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Diphasiastrum, a new genus in *Lycopodiaceae*

Diphasiastrum, nový rod čeledi *Lycopodiaceae*

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The *Lycopodium complanatum* agg. s.l. is a natural and well defined group of closely related species in *Lycopodiales*, characterized by a special dorsiventral structure of branchlets, a common basic chromosome number ($x = 23$) and a special type of the natural prothallium („*Complanatum*“-type). The group represents a distinct evolutionary branch in the *Lycopodiaceae* s.s. and is therefore accepted here as a separate genus — *Diphasiastrum* Holub. A generic description is provided, based mostly on a discussion of characters separating this genus from other natural groups of *Lycopodiaceae* s.s.; especially the differences from the *Lycopodium scariosum* agg. = *Diphasium* C. Presl, with which it has been erroneously united, are considered. *Diphasiastrum* contains about 30 species (inclusive of interspecies). New nomenclatural combinations for 22 of these are proposed and their classification to area types is given.

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INTRODUCTION

The club-mosses, placed at the beginning of the classification systems of recent vascular plants, have always attracted the interest of botanists. As far as the taxonomic classification is concerned, much attention was paid, especially by European botanists, in addition to the generic problems, to the difficult *Lycopodium complanatum* agg. s. l. Still, this group is inadequately known. The present author has been studying the club-mosses extensively for years and a paper on *Diphasium* has been in preparation since 1964 (see Holub 1964 : 128). Various reasons made it necessary to postpone its publication, as for instance the preparation of a monograph of this taxonomic group by Wilce (1965), the study of Slovak representatives of the group by Futák (1963, 1967), and of Czech taxa by Rauschert (1967). To solve the generic problem, it was necessary to investigate also various extra-European species, poorly represented in Czechoslovak herbaria. As the Czech and Slovak species were studied by Kubát (1974) and Futák (1963, 1967), who provided distinguishing characters of all taxa and distributional data on interesting taxa, the present paper will discuss mainly the problems of generic classification. With regard to the papers by Kubát and Futák the publication of a more detailed study of Czechoslovak representatives of the genus has been postponed. A review of generic problems in *Lycopodiales* and notes on some species of *Diphasiastrum* will also be found in separate papers.

HISTORICAL REVIEW

Linnaeus (1753) included the *Lycopodium complanatum* agg. s.l. in his broadly circumscribed genus *Lycopodium*, containing, in addition to 12 species of club-mosses belonging to *Lycopodiales* in modern systems, also representatives of the genera *Selaginella* s.l. (11 species) and *Psilotum* (1 species). To my knowledge, the group under consideration had never been excluded as a separate genus in the pre-Linnaean literature. Even PALISOT DE BEAUVOIS, who was the first author to propose generic subdivision of the huge LINNAEUS's genus in 1803—1805, did not separate the group from the proper club-mosses named *Lepidotis* by him. It is true that NECKER (Elem. Bot. 3 : 335, 1791) had subdivided *Lycopodium* L. into two "species naturales" — *Lycopodium* and *Acopodium*. The latter contained species with distichous leaves and might have included the group studied here; it did, however, include most species of the present *Selaginella* s.l. The monographer of the *Lycopodiaceae*, SPRING (1842, 1849) also retained *Lycopodium* in a broad sense corresponding to *Lycopodiales* of the modern authors excluding, however, all heterogeneous elements of the original LINNAEUS's concept, belonging to other orders. This SPRING's circumscription as the concept given by the monographer gained a general recognition and prevails also at the present time, except for a few modern, mostly European taxonomists.

C. PRESL (1845) was the first author to establish the group in question as a separate genus. He named the genus *Stachygynandrum*; however, this name had been proposed by PALISOT DE BEAUVOIS for an entirely different genus belonging to *Selaginellaceae*. PRESL did not mention PALISOT DE BEAUVOIS (though his generic name was apparently known to him) and provided a short diagnosis of the genus of his own. This differs from that of the homonymic genus by PALISOT DE BEAUVOIS especially by a reference to the isosporous character („spicae solummodo antheridia reniformia gerentes"). PRESL's genus accomodates *Lycopodium complanatum* L., *L. wightianum* HOOK. et GREV., *L. thyoides* WILLD. and *L. alpinum* L. PRESL did not exclude the possibility that further species might be referred to his genus. In his circumscription, *Stachygynandrum* corresponds to what is described here as a new genus *Diphasiastrum*. PRESL's diagnosis refers to the arrangement of the leaves ("stipulae enim uniseriales in utraque pagina rami, folia cum ramo coadunata"). In spite of its natural character the proposed classification has not been accepted. The generic name used is illegitimate with regard to the existence of a homonym validly published earlier. PRESL also clearly delimited *Stachygynandrum* against *Diphasium*, described by him as a new monotypical genus in the same paper. His *Diphasium* is based on *Lycopodium jussiaei* DESV. resembling somewhat *Stachygynandrum* C. PRESL. Unfortunately, this fact was misunderstood by ROTHMALER (1944). His broad concept of *Diphasium* C. PRESL (including the *L. complanatum* agg. s.l.), has been accepted by many authors to designate the latter group, which was due to the geographical limitation of their studies.

After PRESL, the group of species under discussion was classified as an infrageneric taxon, either as a section *Complanata* M. VICTORIN 1925, or a subgenus *Thujophyllium* BÖRNER 1912, in both cases in a taxonomically justified circumscription. The taxonomic correctness of the circumscription of these two taxa may be, however, questionable because of the geographical limits of the area covered. The circumscription proposed by HERTER (1909) appears less correct from the taxonomic viewpoint, because his *Lycopodium* subgen. *Complanatostachys* included some heterogeneous elements as for instance *L. scariosum* R. BR. and *L. volubile* FORST. f. The same may be said of the concept by WALTON et ALSTON (in VERDOORN 1938), including, in addition to these species, also *L. casuarinoides* SPRING. BAKER (1887) adopted PRESL's name *Diphasium* (with its type species) to designate one of his four subgenera in *Lycopodium*. His concept of this taxon, is, however, exceedingly heterogeneous, including all species of *Lycopodiaceae* s.s. with dorsiventral structure of branchlets (or of the main stem), which belong to very different evolutionary lines. The representatives of the genera *Lycopodiella* (*L. carolinianum* L.), *Diphasium* (*L. scariosum* FORST. f.), *Diphasiopsis* (*L. volubile* FORST. f.) and *Diphasiastrum* (*L. complanatum* L. s.l., *L. wightianum* HOOK. et GREV.) are included in BAKER's subgenus *Diphasium*. Isophyllous or slightly heterophyllous taxa of *Diphasiastrum* (such as *L. alpinum* L., *L. sitchense* RUPR.) are found referred to the subgenus *Lepidotis* together with the type species of *Lycopodium* L. — *L. clavatum* L. To a certain extent, BAKER's concept is dependent upon the classification of *Lycopodium* as proposed by the monographer SPRING, who, however, did not give any names to the majority of subgroups of his infrageneric classification. BAKER's rapprochement of *L. scariosum* FORST. f. and the *L. complanatum* agg. s.l. led probably ROTHMALER (1944) to merge these two different elements into one genus. ROTHMALER, however, justifiably excluded other species with dorsiventral structure of branchlets from this taxon and transferred them (not always correctly) to other groups.

The *Lycopodium complanatum* agg. s.l. was reclassified as a genus only hundred years later by ROTHMALER (1944) who united this group with *Diphasium* C. PRESL, subdividing the resulting genus into two infrageneric taxa at the serial level: ser. *Complanata* ROTHM. and ser. *Jussiaea* ROTHM., the latter one containing the type of the genus. ROTHMALER considered this genus to be a very natural one. The fusion of two unrelated elements (based especially on the flattened branchlets) into one genus (which unfortunately received the name of the group with lower species number and more limited geographical distribution) is, however, a taxonomic failure. C. PRESL, the classic of pteridological classification, describing *Diphasium* in 1845, made it clear that this genus was different from *Stachygynandrum* C. PRESL ("E numero *Stachygynandri* specierum eliminari debet *Lycopodium Jussiaei* . . .") because it is defined by a different type of the foliar arrangement in the branchlets. The present author considers Presl's concept fully justified not only morphologically, but also phylogenetically, as will be shown below. *L. jussiaei* Desv. — the type species of *Diphasium* C. Presl — belongs to the *L. scariosum* agg., a South American — South Pacific taxonomic group which has not been sufficiently known to most authors involved in the taxonomy of Boreal (or European) representatives of the *L. complanatum* agg. s.l. who accepted Rothmaler's circumscription of *Diphasium* without any further revision. Rothmaler (1962) later applied the name *Diphasium* direct to the *L. complanatum* agg. s.l. which led some authors to suppose that the type species of *Diphasium* C. Presl is *Lycopodium complanatum* L. (Kukkonen 1967 : 465), a species not at all included in the original concept of *Diphasium* by C. Presl.

In recent years, Rothmaler's partial circumscription of the genus *Diphasium* has been increasingly used which may be due to its acceptance in various handbooks (e.g. Dostál 1958; Rothmaler 1963 etc.) and especially in "Flora Europaea". The monographer of the group, Wilce (1965, 1972) opposes the recognition of *Diphasium* as a separate genus, especially in the delimitation accepted by Rothmaler. Her criticism of the emphasis laid on the nature of gametophyte is based on the results of "in vitro" cultivation and appears justified, at least to a certain extent. This can hardly be said, however, of her criticism of the dorsiventral structure of branchlets as a taxonomic character. Dorsiventral structure of branchlets occurs in various groups of *Lycopodium* s.l. but the type found in the *L. complanatum* agg. s.l. is quite different. Wilce also considered the chromosome number insufficient to separate the taxon in question as a genus, even though it is of principal importance in *Lycopodiales* and has been used even by Rothmaler (1962) in delimitation of his concept of *Diphasium*. The primary want of Wilce's approach, who succeeded in collating important factual material relating both to the knowledge of the *L. complanatum* agg. s.l. and the generic classification of *Lycopodium* s.l., is the non-phylogenetical (pragmatical) approach to the use of the generic classification unit.

CHARACTERISTICS OF THE *LYCOPODIUM COMPLANATUM* AGG. S.L.

The *L. complanatum* agg. s.l. is relatively well defined morphologically and most taxa may be recognized as belonging to it at first sight. Sterile branchlets of the most species have a dorsiventral structure and are more or less flattened (especially at the ventral side). The leaves are opposite and decussate, arranged in three planes and are termed dorsal (1), lateral (2) and ventral (1). The pairs of identical lateral leaves alternate with pairs consisting of one ventral and one dorsal leaf. Leaves of sterile branchlets are trimorphous and rarely dimorphous. Lateral leaves are carinate and adnate to stem by their elongated bases and are responsible for the general appearance of sterile branchlets. In taxa with more flattened branchlets the ventral leaves differ considerably from other leaves providing important distinguishing characters. Generally, dorsiventral structure of branchlets is a secondary feature in club-mosses and so it is in the group concerned. It seems to have arisen several times in various evolutionary lines of *Lycopodiales*. However, the structure of sterile branchlets found in the group discussed here is unequalled in the club-mosses. The original more or less spiral arrangement of isomorphous leaves is retained on the main stem (or on the rhizome) and on the peduncles. In aerial shoots this arrangement is substituted by a decussate arrangement of anisomorphous leaves. The decussate arrangement of leaves on sterile branchlets can be changed to the spiral arrangement under special conditions, for instance when the shoots are shaded, as has been experimentally proven by Goebel (1928 : 618). The original spiral arrangement of leaves in the whole plant is preserved in three species (*L. sitchense* Rupr., *L. nikoënse* Franch. et Savat. and *L. veitchii* Christ) which are probably closely related to the archetype of this taxonomic group. Their leaves are arranged in 5—6 vertical rows, partly adnate to the stem, whereas in isophyllous representatives of *Lycopodium* s.s. the leaves are in 6—10 vertical rows and free. According to DOSTÁL (1971) a disturbance of the decussate arrangement of leaves is also known to occur in *L. alpinum* L., which may be due to environmental conditions. These deviations do not affect the natural character of the group discussed, because plants with spirally arranged isomorphous leaves are closely related to those with decussate leaves of a differentiated form and isophyllous taxa have been treated as infraspecific variants of anisophyllous species by some authors. In addition, there are also intermediates (intertypes, intertaxa, interspecies) between isophyllous and anisophyllous species, probably of a hybridogeneous origin which is another proof of the close relationships between representatives of the two morphologically different subgroups. The decussate leaf-arrangement and anisophylly are trend features of a phyletic line, proper to 90% of taxa in the group. Phylogenetically, they are important features of the whole phyletic line, which constitutes a relatively well defined group.

The basic chromosome number, and to a certain extent the size of chromosomes, is important for the generic classification of club-mosses. Owing to the technical difficulties the karyological investigation of this group proceeded slowly, and many chromosome numbers reported by earlier authors proved to be inaccurate or erroneous and some need a revision. In recent years a considerable progress has been made. At present, chromosome numbers are available for all main groups of *Lycopodiales*, and may be considered for taxonomic purposes. The chromosome numbers of $2n = 46$ was stated in several species of the *L. complanatum* agg. s.l. (*L. alpinum* L., *L. complanatum* L., *L. digitatum* A. BR. = *L. flabelliforme* (FERN.) BLANCHARD, *L. issleri* (ROUY) DOMIN, *L. sitchense* RUPR., *L. tristachyum* PURSH, *L. zeileri* (ROUY) and a comparable number of $n = 48$ (? 46) has been reported for *L. wightianum* HOOK. et GREV. (NINAN 1958). The latter is the only polyploid number hitherto reported for the group in question. Judging from the size of the spores, a polyploid condition may be expected to occur in *L. zanclophyllum* WILCE only (WILCE 1965). SORSA (1963) counted 22—24 pairs of meiotic chromosomes in *L. alpinum* L. and DAMBOLDT (1963) suggests that this may be an evidence of a certain instability of the number or that B chromosomes may be involved. Considering that the chromosome number of $2n = 46$ has been repeatedly found by various authors (DAMBOLDT, LÖVE, SORSA, WILCE etc.) in many taxa belonging to various subgroups of the group concerned and that other data do not differ much from this number (NINAN), $x = 23$ may be regarded as the basic chromosome number in this taxonomic group. The basic chromosome numbers in other main taxonomic groups of *Lycopodiales* are as follows: $x = 11$ (*Huperzia* s.s.); $x = 13$ (*Lycopodiella, Palhinhaea*); $x = 17$ (*Phlegmariurus, Lycopodium*, most likely also *Diphasium*). The basic number of $x = 23$ is certainly a secondary one; however, it cannot be derived from any other basic number in the now existing club-mosses.

WILCE (1965), considering the close relationships of this taxonomic group to *Lycopodium* s.s. ($x = 17$) attempted to derive the basic numbers of the two groups from the more archetypal basic numbers of $x = 11$ or $x = 12$ (or also $x = 6$). The basic number of $x = 23$ may have arisen by a doubling of $x = 11$ accompanied by the addition of one chromosome — $23 = (2 \times 11) + 1$, and $x = 34$ in *Lycopodium* s.s. by a tripling of $x = 11$ accompanied by the addition of one chromosome — $34 = (3 \times 11) + 1$. Alternatively $x = 12$ may have given rise to $x = 23$ by a doubling accompanied by the loss of one chromosome — $23 = (2 \times 12) - 1$, and to $x = 34$ by a tripling of $x = 12$ accompanied by the loss of two chromosomes — $34 = (3 \times 12) - 2$.

Which hypothesis concerning the archetypal chromosome number is correct, remains to be seen. For the purposes of taxonomic classification, it is necessary to start from the real (not hypothetic) basic number of this group which is $x = 23$. This is the highest basic number encountered in recent club-mosses and the species studied are mostly diploid; tetraploid condition seems to be very rare in the group concerned. It is interesting to note that diploids have not at all been reported for any other group of club-mosses. The chromosome numbers are $4x$ in *Lycopodium* s.s. and *Diphasium* (rarely $8x$ in *Lycopodium* s.s.), $6x$ and $12x$ in *Lycopodiella*, $16x$, $24x$ and $32x$ in *Palhinhaea*, and $8x$, $24x$ and $48x$ in *Huperziaceae*. Chromosome numbers within a taxonomic group of club-mosses are surprisingly uniform and are good markers of phylogenetically natural units. The generic separation of the group discussed here is thus corroborated. The chromosome number of the isophyllous *L. nikoënse* FRANCH. et SAVAT. will have to be re-examined because this species is closely related to the archetype of the *L. complanatum* agg. s.l. and deviating chromosome number of $2n = 68$ was reported for it by MEHRA and VERMA (sec. Á. et D. LÖVE 1958); this number points to $x = 17$, i.e. rather to the group *Lycopodium* s.s. The other isophyllous species *L. sitchense* RUPR. (to which *L. nikoënse* FRANCH. et SAVAT. was referred by WILCE 1965) has, however, $2n = 46$. *L. jussiaei* DESV., the type species of *Diphasium* C. PRESL, has been shown to have $2n = 34-36$ (WILCE, 1972), suggesting that this species has nothing to do with the group under discussion. There is also a difference in the size of chromosomes between *Lycopodium* L. s.s. and the *L. complanatum* agg. s.l., the latter having smaller chromosomes — see Á. et D. LÖVE (1958) and WILCE (1965).

When classifying club-mosses at generic level, the present century students of *Lycopodium* have laid stress upon differences in the structure of the gametophytes. This approach needs a revision in the light of results obtained recently "in vitro". It would be, however, hardly possible to reject completely the characters of natural prothallia as entirely unimportant for taxonomic classification, as it might follow from the argumentation by WILCE (1972). The gametophyte of the representatives of the *L. complanatum* agg. s.l. found in nature differs from prothallia of other groups of *Lycopodiales* by its complex structure and differentiated tissues. In cultivation "in vitro", prothallia of this type approach those of the other groups of club mosses losing their characteristic napiform shape with a differentiated corona at the top, where the sunk antheridia and archegonia are found. Archegonia of cultivated prothallia have also a shorter neck than those found in nature. Cultivation experiments would suggest that the shape and the structure of natural prothallia are greatly influenced by symbiosis with fungi. Symbiosis has also been observed in the sporophytes of club-mosses (BARROWS 1935). Fungi have been found not only in roots, but even in stems and peduncles of strobiloids, suggesting that the morphology of sporophytes may also be modified. Because all main groups of *Lycopodiales* are defined by a certain type of natural prothallium, it may be conveniently used as a complementary character to define the group in question. (For a description of the prothallium of the "*Complanatum*"-type, see BRUCHMANN 1908). Care should be taken in weighting this character, however, because the natural prothallium has been examined in few species only.

In the following text the group under discussion will be compared with other segments of the family *Lycopodiaceae* s.s., representing, in my opinion, natural genera. The relevant generic names are taken from my unpublished study (HOLUB, in prep.); at the specific level, names valid in *Lycopodium* s.l. are used.

Phylogenetically, the *L. complanatum* agg. s.l. appears closely related to *Lycopodium* L. s.s. (type species — *L. clavatum* L.). The main distinguishing feature is the phyllotaxis (the leaves of branchlets are normally opposite, decussate, dimorphous or trimorphous in the *L. complanatum* agg. s.l., but are more or less spirally arranged and normally monomorphous in *Lycopodium* s.s.).Isophyllous species of the group studied approach some representatives of *Lycopodium* s.s. (e.g. *L. obscurum* L.) but differ in having only 5—6 vertical rows of leaves (6—10 in *Lycopodium* s.s.). Also, the leaves are partially adnate to the stem (free in *Lycopodium* s.s.), the chromosome number is $2n = 46$ (98), ($2n = 68$ (136) in *Lycopodium* s.s.) and the chromosomes are smaller. There are also differences in natural prothallia (napiform, with a well differentiated corona in the *L. complanatum* agg. s.l.; flattened, disc-shaped or pan-shaped, undulate, with thickened margins in *Lycopodium* s.s.).

The monotypic genus *Diphasiopsis* (HOLUB, in prep.), based on *L. volubile* FORST. f., differs from the group discussed by its habit, phyllotaxis, form and colour of sporangia, the type of their opening and by characters of natural prothallium. Members of *L. complanatum* agg. s.l. are terrestrial plants with a repent main stem or rarely with a rhizome; *L. volubile* is a vine with a wire-like main stem up to 20 m long, climbing on shrubs and trees. Unlike the taxa of the *L. complanatum* agg. s. l. the fertile part with a great number of strobiloids is separated. The arrangement of the leaves in the two groups compared is in the main similar. The leaves are arranged in three parallel planes, but in *L. volubile* the lateral leaves are not distinctly opposite and the ventral leaves are less numerous than the dorsal ones. The regular alternation of pairs of lateral leaves with pairs consisting of one dorsal and one ventral leaf, which is characteristic of the majority of species of the *L. complanatum* agg. s.l., does not occur in *L. volubile*. The radially arranged branchlets of isophyllous species of the *L. complanatum* agg. s.l. differ substantially from the flattened heterophyllous branchlets of *L. volubile*. Sporangia in the *L. complanatum* agg. s.l. are reniform, yellow and opening into two equal valves by a fissure at the top. In *L. volubile* they are transversely ellipsoidal-globose, brownish and opening in their abaxial side; the valves are therefore not equal. The natural prothallia of *L. volubile* resemble those of the "*Clavatum*"-type (HOLLOWAY 1920; sec. WILCE, 1965).

The genus *Diphasium* C. PRESL (consisting only of one species aggregate — the *L. scariosum* agg.) differs from the *L. complanatum* agg. s.l. by an entirely different phyllotaxis, another type of anisophylly and the chromosome number, to a certain extent also by the structure of the exospore and by the natural prothallium. Unlike the leaves of the *L. complanatum* agg. s.l. which are opposite, decussate and arranged in three parallel planes (dorsal, lateral, ventral) in most species of the group, the leaves of *Diphasium* are arranged into two parallel planes, a dorsal and a ventral one. By their shape and size the leaves of the dorsal plane are similar to the lateral leaves of the *L. complanatum* agg. s.l. Those of the ventral plane are scale-like. Dorsal leaves are not opposite (perhaps with exception of *L. comptonioides* DESV.), as in the *L. complanatum* agg. s.l. and the scale-like ventral leaves are usually in in several rows, but in one row in the *L. complanatum* agg. s.l. The terms "dorsal" and "ventral" for designation of the two planes in *Diphasium* are often used in opposite senses; the present author follows PRESL (1845). The chromosome number in *Diphasium* $n = 34—36$ (WILCE 1972) compared with the normal one $2n = 46$ in the *L. complanatum* agg. s.l. The spores of both the groups are of the reticulate type, the meshes in *Diphasium* are larger and less numerous in the distal side of the spore than in spores of the *L. compla-*

natum agg. s.l. and are absent from the proximal side of the spore (in the *L. complanatum* agg. the meshes are well developped there). The prothallium of *L. scariosum* is of the "*Clavatum*"-type (HOLLOWAY 1920; sec. WILCE 1965), that of the *L. complanatum* agg. s.l. belongs to its own "*Complanatum*"-type.

L. casuarinoides SPRING, the sole representative of the monotypical genus *Lycopodiastrum* (HOLUB, in prep.) differs substantially by its habit, leaf-arrangement and by spores. It is a vine with a stiff wire-like stem up to 20 m long. The plant is differentiated into a sterile and a fertile part with bunches of strobiloids. Plants of the *L. complanatum* agg. s.l. are terrestrial plants with a repent main stem or rarely with a rhizome, never climbing; the plants are not differentiated into a sterile and fertile part. Mature leaves of *L. casuarinoides* are monomorphous, scale-like and arranged more or less spirally; in the *L. complanatum* agg. s.l. the leaves of sterile branchlets are in mostly di- or trimorphous and decussate; in isophyllous species of this group they are setaceous. *L. casuarinoides* is the only species of *Lycopodiales* having scabrate spores (WILCE 1972); spores in the *L. complanatum* agg. s.l. are reticulate.

L. deuterodensum HERTER, the only member of the genus *Pseudolycopodium* (HOLUB, in prep.) differs especially by its "spinose" (baculate, WILCE 1972) spores, which are not met with in any other species of the order *Lycopodiales*. They resemble somewhat the spores of *Selaginellaceae*. The spores of the *L. complanatum* agg. s.l. are reticulate. The habit and foliar arrangement in *L. deuterodensum* are also different from those in the *L. complanatum* agg. s.l.

The genus *Lycopodiella* HOLUB 1964 differs from the *L. complanatum* agg. s.l. by the morphology of sporangia and spores, chromosome number and natural prothalium. Representatives of the group studied here have reniform sporangia, opening by a fissure across the top, with equal valves. Spores are reticulate, of the "*Clavatum*"-type (WILCE 1972). The basic chromosome number is $x = 23$, plants are mostly diploid. Natural prothallia are saprophytic, subterraneous, with a well differentiated corona. In *Lycopodiella* the sporangia are usually transversely ellipsoidal-globose or rarely reniform, opening by a fissure in the abaxial side, valves are unequal. Spores are rugulate ("*Carolinianum*"-type; WILCE 1972). The basic chromosome number is $x = 13$, and all the species counted hitherto proved polyploid ($4x$, $8x$). The natural prothalium is hemiautotrophic, lobate at the top. The leaf-arrangement is also different.

The genus *Palhinhaea* A. FRANCO et CARVALH. 1967 (represented by the exceedingly variable *L. cernuum* species aggregate) differs from the group studied by its habit, margin of the stegophyll, shape and opening-type of sporangia, basic chromosome number, characters of the spores, structure of the natural prothallium, etc. Members of the *L. complanatum* agg. s.l. lack the arborescent habit of the lateral (= aerial) stems; margins of stegophylls are more or less entire; sporangia are reniform, opening by a fissure with smooth margins across the top of the sporangium, valves are equal. Spores are of the "*Clavatum*"-type (WILCE 1972). The basic chromosome number is $x = 23$ and the numbers hitherto known are either diploid or rarely tetraploid. Natural prothallia are saprophytic, subterraneous, with a differentiated corona and without lobes. Members of *Palhinhaea* have an underground stem (rhizome) producing arborescent lateral stems up to 0,4—2 m long (high), with solitary sessile pendulous strobiloids in the ends of branchlets; stegophylls are laciniate or dentate in the margins; sporangia are transversely ellipsoidal-globose, opening on the abaxial side by a fissure with laciniate margins, valves are unequal. Spores are of the ,,*Carolinianum*"-type (WILCE, 1972). The basic chromosome number is $x = 13$; only high ploidy levels ($16x$, $24x$, $32x$) are known in this group. Natural prothallia are hemiautotrophic, without a special corona but usually lobate at the top.

The genus *Lateristachys* (HOLUB, in prep.) consisting of the only *L. laterale* species aggregate differs from the group studied in having single lateral strobiloids on erect lateral stems. Sporangia open in the abaxial side, valves are not equal. Members of the *L. complanatum* agg. s.l. have terminal strobiloids and sporangia opening by a fissure across the top of the sporangium; valves are equal. There are also differences in the foliar arrangement, spores etc.; the leaves are spirally arranged in *Lateristachys*, but decussate in the most members of the *L. complanatum* agg. s.l.

It follows from the above discussion that the *L. complanatum* agg. s.l. is a well distinct group of *Lycopodiaceae* s.s., defined by a number of various characters. It represents a separate evolutionary line, the constituent members of which are closely related to each other. The distinct character of the group (including isophyllous species) speaks in favour of its separation at the generic level. Its fusion with groups having a dorsiventral structure of shoots cannot be justified on the grounds of morphology and evolution. Evolution of the dorsiventral structure of sterile branchlets seems to have proceeded parallelly in several independent phyletic lines in *Lycopodiales*, leading to different morphological features in each line. The group in question is most closely related to *Lycopodium* s.s. The generic separation of the *L. complanatum* agg. s.l. from *Lycopodium* s.s. is supported by karyological differences and the trend towards a special phyllotactic arrangement and anisophylly in this phyletic line.

Based on the above discussion of the distinguishing characters and relationships, the *L. complanatum* agg. s.l. is here described as a new genus *Diphasiastrum*. Its diagnostic description follows:

Diphasiastrum HOLUB, genus novum

Plantae terrestres; caule ramoso, in caulem primarium atque ramos laterales ramificato; caule primario horizontali, ad terrae superficiem repente vel subterraneo (rhizoma), foliis alternis; ramis lateralibus erectis, modo dichotome ramificatis, ramulos steriles atque fertiles strobiloideis instructis gerentibus; ramulis sterilibus subteretibus vel subplanis, dorsiventralibus; foliis ad ramulos partibus basalibus coadunatis, quadrifariis, diformibus vel triformibus in planitiebus tribus parallelibus dispositis (folia dorsalia, lateralia et ventralia), decussatis; folia dua lateralia cum duobus foliis facialibus (unum folium dorsale et unum folium ventrale) alternantia; raro ramulis sterilibus radiatim symmetricis, multifariis (5—6), cum foliis aequalibus, ± spiraliter dispositis; strobiloideis distincte a ramulis sterilibus differentibus, terminalibus; stegophyllis in margine ± integerrimis; sporangiis reniformibus, luteis, fissura transapicali dehiscentibus, marginibus fissurae glabris, valvis aequalibus; sporodermate in facie sporae distali atque proxima reticulato, luminibus pluribus, minoribus ("*Clavatum*"-typus); numero basali chromosomatum $x = 23$; taxa plurime diploidea ($2x = 2n = 46$); chromosomatibus minoribus; (prothaliis naturalibus typi "*Complanatum*", subterraneis, heterotrophicis, pluriennibus, napiformibus, sulco horizontali sub apice in regiones duas, in regionem vegetativam in parte inferiori et in regionem generativam in parte superiori divisis; regione generativa quoad corona evoluta, antheridiis atque archegoniis instructa; archegoniis longicollibus).

Typus: *Lycopodium complanatum* L. 1753.

Etymology: The name of the new genus is derived from that of the genus *Diphasium* to which the species concerned have been referred. The termination "*-astrum*", added to the radical of the name *Diphasium*, denotes the similarity of those two genera.

Synonyms: *Stachygynandrum* PRESL, Abhandl. Böhm. Ges. Wiss. 5/3 : 582, 1845 (nomen illegitimum), non *Stachygynandrum* PAL. BEAUV. apud MIRBEL et LAM. 1803. — *Lycopodium* L. subgen. *Complanatostachys* HERTER, Engler Bot. Jahrb. 43, Beiblatt 98 : 29, 1909 [p. p.]. — *Lycopodium* L. subgen. *Thujophyllium* BÖRNER Fl. Deutsch. Volk., 110, 1912. — *Lycopodium* L. * *Heterophylla* SPRING sect. *Complanata* M. VICT., Contrib. Laborat. Bot. Univ. Montréal 3 : 34, 89 (descriptio!), 1925. — *Diphasium* C. PRESL ser. *Complanata* ROTHM., Fedde Repert. 54 : 64, 1944.

Diphasiastrum is a well defined group encompassing about 25—30 closely related species (including intertypes, classified here as species, i.e. interspecies). Correct binomial names for 22 species of *Diphasiastrum* will be found below. The subdivision of *Diphasiastrum* into infrageneric taxa present serious difficulties. There are intermediate situations (intertaxa) even between species which are morphologically clear-cut; the intertaxa correspond by their features to the stabilized hybrids in flowering plants. Owing to the distinct character of the genus and the close relationships of the constituent species (possibly with regard to reticulate evolution) no subgenus, nor section may be described within *Diphasiastrum.* A treatment at the series level, based for instance on *D. sitchense*, *D. alpinum* and *D. complanatum*, might perhaps be considered. However, the intertaxa make any infrageneric classification virtually impossible. This is another testimony of the close relationships within the genus and of its natural character. Phylogenetically, isophyllous species with leaves arranged more or less spirally are close to the archetype of the genus. Taxa (mainly tropical) with a distinct dorsiventral structure of branchlets are clearly advanced.

In *Diphasiastrum* it is very difficult to decide whether the species with peduncled or sessile strobiloids are primitive or advanced. WILCE (1965) maintains that sessile strobiloids are an evidence of specialization in this genus, because in *Lycopodium* s.s. (from which *Diphasiastrum* seems to have evolved) they are peduncled. However, peduncled strobiloids are absent in some representatives of *Lycopodium* s.s., as for instance in *L. annotinum* L. and *L. obscurum* L. Peduncled and sessile strobiloids are found in various phyletic branches of club-mosses and appear to have arisen several times in some of them. It is hardly possible to resolve this problem only on the basis of the study of this feature itself. It is interesting to note, that in northern (Arctic and Subarctic) regions a trend towards the shortening of peduncles may be seen, suggesting that the environment may have played an important role in the evolution of this feature; this shortening of peduncles is, however, certainly a secondary phenomenon.

Close relationships between isophyllous *D. sitchense* and heterophyllous *D. sabinifolium* led FERNALD, BOIVIN and CALDER et TAYLOR to unite these two taxa into one species. WILCE (1965) considers *D. sabinifolium* to be a product of hybridization between *D. sitchense* and *D. tristachyum*. Intertypes between individual species do not form an entirely continuous series of transitory individuals. The major part of material belonging to an intertype is of an intermediate position between the presumed parental species. The origin of intertypes is not clear. It has been proposed that they are due to hybridization. This hypothesis is supported by morphological evidence, occasional coincidence of several species in a locality, identical chromosome number and high percentage of abortive spores. It may be argued that hybridization is unlikely to take part in nature in this group because prothalia are subterraneous and are extremely rare. Intertypes have also been reported for American taxa of *Lycopodiella*. GILLESPIE (1962) suggests that hybridization followed by an introgression of the four basic taxa was involved. The intertypes in *Diphasiastrum* may well be of a hybridogeneous origin but the majority of them seem to have arisen in the past. They gradually assumed the character of separate species and occupied their own distribution areas, to a certain extent also their own ecological niches. Some of them even show a certain amount of variation, as for instance *D.* /×/ *zeileri* with its northern populations. Longevity of polycormons should also be taken into account. The lowered fertility of interspecies (combined with the "juvenile" character of the plants) constitutes barrier and provides for the conservation of their intermediate position between parental species. Interspecies between species with peduncled strobiloids and those with sessile strobiloids differ by having lax strobiloids and stegophylls more distant in their lower part.

The hybridogeneous character of interspecies is also supported by phytogeographical evidence. The interspecies are only known among the species of the Palearctic region, where several basic species occur sympatrically and where also drastic changes of distribution areas occured during the Pleistocene. These changes made it possible for a number of diverse basic species once separated geographically or ecologically to come into contact. So far, no interspecies are known to occur in the tropics and in southern hemisphere where the distribution pattern is largely allopatric. Evolution in tropical taxa occurring in isolated mountains and islands proceeded independently of other members of the genus.

The relatively high number of intertypes found in the temperate region of northern hemisphere is responsible for difficulties in identifying specimens. This is obvious from taxonomic classification of some authors who refer quite different taxa to one species. Based on the available information, the present author proposes to treat as separate species all the morphological intermediates between basic species of *Diphasiastrum* showing the properties of natural units. Because their hybridogeneous origin has not been proven, it is suggested that the sign "/×/" be placed in their binomials; in the parental formula the sign "—" may be used. An example follows: "*Diphasiastrum* /×/ *issleri* = *D. alpinum*—*D. complanatum*". The existence of intertypes (possibly combined with introgression) present problems in both determination and classification. Another source of difficulties is the modifiability of plants responding readily to the changes of environment (shading, insolation, watter supply, density of the plant cover, etc.). Extreme environmental conditions may cause sterility and produce special ecomorphoses (mostly sciomorphoses). Even specific diagnostic characters may be modified, making a safe identification of the material impossible. The influence of mycorhyzic fungi upon the morphology of host plants should also be taken into account.

The distribution area of *Diphasiastrum* is very extensive (for a distribution map see LAWALRÉE 1972). The members of the genus are absent from Australia, New Zealand and southern part of South Africa. Based on the geographical distribution of 22 species and interspecies given below, following data on the distribution pattern of *Diphasiastrum* can be given. The largest number of species — nine — occur in North America; seven species are found in southeastern Asia (from the Himalaya and Japan to New Guinea) and six in Europe. Examining the occurrence in phytogeographical zones, the highest number of species will be found in the tropical and northern subtropical (= meridional) zones (11 spp. in each zone), and in the septentrional zone (9 spp.). The distribution areas of species are usually of a medium size (mesoareas) covering, for instance one continent (11 spp.) or of a minor size (microareas), including also insular areas (7 spp.). Circumpolar or transcontinental distribution areas (macroareas) are known for five species only. The distribution areas of the most species belong to various area types. Similar distribution patterns can be found in *D.* /×/ *issleri* and *D. complanatum* (septentrional zone; the first species, however, is largely confined to Europe), *D. angustiramosum* and *D. novoguineense* (New Guinea), *D. digitatum*, *D. sabinifolium*, *D.* /×/ *habereri* and *D. tristachyum* (American part of the distribution area) (eastern North America) and *D. tristachyum* and *D.* /×/ *zeileri* (eastern North America, Europe). The distribution pattern of taxa of allegedly hybridogeneous origin is similar to that of one or both putative parents. The Latin designations of area types (see proposals by HOLUB et JIRÁSEK 1968) of 22 species of *Diphasiastrum* follow:

D. alpinum: AT arcto—oreo—septentrio—suprameridionalis
D. angustiramosum: AT novoguineensis
D. carolinum: AT oreo—tropico—africanus
D. complanatum: AT septentrionalis
D. digitatum: AT infraseptentrio—suprameridio—atlantico—americanus
D. fawcettii: AT caribaeus
D. /×/ *habereri:* AT infraseptentrio—suprameridio—atlantico—americanus
D. henryanum: AT tropico—pacificus
D. /×/ *issleri:* AT septentrionalis
D. madeirense: AT macaronesicus
D. multispicatum: AT austro-orientali-asiatico—philippinensis
D. nikoënse: AT japonicus
D. novoguineense: AT novoguineensis
D. platyrhizomum: AT malesiacus
D. sabinifolium: AT infraseptentrio—suprameridio—atlantico—americanus
D. sitchense: AT septentrio—americanus
D. thyoides: AT neotropicus
D. tristachyum: AT infraseptentrio—suprameridio—atlantico—euro—americanus
D. veitchii: AT oreo—austro-orientali-asiaticus
D. wightianum: AT orienti-asiatico—malesiacus
D. zanclophyllum: AT madagassico—austroafricanus
D. /×/ *zeileri:* AT septentrio—suprameridio—atlantico—euro—americanus.

Of the six European species five occur in Czechoslovakia; the sixth one, *D. madeirense*, is confined to Madeira. The Czechoslovak species are as follows:

D. alpinum: Scattered in higher mountains, mostly in the Supramontane and Alpine belts.

D. /×/ *issleri:* Rare to scattered, decreasing from west to east: most frequent in Bohemia, but known only from four localities in Slovakia; mostly in the Montane and Supramontane belts, rare in lower altitudes.

D. complanatum: Scattered in the Hercynian-Sudetic region, rather rare in the Carpathians; absent from warm lowlands; most frequent in moderately shady coniferous woods; extending from lowlands to the Montane belt, rarely higher.

D. /×/ *zeileri:* Rare to scattered in the Hercynian-Sudetic region, only one single locality is reported in Slovakia; spread from lowlands to the Submontane (? Montane) belt.

D. tristachyum: Very rare (11 localities), confined to Bohemia and western and northern Moravia, mostly in light coniferous woods or in open places from the hilly country to the Montane belt.

The decrease of abundance in the eastern direction is interesting. While in Bohemia all five species are relatively the most abundant, in Moravia the degrees of comparable abundance are distinctly lower. In Slovakia the species of *Diphasiastrum* are rare, *D.* /×/ *issleri* and *D.* /×/ *zeileri* very rare and *D. tristachyum* is absent.

New combinations in *Diphasiastrum*

Diphasiastrum alpinum (L.) HOLUB, comb. nova. — Bas.: *Lycopodium alpinum* LINNAEUS Spec. Plant. 2 : 1104, Holmiae 1753.

Diphasiastrum angustiramosum (ALD. ROSENB.) HOLUB, comb. nova. — Bas.: *Lycopodium complanatum* L. var. *angustiramosum* ALDERWERELT ROSENBURGH, Bull. Jard. Bot. Buitenzorg, Ser. 2, 24 : 6, 1917. — Syn.: *Lycopodium angustiramosum* (ALD. ROSENB.) HERTER Index Lycopod., 4, 1949.

Diphasiastrum carolinum (LAWALRÉE) HOLUB, comb. nova. — Bas.: *Diphasium carolinum* LAWALRÉE, Bull. Soc. Naturalist. Luxembourg. 76 /1971/ 1 : 3, Luxembourgh 1972.

Diphasiastrum complanatum (L. restr. WILCE) HOLUB, comb. nova. — Bas.: *Lycopodium complanatum* LINNAEUS Spec. Plant. 2 : 1104, Holmiae 1753, restr. WILCE, Nova Hedwigia 3 : 97, Weinheim 1961.

Diphasiastrum digitatum (A. BR.) HOLUB, comb. nova. — Bas.: *Lycopodium digitatum* [DILLENIUS] A. BRAUN, Amer. Journ. Sci. Arts 50 : 681, New Haven 1848. [= *Lycopodium flabelliforme* (FERN.) BLANCHARD 1911.]

Diphasiastrum fawcettii (LLOYD et UNDERW.) HOLUB, comb. nova. — Bas.: *Lycopodium fawcettii* LLOYD et UNDERWOOD, Bull. Torrey Bot. Club. 27 : 167, New York 1900.

Diphasiastrum /×/ *habereri* (HOUSE) HOLUB, comb. nova. — Bas.: *Lycopodium habereri* HOUSE, New York State Mus. Bull. 176 : 36, 1913. [= *Diphasiastrum digitatum* (A. BR.) HOLUB — *D. tristachyum* (PURSH) HOLUB.]

Diphasiastrum henryanum (E. BROWN) HOLUB, comb. nova. — Bas.: *Lycopodium henryanum* E. BROWN, Bernice P. Bishop Mus. Bull. 89 : 106, Honolulu 1931.

Diphasiastrum /×/ *issleri* (ROUY) HOLUB, comb. nova. — Bas.: *Lycopodium alpinum* (L.) SCHK. race *issleri* ROUY Fl. France 14 : 489, Paris 1914. — Syn.: *Lycopodium issleri* (ROUY) DOMIN, Věda Přír. 18 : 204, 1937. [= *Diphasiastrum alpinum* (L.) HOLUB — *D. complanatum* (L., restr. WILCE) HOLUB.]

Diphasiastrum madeirense (WILCE) HOLUB, comb. nova. — Bas.: *Lycopodium madeirense* WILCE, Nova Hedwigia, 3 : 111, Weinheim 1961.

Diphasiastrum multispicatum (WILCE) HOLUB, comb. nova. — Bas.: *Lycopodium multispicatum* WILCE, Nova Hedwigia 3 : 103, Weinheim 1961.

Diphasiastrum nikoënse (FRANCH. et SAVAT.) HOLUB, comb. nova. — Bas.: *Lycopodium nikoënse* FRANCHET et SAVATIER Enum. Plant. Japon. 2 : 198, Paris 1879, nomen, et 613 ut var. *L. alpini* L. (descriptio).

Diphasiastrum novoguineense (NESSEL) HOLUB, comb. nova. — Bas.: *Lycopodium alpinum* L. var. *novoguineense* NESSEL, Fedde Repert. 39 : 69, Berlin-Dahlem 1936 (‘*novo-guinensis*’). — Syn.: *Lycopodium novoguineense* (NESSEL) HERTER Index Lycopod., 30, 1949.

Diphasiastrum platyrhizomum (WILCE) HOLUB, comb. nova. — Bas.: *Lycopodium platyrhizomum* WILCE, Nova Hedwigia 3 : 99, Weinheim 1961.

Diphasiastrum sabinifolium (WILLD.) HOLUB, comb. nova. — Bas.: *Lycopodium sabinifolium* WILLDENOW Spec. Plant. 5 : 20, Berolini 1810 (‘*sabinaefolium*’).

Diphasiastrum sitchense (RUPR.) HOLUB, comb. nova. — Bas.: *Lycopodium sitchense* RUPRECHT, Beitr. Pflanzenk. Russ. Reich. 3 : 30, St.-Petersburg 1845.

Diphasiastrum thyoides (WILLD.) HOLUB, comb. nova. — Bas.: *Lycopodium thyoides* HUMBOLDT et BONPLAND ex WILLDENOW Spec. Plant. 5 : 18, Berolini 1810.

Diphasiastrum tristachyum (PURSH) HOLUB, comb. nova. — Bas.: *Lycopodium tristachyum* PURSH Fl. Amer. Septentr. 1 : 653, Londini 1814.

Diphasiastrum veitchii (CHRIST) HOLUB, comb. nova. — Bas.: *Lycopodium veitchii* CHRIST, Bull. Acad. Internat. Géogr. Bot. 15 : 141, Le Mans 1905.

Diphasiastrum wightianum (GREV. et HOOK.) HOLUB, comb. nova. — Bas.: *Lycopodium wightianum* WALLICH ex GREVILLE et HOOKER, Hooker's Bot. Miscell. 2 : 379, London 1831.

Diphasiastrum zanclophyllum (WILCE) HOLUB, comb. nova. — Bas.: *Lycopodium zanclophyllum* WILCE, Nova Hedwigia 3 : 108, Weinheim 1961.

Diphasiastrum /×/ *zeileri* (ROUY) HOLUB, comb. nova. — Bas.: *Lycopodium complanatum* (L.) SCHK. race *zeileri* ROUY Fl. France 14 : 491, Paris 1914. — Syn.: *Diphasium zeileri* (ROUY) DAMBOLDT, Ber. Bayer. Bot. Ges. 36 : 26, 1963.

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SUMMARY

The group of species around *Lycopodium complanatum* L. has always attracted the attention of taxonomists because it presents interesting problems at both the generic and the specific level. The present paper discusses especially generic concepts, taxonomic problems at the species level having been thoroughly studied by WILCE. The geographical distribution of the Czechoslovak taxa has been investigated by FUTÁK and KUBÁT.

The *L. complanatum* agg. s. l. is a separate evolutionary line within *Lycopodiales* and is closely related to *Lycopodium* s.s. It was first recognized as a distinct taxonomic unit by the Czech botanist K. B. PRESL who named it *Stachygynandrum*; however, his name is a homonym and is therefore illegitimate. His concept, though taxonomically correct, has never been accepted. Almost hundred years later ROTHMALER reclassified this group as a genus, uniting it with the genus *Diphasium* C. PRESL which was based on the South American species *Lycopodium jussiaei* DESV. However, the latter species belongs to a quite different species aggregate and characters separating it from other taxa (structure of branchlets, type of spores, basic chromosome number, type of natural prothallium) may be used to define genera in *Lycopodiales*. The *L. complanatum* agg. s.l. is very distinctive and the combination of the characters is unequalled within the order. Therefore its separation at the generic level appears justified. Because no generic name is available, a new name *Diphasiastrum* is proposed. The branchlets of the majority of species of *Diphasiastrum* have a dorsiventral structure. The leaves are arranged in three parallel planes (dorsal, lateral, ventral), they are dimorphous or trimorphous, opposite and decussate; pairs of lateral leaves alternate with pairs consisting of one dorsal and one ventral leaf. Only few species have isomorphous leaves arranged more or less spirally in 5—6 vertical rows. The basic chromosome number $x = 23$ is the highest one in the *Lycopodiales*; however, only lower ploidy levels $2x$, rarely $4x$ are hitherto known to occur. The natural prothallia (of the "*Complanatum*"-type) have the most complex structure of all living pteridophytes.

The genus comprises about 30 species (including interspecies) with an almost world-wide distribution. New nomenclatural combinations with the generic name *Diphasiastrum* are proposed for 22 of them; according to their distribution areas, they are also referred to area types. Interspecies are found in areas where two or more species occur sympatrically and seem to be of a hybridogeneous origin. It is proposed that they be designated by the sign "/ × /" placed between the generic name and the specific epithet in the binomial and by "—" inserted between the names of presumed parents in the parental formula. Of the Czechoslovak taxa, *D.* / × / *issleri* and *D.*/ × / *zeileri* are shown to belong to interspecies.

SOUHRN

Skupině druhů kolem *Lycopodium complanatum* L. byla a je stále věnována poměrně velká pozornost z nejrůznějších hledisek. Z hlediska taxonomického v ní existují zajímavé problémy jak na úrovni rodu, tak na úrovni druhu. V této studii je řešena hlavně problematika rodová, protože taxonomická problematika na úrovni druhové byla podrobněji studována nedávno americkou badatelkou Wilceovou (WILCE). Chorologickým poměrům československých zástupců tohoto okruhu věnovali pozornost FUTÁK a KUBÁT.

Skupina *Lycopodium complanatum* agg. s.l. představuje jednu z vývojových větví uvnitř řádu *Lycopodiales*; příbuzensky navazuje na rod *Lycopodium* L. s.s. Její taxonomickou samostatnost pochopil jako první český botanik K. B. PRESL, jenž ji popsal jako rod pod ilegitimním jménem *Stachygynandrum*; jeho taxonomicky správné pojetí nebylo však až dosud vůbec přijato. Téměř o sto let později ROTHMALER přijal tuto skupinu opět jako rod, zároveň ji však spojil s rodem *Diphasium* C. PRESL, založeném na jihoamerickém druhu *Lycopodium jussiaei* DESV. Tento druh patří však do zcela jiného příbuzenského okruhu než *L. complanatum* L. a liší se ve všech základních znacích, jež mohou sloužit v řádu *Lycopodiales* pro vylišování taxonomických skupin na klasifikační úrovni rodu (typ stavby prýtu, typ spor, základní chromozómový počet, typ přírodního prothalia). Skupina *L. complanatum* agg. s.l. vykazuje zcela samostatné postavení, protože vytváření těchto znaků v této skupině je pro ní zcela specifické. Při revizi klasifikace řádu *Lycopodiales* na úrovni rodu je proto oprávněné vyčlenit tuto skupinu jako samostatný rod. Vzhledem k tomu, že pro ni neexistuje žádné rodové jméno, je skupina popsána jako nový rod pod jménem *Diphasiastrum*. Větévky většiny zástupců rodu *Diphasiastrum* jsou dorsiventrálně stavěné, jejich listy jsou rozloženy ve 3 paralelních rovinách (dorsální, laterální, ventrální), jsou dimorfní až trimorfní, vstřícné, křižmostojné, se střídáním dvojic listů — 2 laterální — 1 dorsální + 1 ventrální. Malá skupina druhů s isomorfními listy v ± spirálním uspořádání je má rozmístěny pouze v 5—6 vertikálních řadách. Základní počet chromozómů je $x = 23$, nejvyšší v řádu *Lycopodiales*; stupeň ploidie je naopak nejnižší — $2x$, zřídka $4x$. Přírodní gametofyt tohoto rodu (typ „*Complanatum*") má nejsložitější strukturu mezi všemi kapraďorosty.

Rod zahrnuje asi 30 druhů (včetně interspecií), rozšířených téměř po celé zeměkouli; pro 22 z nich jsou navrženy příslušné nomenklatorické kombinace s rodovým jménem *Diphasiastrum* a jsou také zařazeny do areálových typů. V oblasti výskytu více druhů se nacházejí interspecie, nejpravděpodobněji hybridogenního původu; pro jejich označení je užito značky „/ × /", vložené mezi rodové jméno a druhové epiteton a dále pak pomlčka, vložená mezi jména předpokládaných rodičů. Z československé květeny sem patří *D.* / × / *issleri* a *D.* / × / *zeileri*.

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