# Pochodzenie torfowców

*The origin of the Sphagna.*

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## Introduction.

The determination of the primary and secondary centres of origin of a certain systematic group is — as is generally known — a very difficult task, and its solution is most often hypothetical because of the lack of fossil remains. Nevertheless this is a very important problem in the geography of plants since its adequate solution gives the key to the understanding of the present ranges of plants.

We meet in literature with two hypotheses on the placing of the areas in which the *Sphagna* originated: The first, formulated by Gams (2) accepts South America to be the centre of origin of the *Sphagna,* as it is in Brazil that most species of the *Sphagna* are living now. The other supposition, contrary to that of Gams, was put forward in general only by A. Le Roy Andrews (6) in his criticism of the species of the *Sphagna* described by Warnstorf; he accepts the northern temperate zone as the primary place of origin of the *Sphagna.* Many Brazilian species described by Warnstorf are regarded by Andrews as identical with the Holarctic species, hence the number of species in Brazil given by Warnstorf were over-rated. It seems to me, however, that Andrews' levelling systematic statements, although right and accurate in principle, are perhaps in some cases too far-reaching and of a lesser value for the problem of the placing of the centre

of origin of the *Sphagna,* because in this case the predominance of the endemic forms is more decisive than the general number of the species in a given territory.

To me the theory of G a m s suggesting South America as the primary centre of origin of the *Sphagna* is more convincing, as I shall try to explain below.

It has been just mentioned that we do not possess any paleobotanical material of the *Sphagna* from the older strata; that is why I had to base my considerations upon the following data:

1) The morphological-systematic character of our species. (I submitted a view of the systematic relations of the *Sphagna* in my paper (9) entitled: „An attempt at the explanation of the phylogenetic relation in the sections of the *Sphagna*". Therefore I do not discuss these matters here, but if need be I immediately quote the conclusions arrived at there).

2) A statistic comparison of the distribution of all species on the globe according to the supposed phylogenetic sequence of the sections.

3) The cartographic material obtained by means of entering in the maps the distribution given by W a r n s t o r f in „Sphagnologia universalis" (12) and completed by the recent literature. (The cartographic material is not given here for the sake of economy of space).

## 1. *An Outline of the General Distribution of the Sphagna, their primary and secondary centres of development, the history of their migrations.*

The *Sphagna* appear nowadays most abundantly (but not with respect to the number of species) in the temperate areas of America and Eurasia near the oceans. They are met with more seldom in the arctic and antarctic regions (H e r z o g 3). The *Sphagna* develope less abundantly in tropical countries, but instead they appear in a great wealth of forms (W a r n s t o r f 12, H e r z o g 3). In the areas between the tropics they grow mostly in the mountains and only exceptionally in the lowlands, for instance in south eastern Brazil (Rio de Janeiro, U l e 10).

The following represents a statistic comparison of the distribution of the species of *Sphagna* as well as the number of the endemic forms on the particular continents:

North America possesses 96 species, 38 of which are endemics
South America „ 125 „ 104 „ „ „ „ (78 in Brazil)
Europe (the Azores) „ 60 „ 9 „ „ „ „
Asia (the Malayan territory) possesses 64 species, 33 endemics (18 in Japan)
Australia and Oceania possess 49 species, 44 of which are endemics
Africa (the Canary Islands) possesses 61 species, 45 of which are endemics
(The above data are drawn from Herzog and Warnstorf).

In the above mentioned comparison the fact (to which Warnstorf (12) and Herzog (3) have drawn attention) strikes us that as far as the number of endemic species is concerned there are two distinct belts:

1) The southern belt including South America, Africa and Australia where the endemics predominate (especially in the sphere between the tropics).

2) The northern belt including North America and Eurasia where we meet mostly wide-spread species and instead a lesser number of endemics, especially in Europe, North America as well as in western and northern Asia. Eastern Asia, and especially Japan, forms a sort of transitory sphere because a greater number of endemic forms already grow there. The cause of this phenomenon is most probably the fact that for long periods of time this area did not undergo any greater climatic changes; neither was it reached by Diluvial glaciations.

The presence of a predominant amount of endemics in South America, Africa and Australia may be to a certain extent explained as follows: the respective parts of the southern continent have been isolated since the Oligocene, therefore the development of the *Sphagna* proceeded separately on each continent, while the areas of the northern belt were united throughout the whole of the Tertiary, and their separation followed — as is supposed — as late as in the Great Interglacial Period (Masovien I, Szafer 8). Therefore the exchange of the flora there might have proceeded in the later periods almost without any interruption. Further on this uninterrupted vegetational period in the areas between the tropics caused a quicker change and a greater abundance of forms (Irmscher 4, p. 294).

However, this is not a sufficient explanation, because observations prove that the vegetation in historically older territories usually shows a greater amount of endemics, while in the areas which have been occupied by the plants not so long ago an insignificant amount

of endemics is met with. For this reason we may suppose that the *Sphagna* have been rather long and well settled in the southern belt, as we find there quite a number of endemic forms (over 80% of species). In the northern belt, however, where from the geological point of view they are more recent new-comers, the differentation of forms has been accomplished only in a very small degree (about 30%, in Europe only 15%).

The wide intercontinental distribution of some species (Eurasia, America, Australia) speaks against a quicker change of forms of the *Sphagna* in the area between the tropics, for instance *Sph. magellanicum, cuspidatum*. This fact proves that long periods of time are necessary for the *Sphagna* to change their forms. Most probably this is connected with lesser genetic possibilities appearing in the lower plants (H e r z o g 3, page 215, I r m s c h e r 4, page 293). Thus the appearance of a larger quantity of endemics among the *Sphagna* points to the long establishment of this flora in the given territory.

The statistic-geographic facts speak in favour of looking for the primary centre of origin of the *Sphagna* in the belt of the southern continents. A great concentration of endemic species being met with today in the territories of South America situated below the Equator (in Brazil * grow — 78 endemic species out of the 125 which live in the whole territory of South America), we should consider the humid areas of the south-eastern Atlantic part of the Brazil Uplands as the probable and hitherto preserved part of the primary centre of origin of the *Sphagna,* from which they migrate to the colder territories southwards as well as northwards. In this way I r m s c h e r (4) explains the bipolar range of some species, for instance *Sph. fimbriatum*.

In favour of this supposition may also speak the lack of the *Sphagna* in the Carboniferous Period in England (W a l t o n 11) which most probably is not accidental, because according to geological data the *Sphagna* might have migrated to Europe from the supposed centre of origin in South America as late as in the Upper Eocene (1). However, it is not out of the question that the *Sphagna* being easily subject to decomposition they might have not been preserved in the fossil state. We are not able, for lack of fossil

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* Even if according to A n d r e w s' views the number of species is reduced, we still find there a predominating quantity of endemics.

remains of *Sphagna* in the older strata, to determine the time of their origin more accurately. As however, according to what I have mentioned above — we already know the accurately determined fossil remains of Bryophytes from the Upper Carboniferous Period (although there are no *Sphagna* among them, and only Hepaticae and Bryales corresponding in their form more or less to the living ones have been found there) we are able to ascribe an at least approximate age to the *Sphagna*. Since further more we know from the biology of the *Sphagna* that today they develope most exuberantly in temperate zones on post-glacial soils, we therefore may assume with a certain degree of probability that the origin of the *Sphagna* dates back to the Permo-Carboniferous Glaciation of the southern hemisphere.

The migration of the *Sphagna* from the South American centre to North America might have taken place as late as at the beginning of the Tertiary, as is known, and even then for not a long period of time, and the present connection of both continents (the Panama) originated no sooner than in the Upper Pliocene. This period of unity of both American continents, short from the geological point of view, explains why we find only 9 species common to both continents, and why it is in North America (especially in its southern part) that we meet a rather high number (38) of endemic species. It is probably for this reason that there originated in North America a secondary centre of development of new forms of the *Sphagna,* hencefrom they migrated to Eurasia.

The appearance of *Sphagna* in Europe followed of course later than in North America. They have been stated paleobotanically in Europe as late as in the Upper Pliocene (K i r c h h e i m e r 5). The small number of endemic forms in the western European refuges points to a comparatively late appearance of the *Sphagna* in Europe although the possibility of their immigration there existed already in the Upper Eocene.

It is possible that a part of the species (the Atlantic element) reached Europe straight from North America in the periods of the connection of both these continents (in the Miocene?). The existence of 80% of common species (51 out of the 60 growing in Europe) points to tnis fact... It seems that they might have migrated from America to Europe via Greenland and Iceland in the Diluvium when there followed the final detachment of Greenland from Europe. This is also proved by the present fairly abundant appearance of the

*Sphagna* on the southern coasts of this island. But the majority of species migrates to Europe by way of Asia through the present Behring Straits and next through southern Siberia. This proceeded most probably in the Upper Tertiary. These specimens have today a wide distribution in the whole of the Holarctic.

Besides the American centre of development of the *Sphagna* there originated a secondary one, poorer than the former, that is the East-Asiatic centre, as it is indicated by the fairly considerable number of the endemics in Japan. The comparison below represents the relation in which the latter centre stands to its neighbouring territories:

| | | |
|---|---|---|
| In Asia we have | 63 | species |
| in common with Europe and North America | 22 | { [one of them also in Java] |
| in common only with Europe | 2 | species |
| in common with Europe, North America and Australia | 5 | ,, |
| in common with the Philippine Islands, Java and New Guinea | 1 | ,, |
| Endemic species in Asia | 33 | ,, |
| out of which in Japan and China | 18 | ,, |
| in the Himalayan Mountains | 3 | ,, |
| in Ceylon | 1 | ,, |
| in the Malayan territory | 9 | ,, |
| in the Philippine Islands | 1 | ,, |
| In south-eastern Asia (China, Japan, the region of Malaya | 1 | ,, |

The presence of only two species *(Sph. Jensenii* and *hakkodense)* common in Eurasia and not growing in North America proves how slight is the influence of this centre on the flora of the *Sphagna* in Europe. The small systematic value of these species which differ slightly from their relative species *(Sph. Jensenii* is similar to *Sph. obtusum* and *Dusenii,* and *hakkodense* to *Sph. palustre)* points to their recency and therefore to the comparatively late separation of America from Asia. We do not possess a single species common only to America and Asia, but instead we have quite a number of species (27) growing in all three continents of the Holarctic, the conclusion from which is that these species of the *Sphagna* are also of American origin although their migration from America to Europe proceeded to a considerable degree by way of Asia.

It is also surprising how feeble is the sphagnologic connection between Asia and the islands of the Melanesian Archipelago. Out

of the species growing in Asia only *Sph. Girgensohnii* is met with in Java, and *Sph. Junghunianum* in Java and New Guinea. But on the other hand they do not grow in Australia. This fact might indicate that they have come to these islands not very long ago, in the Diluvium or perhaps in the Postglacial period, because according to present opinion the separation of New Guinea from Australia took place some time in that period. This would also explain the absence of these species on the continent of Australia.

Five Eurasiatic species growing in Australia *(Sph. palustre, centrale, magellanicum, papillosum, cuspidatum)* are common in North America from where they might have migrated to Asia, and this seems the more certain that we do not meet them at all in the islands of Melanesia. But instead the presence of these species in Australia is explained if we place the primary centre of their origin on the southern continents and if we accept Wegener's theory of the shifting of lands.

*2. The Quantitative Condensation in the Distribution of species of Sphagna on the continents, together with their supposed phylogenetic development from the point of view of Wegener's theory.*

The gigantic southern continent (Gondwana Land) which on the ground of the above data has been acknowledged by us to be the probable primary centre of origin of the *Sphagna,* according to W e g e n e r's theory of the shifting of the socles of lands, in the Mesozoic slowly fell asunder into three separate units: the American, the African-Indian and the Australian continents. From Table 1 in which the quantitative condensation of species of *Sphagna* is shown (in the order of sequence of the phylogenetic development of the sections, S z a f r a n 9), we may see on the continents an amazing conformity between the disintegration of the continents (corresponding to Wegener's theory), and the quantitative condensation of species on the respective continents, as well as their probable phylogenetic development.

The section *Subsecunda,* which is specifically the richest and phylogenetically the oldest, appears in a great quantitative condensation (30, 14, 21) on all the three southern continents. This would correspond to the situation of the lands up to the Trias (I r m s c h e r 4, p. 26) that is to the period while the three continents formed one whole. The phylogenetically younger section *Cymbifolia* shows

a greater quantity of species only in America (43) and in Australia (14), but in Africa there are only three. This is in accordance with the changes of continents which according to W e g e n e r took place from the Jurassic Period to the Eocene when the separation of South America and of the Arctic-Australian land from Africa occured, while the connection of Australia with America by means of the Antarctic still existed. According to I r m s c h e r there was in the Cretaceous Period a connection especially favourable for the migration of plants, when the position of the South Pole was such as to leave a broad belt of the northern Antarctic Land free of ice.

Lastly, during the later geological periods there followed a slow but total isolation of all the three continents, and in connection with this we notice that on the American continent, now distant, and in Australia which is now removed far to the east there dominate quantitatively two different sections, namely the species of the section *Acutifolia* develope strongly in South America, and those of the section *Cuspidata* thrive in Australia. We know that the section *Cuspidata* is most closely related to the section *Acutifolia,* hence we may infer that the rather sudden change of climatic conditions in Australia, now remote, was no doubt a stimulus which brought about a change of forms grouped in the section *Acutifolia* into forms which today are reckoned among the section *Cuspidata.* This supposition is corroborated by the total absence of the species of the section *Acutifolia* on the Australian continent. (Only *Sp. fimbriatum* grows in New Zealand and *Sph. Junghunianum* in New Guinea).

The supposition that the forms of the section *Cuspidata* originated in Australia, as well as the total lack of intermediate localities on the islands of Melanesia between East Asia and Australia, exludes the possibility of migrations of the *Sphagna* from Australia to Asia along this route, which forms one of W e g e n e r's claims, and necessitates looking for the routes of migrations of the Australian forms through the lands of the Antarctic and South and North America to Eurasia.

According to I r m s c h e r there existed geologically the possibility of a migration from Australia to South America through the Antarctic Land in the Cretaceous. The comparison of distribution in Table 1 also speaks in favour of this route; there we see that 4 species of the section *Cuspidata* appear in the Antarctic America, and 6 in South and Central America.

### *3. The Sphagna as a Geographical Element.*

As is generally known the *Sphagna* grow nowadays on all continents but they develop in a mass above all in the coastal areas subject to the influence of oceans and seas characterized by their humid (oceanic) climate and not too low a temperature. They often penetrate, in ranges larger or smaller and sometimes detached, into the interior of the continents making use of any kind of territory where moisture is available in large quantity, such as river valleys, higher mountains, etc. Most often they grow in a complex of special plant societies passing under the name of „peat-bogs". But they are almost never met with in continental or desert territories.

As is evident from the data given in the first chapter, certain facts speak in favour of the *Sphagna* being of South-American origin, since at the present time they develop most abundantly on the shores of the southern hemisphere, and for this reason G a m s (2) reckons them among the oceanic or hygrothermic element which he considers to be the oldest in the Bryophyte flora of the Holarctic.

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TABLE 1.

The quantitative Condensation in the Distribution of Sphagna on the continents, according to sections, in the order of their supposed phylogenetic development.

| | Subsecunda | Mollusca | Cymbifolia | Eurigida | Polyclada | Squarrosa | Truncata | Fimbriata | Euacutifolia | Eucuspidata | Laciniata | Sericea | Mucronata | Together |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. North America, Eurasia | 3 | 1 | — | 1 | 1 | 2 | 1 | — | 7 | 5 | 1 | — | — | 22 |
| 2. North America | 19 | — | 5 | — | — | — | — | 2 | 5 | 5 | 1 | 2 | — | 38 |
| 3. Eurasia | — | — | 1 | — | — | — | — | — | — | 1 | — | — | — | 2 |
| 4. Asia (Japan) | 10 | — | 4 | — | — | — | — | 1 | 6 | 3 | — | — | — | 24 |
| 5. North America, Europe | 10 | — | — | — | — | — | — | — | 4 | 3 | — | — | — | 17 |
| 6. Europe (the Azores) | 5 | — | — | — | — | — | — | — | 2 | 2 | — | — | — | 9 |
| 7. North and South America, Eur. Austr. | — | — | 1 | — | — | — | — | 1 | — | 1 | — | — | — | 3 |
| 8. North America, Europe, Australia | — | — | 3 | — | — | — | — | — | — | 1 | — | — | — | 4 |
| 9. North and South America, Eurasia | — | — | 1 | — | — | — | — | — | 1 | — | — | — | — | 2 |
| 10. South America, Eurasia, Malaya | — | — | — | — | — | — | — | 1 | — | — | — | — | — | 1 |
| 11. North Central America, North Africa | — | — | — | — | — | — | — | — | — | — | 1 | — | — | 1 |
| 12. North and South America, Europe | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 |
| 13. North and South America | 4 | — | 1 | — | — | — | — | — | — | — | — | — | — | 5 |
| 14. Antarctic, North America, Europe | — | — | — | — | — | — | — | — | — | 2 | — | — | — | 2 |
| 15. Asia, the Malayan territory | — | — | — | — | — | — | — | — | 1 | — | — | — | — | 1 |
| 16. South America | 30 | — | 43 | — | — | — | 1 | — | 26 | — | — | — | — | 100 |
| 17. South and Central America | — | — | — | — | — | — | — | — | — | 6 | 1 | — | — | 7 |
| 18. Australia, Oceania | 14 | — | 14 | 2 | — | — | — | 1 | — | 18 | 2 | 1 | 1 | 53 |
| 19. Equatorial America | 21 | 1 | 3 | 3 | — | — | — | — | 5 | 9 | — | — | 3 | 45 |
| 20. Antarctic America | — | — | — | — | — | — | — | — | — | 4 | — | — | — | 4 |
| 21. Antarctic America, Australia | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 |
| the Sum: | 116 | 2 | 76 | 8 | 1 | 2 | 2 | 5 | 58 | 60 | 5 | 3 | 4 | 342 |