenus, *Megalocranion*. Mackenzie (1931–35) considered the monostachyous species to be partly primordial. In his treatment of North American species, he discards subgenera altogether but, in all other respects, generally agrees with Kükenthal. Mackenzie described over 500 species of North American *Carex*. By this time there were between 1,800 to 2,000 species of *Carex* throughout the world.

For most of this century, caricology has been dominated by the studies in Asia and

Eurasia. Prominent among them are the works of Chu (1938), Ascherson and Graebner (1905), Don (1925), Kabanov (1935), Komarov (1908–1914), Ostenfeld (1902), and Nelmes (1939–55). Ultimately, the Japanese scholars had a profound influence in the taxonomic treatment of *Carex*. The Japanese tradition began with Thunberg (1784), another of Linnaeus' star pupils, who reported seven species of *Carex* from Japan; Steudel (1855) cited 15 species originating from Japan, and Boott (1860) also described many new species from that country. Until the 20th century our knowledge of Japanese *Carex* relied almost entirely on resident and nonresident European scholars in the 19th century. But the systematic studies of *Carex* by Japanese scholars gradually emerged at the turn of this century with the works of Nakai (1911–52), Hayata (1911–12), Koidzumi (1910–30), Kudo (1922), Honda (1929–39), Akiyama (1932–55), and Ohwi (1930–65). Akiyama (1933–42) carried out an extensive morphological study on the systematic anatomy of the leaves of *Carex* which complemented his taxonomic studies of the Japanese species. Ohwi (1936) also carried out a revision of *Carex* from a more extensive range, including Japan, Kuriles, Sagkalin, Korea and Formosa. In his work he agreed with Kreczetowicz (1935) on the taxonomic status of *Primocarices* and incorporated them into two subgenera, *Vignea* and *Eucarex*. Because of the similarities of the perigynia in *Indocarex* and the section *Hymenochlaeneae*, all the *Indocarices* were placed in *Eucarex*. In a more recent monograph on Japanese *Carex*, Akiyama (1955) noted that, cytologically, *Carex* is a remarkable example of heteroploidy; that, in general, the process of classification is somewhat mechanical and to be criticized whether it is natural or not. Consequently, he adopted the view which abolishes subgenera, but chose to retain sections.

Nelmes (1952) based his classification on more detailed phylogenetic principles than his predecessors and attempted to reinstate the subgenera *Indocarex* and *Primocarex*; apparently with little success. Nelmes concluded that *Eucarices*, with racemose inflorescences, derived from paniculate spikelets of *Indocarices*. The *Primocarices* he considered to be a mixture of primitive and reduced forms and, in general, closely allied with *Kobresia*. In fact, the analogy was so close that he placed *C. obtusata* and *C. rupestris* in *Kobresia*. Savile and Calder (1953) took a novel approach to the phylogeny of *Carex* based on the parasitic relationship of smut fungi (*Cintractia* and *Planetella*) of infected *Carex*. They also concluded that *Carex* was monophyletic and derived from a *Kobresoid* ancestor which, on a separate line, also included the closely related genus *Schoenoxiphium*. To them *Carex* included five subgenera, all derived from *Kobresia: Indocarex* which evolved on a separate line, *Primocarex* from which diverged *Vignea, Eucarex*, and a new subgenus designated *Kükenthalia*. The genus *Uncinia* was considered a specialized side branch of the evolutionary line giving rise to *Kükenthalia*. From this branch line, the section *Pauciflorae* diverged and is included in *Kükenthalia*. *Indocarex* was placed on a separated evolutionary branch line because the point of divergence was unclear; being placed below *Primocarex* because the complex inflorescence and uniformly tristigmatic pistillate spikelets were considered more primitive. The *Primocarex* comprised only 27 of the 60 species originally assigned to it by Kükenthal (1909). However, 30 species were transferred from other subgenera, plus some new ones, e.g., *Filifoliae*. These were considered primitive species in possession of a rachilla. Some species with rudimentary rachillas were placed low in *Eucarex*, partly on the smut relationship and because their evolutionary divergence was considered tentative pending further data on smut records. The sections *Phyllostachyae* and *Scirpinae* were considered reduced rather than primitive because their smuts are related to those of the section *Limosae*. Twelve sections were comprised mainly of aquatic or semi-aquatic species with inflated perigynia and persistent style. One species, *C. microglochin*, has a projecting rachilla which was viewed as a digressive reduction from the genus *Uncinia*. Accordingly, the adoption of an aquatic environment resulted in an evolution from a slender, subulate perigynia to an inflated one adapted to dispersal by water. The occurrence of dry land species (Hirtae) in *Kükenthalia* was

superficially explained as evidence of hybrid origin. Savile and Calder's theory has not been widely accepted but, perhaps, as with Drejer, we have not seen the full wisdom of their concept; for while their work is speculative they, nevertheless, point to a new direction in the phylogeny of *Carex*.

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