

THE IMPORTANCE OF ECOLOGY FOR GENERIC AND SPECIFIC DIFFERENTIATION IN THE ARACEAE-AROIDEAE

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It is Meusel's (1951) merit to have pointed out the significance of growth-habit for interpreting the evolution of a particular group of plants. In his paper he chose Araceae and Lemnaceae as striking examples to prove his point. While it is rather difficult to translate the German terminology he used for those plants which produce persistent parts above the ground, the term "geophytes" fits well for all those which persist with their subterranean parts alone. Among Araceae, rhizomatous and tuberous geophytes are known. Subfamily Aroideae is composed almost entirely of members of the latter group with the exception of plants growing in water or at least swampy ground, like *Lagenandra*. While, according to Meusel, intermediates between rhizomatous and tuberous geophytes are found in Colocasioideae, geophytes are rare or absent in the rest of the family.

Advantages of geophytic growth habit are obvious; it is possible for the plant to survive during unfavorable periods in a very reduced state underground. The ecological implications of this advantage can easily be seen: not only habitats different from those colonized by members of Araceae devoid of it can be conquered but the whole area of distribution can be extended considerably. Araceae are primarily a group of tropical and subtropical plants growing in areas in which seasonal changes of tem-

perature are slight and there is no period of more or less extreme drought even during the dry season. Where subterranean parts alone are responsible for the survival of an individual, periods of drought and/or low temperatures can be bridged without any harm.

There is little doubt that extratropical Aroideae evolved from tropical ancestors, and several tribes (for an updated system of the family based on Engler, 1920, see Bogner, 1978) are confined to tropical areas even today. There is, however, a marked preference for more extreme habitats such as high altitudes, slopes, etc., even in these. Genera like *Spathantheum* are confined to the upper levels of the Andes in Bolivia and Peru; for species like *Asterostigma lividum* (Lodd.) Engl. we find label data noted by the collector of the type cited by Engler, l.c., 'in den Waldungen des Corcovado an abschüssigen Stellen' (in the forests of Corcovado on steep slopes.)

Being more experienced in extratropical regions of the Old World I may be excused if the ideas developed in this paper are centered on tribe Areae with its mainly extratropical distribution. The tropical species included here are further examples of ecological specialization, often growing in mountainous districts. In the whole group, *Arisaema* Mart. is not only the genus with the greatest number of species by far within the group, but also

with the widest ecological and geographical range of distribution. Two or three characters can be mentioned as comparatively primitive: the number of ovules in one ovary is greater than one as a rule, the filiform, sterile male flowers are developed upwards to the apex of the spadix in some species (the osmophores on the club of *Arum*, for instance, can be derived morphologically from the bases of extremely reduced staminodial flowers), and some of the species are dioecious. Series *Fimbriata* Engl. with numerous staminodial flowers up to the top of the spadix has a south-eastern Asiatic distribution in Malaysia and Indonesia in the zone of the monsoon forests.

Prime (1960) raised the question of whether genera with a very limited distribution within the Araceae are primitive relics or rather very young, advanced groups which could not spread more widely during the comparatively short time of their existence. In the case of *Helicodiceros* Schott, the first alternative seems to be more likely for the same reasons we mentioned in *Arisaema*. The whole distal part of the spadix is covered with subulate staminodial flowers. There are up to six ovules in each ovary, and female flowers are numerous. The only species grows on coastal rocks on a few Mediterranean islands such as Corsica, Sardinia and some of the Balears.

Ambrosinia L., another monotypical genus, on the other hand has two centers of distribution which are separated by the whole width of the Mediterranean Sea and each of which is comparatively small: Corsica, Sardinia, Calabria and Sicily in Europe, Algeria and Tunisia in North Africa. In Africa, it is confined to a short distance

from the coast and the northern declivities of the adjacent hills. The number of female flowers is reduced to one here, the ovary is multiovulate. The sterile apex of the spadix is reduced. Reduction of the whole plant seems to have gone rather a long way towards Lemnaceae already, though it is certainly not among the ancestors of this family: small size, reduced number of leaves, which are broadly elliptical resembling the first leaves after the cotyledon of other Araceae, the fairly small number of male flowers, which are arranged in two series on one side of the spadix all indicate a long phylogenetic history. It is growing in rocky or sandy places, in grassy vegetation, degraded forests, hedges and especially macchia-like scrub. This is a typical habitat of several Mediterranean Araceae, members of the genus *Arum* like *A. pictum* L.f. with a very similar geographical distribution, *Helicodiceros muscivorus*, or the widespread *Arum italicum* Mill., *Dracunculus vulgaris* Schott, *Arisarum vulgare* Targ.-Tozz. or *Biarum tenuifolium* (L.) Schott.

If we try to discover a general pattern of ecological distribution in Aroideae, we find two principal trends starting from intermediary mesophilic plants, one leading from mesic to semiaquatic and aquatic habitats, another to dry habitats which cannot be colonized by any other group of Araceae. In the first group, *Cryptocoryne* and *Lagenandra* are the extremes which no longer have tuberous, but slender, elongated rhizomes with secondary fibrous roots at the nodes. Their distribution in the zone of monsoon rainfall in southeastern Asia indicates that they can be derived directly from tropical ancestors but

they show a number of unusual morphological specializations. Other Aroids don't go as far as that but prefer moist ground along river banks or in narrow ravines. The driest localities colonized by Araceae are rocky or gravelly places in the Mediterranean region with open vegetation and a resting period during summer. To illustrate my point I shall give a short account on ecological as a parallel to taxonomical differentiation within the genus *Arum*.

Arum creticum Boiss. et Heldr. and *A. pictum* L. f., mentioned already before, stand apart morphologically from all the other species of the genus, but fit well into the pattern of ecology displayed by other Aroids growing in rocky places in the Mediterranean region. They both have a very limited distribution, the first one being confined to Crete and Karpathos, and may well be regarded as ancient relics. The most widespread species, on the other hand, *A. italicum*, grows in similar places, but has a much wider ecological range including moist places. It is a matter of personal opinion whether it should be split into a number of closely related species with a higher degree of ecological specialization, or whether Engler's example should be followed. *Arum italicum* var. *intermedium* Mutel was collected along rivulets on Corsica by Briquet, var. *concinatum* (Schott) Engl. subvar. *wettsteinii* (Hruby) Engl. and subvar. *marmoratum* (Schott) Engl. in moist places on Crete by Reverchon. According to Engler, the typical variety is especially common on moist, loamy soil. Certainly, it is not a species of shady forests but prefers open country, hedges and shrubby vegetation. It seems to avoid ecological extremes, but re-

sist occasional drought for a short time at least. In Bulgaria, Velenovsky found it most often near *Paliurus spina-christi*, a shrub of hot, dry, stony places that gives very little shadow itself. *Arum nigrum* Schott is similar ecologically, growing on stony and bushy slopes in Yugoslavia not too far from the coast, so that it always receives a certain amount of damp air. Other species of the Mediterranean region with similar ecological demands are *A. dioscoridis* Sibth. et Sm., *A. conophalloides* Kotschy ex Schott and *A. hygrophilum* Boiss. According to label-data cited by Engler, they grow near rivulets, springs or waterfalls, *A. hygrophilum* also near mountain tops where water from melting snow is always available. Either humid soil or damp air, commonly both, are essential even for these species, which are growing in normally dry areas.

Arum is one of the few genera within the family that reaches the temperate region of Europe, with *A. maculatum* L., while *A. orientale* M.B. subsp. *alpinum* (Schott et Ky.) H. Riedl is found in eastern and east-Central Europe and *A. italicum* in Western Atlantic Europe. There seem to be no great differences in ecology between *A. maculatum* and *A. italicum* in England, where the latter species has its northern limit. It is interesting to note that it changes its ecological preferences considerably outside the Mediterranean region. Prime, l.c., writes "The rare lords-and-ladies grows in rather similar situations to the common plant, and in some localities the two grow together. It is a plant of light shade, liking a little shelter and requiring a moist, well-drained, fairly calcareous soil." The time of flowering is delayed in the North; it starts in June, when *A. maculatum*

has finished already. The same author characterizes the habitat requirements of *A. maculatum* briefly: ". . . a common British plant which adorns our hedgerows and woods in spring and autumn." According to Oberdorfer (cited by Riedl, 1979) *A. maculatum* grows in various types of deciduous forests in Central Europe, preferring fairly moist localities. Where it meets *A. orientale* subsp. *alpinum* its ecological range becomes more restricted. South of Vienna, where *A. orientale* is near its western limit, *A. maculatum* is confined to woods known as Alno-Padion to plant sociologists, while *A. orientale* subsp. *alpinum* is found in beech-forests, but also in the drier Querceto-Carpinetum, an association of limited distribution filling the gap between the more Atlantic beech-forests and the eastern forest steppes with several species of oaks. Beech-forests are among the favorite habitats of *A. maculatum* in more humid areas. *A. orientale* subsp. *alpinum* has been described from Romania by Schott and Kotschy, and it does not seem to go farther east. *A. orientale* M.B. subsp. *orientale* replaces it to the east, growing in mountain forests and more open, rocky ground of Turkey, the Caucasus and the southern Ukraine. Engler united *A. elongatum* Stev. with *A. orientale*, though it is a quite distinct species that is most common in Turkey and northern Iran. Ecologically, the two species do not seem to be very different from each other, but the available data are not sufficient for my own judgment in this question.

Certainly, resistance against drought is never very great in Araceae. They always retain a certain amount of dependence on air-

humidity, either growing along creeks or in coastal areas even in countries as dry as Libya, where the only endemic species of *Arum* in Africa, *A. cyrenaicum* Hruby, is found in a few places. There are two more genera of rather dry areas in Aroideae, *Biarum* Blume and *Eminium* Schott. Their representatives also seem to prefer comparatively humid localities. On the other hand, there are also examples of Aroids growing in monsoon-influenced countries, that show a tendency towards a moderate drought tolerance such as *Theriophonum zeylanicum* N.E. Brown, which grows in grassy places in the drier parts of Ceylon according to Engler.

How can we try to interpret all these facts in terms of evolutionary steps leading to the differentiation of genera and species as we find them today? As we have seen, the presence of tuberous rhizomes enabled Aroids from tropical areas to migrate northwards beyond the zone of monsoon rainfall. Especially species growing in higher altitudes in the tropics could find similar conditions under a more temperate climate. Obviously, more different combinations of characters like leaf-shape and -division, number of ovules in each ovary and position of the placenta within the ovaries were present in the past, before the genera known today started to differentiate. There were two passages from the African continent available, one in the East and one in the West, when the old Tethys sea began to withdraw more and more. The Indian subcontinent, part of the ancient Gondwana land-mass together with Africa, served as a vehicle itself, when it moved across the sea to join Asia leading eventually to the rise of the Hima-

laya mountains from sediments deposited in the Tethys before. In the West, no changes as drastic as those in the East took place, but there were obviously a few land-bridges that broke down comparatively late, leaving behind as pillars some of the present day Mediterranean islands such as Crete. The drying up of the old Tethys had considerable influence on the climate of the neighboring continents: this effect was less clearly marked in the East, as humid air was barred on its way north from the Indian Ocean by the Himalayas, and most of the humidity was retained in lower latitudes. In the West, the climate north and south of the Mediterranean grew drier and drier all the time, leading to the origin of the Sahara in the warmer southern parts, that made further migrations of plant species impossible. It was the human impact, however, with deforestation of large areas in southern Europe, that strengthened the adverse climatic forces north of the Mediterranean. In terms of plant geography that means that isolation from the tropical ancestors was strong in the West, while these ancestral types themselves could reach higher latitudes in the East and evolve continuously to more advanced taxa. No adaptation to dry habitats was necessary there, but on the contrary, plants with long, creeping rhizomes living in boggy places or submerged in water appeared in subtropical parts of southeastern Asia.

In the West, plants adapted to a warm, moist climate disappeared completely, and only those species could survive which were less sensitive to a changing climate. They withdrew to places where at least a moderate, constant supply of water was secured, and from there adap-

tive evolution started again producing new, ever more resistant taxa. By splitting up of the old continuous area of distribution and extinction of intermediate forms, isolation among the relics of the former, more humid period was considerably strong, so that the number of small, distinct genera is comparatively high, while in the East the genus *Arisaema* spread to nearly all kinds of available habitats. For the plants in the West, three possible ways remained open for the future: they had either to adapt to a more temperate, humid forest climate like *Arum maculatum*, or to a warm, but dry environment like *A. italicum*, or their area of distribution became restricted to a few ecologically specialized localities often separated by long distances like that of *Helicodiceros muscivorus*. Probably, the choice between the first two did not mean such a sharp contrast in the beginning as it does now: before the uprise of human civilization in the Mediterranean region, forests covered most of the land everywhere except on the steep mountain slopes on which bare rocks prevailed. These Mediterranean forests may have been richer in Aroids than the present day Mediterranean environment. The step from there to temperate forests on one side, to the degraded macchia-scrubland and related types of vegetation on the other is comparatively small. Degradation, moreover, took its time, so that adaptation of more advanced taxa was possible. Polyploidization may have played its part in this process. It is not by mere accident that polyploidy is much more important in *Arum* and *Biarum* than in *Arisaema* and other groups of Aroids growing in the East. The appearance of new types of habitats is

one of the strongest forces in the evolution of new taxa by adaptive radiation after a period of isolation of the relics from an earlier age. Things may not be as simple as my explanation of them suggests, but understanding of the more intricate patterns will follow as soon as the prevailing trend has been discovered. This trend, almost certainly, has its origin in the evolution of the environment through interaction of major tectonical and climatological events as outlined above with all their numerous consequences for various ecological factors influencing plant-life as a whole.

Literature Cited

- Bogner, J. 1978. A critical list of the Aroid genera. *Aroideana* 9(3):63-73.
- Engler, A. 1920. Araceae-Aroideae und Araceae-Pistioideae, in *Das Pflanzenreich IV*. 23 F. - Leipzig: Wilhelm Engelmann.
- Meusel, H. 1951. Die Bedeutung der Wuchsform für die Entwicklung des natürlichen Systems der Pflanzen. - *Fedde Rep. sp. n.* 54: 137-172.
- Prime, C.T. 1960. *Lords and Ladies*. - London: Collins.
- Riedl, H. 1979. Araceae, in G. Hegi, *Illustrierte Flora von Mitteleuropa*. 3rd. ed. Vol. II, 1:318-334. - Berlin - Hamburg: Verlag Paul Parey.

SHORT COMMUNICATIONS

At the V International Symposium on Tropical Root and Tuber Crops held in Manila recently, a unanimous decision was taken by all present to have a Committee responsible for unravelling the existing confusion of the taxonomy of aroids, in particular the cultivated species of *Colocasia* and *Xanthosoma*. Dr. Farah D. Ghani was appointed to head the committee.

Any members of the society who have access to direct observations or literature on these plants as they are cultivated in the tropics are urged to communicate with Dr. Ghani at MCR, Wye College, University of London, Wye nr. Ashford, KENT TN25 5AH, England.

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From Mark Moffler: I am interested in obtaining plant material of *Homalomena* for a revision of the neotropical species. I am especially interested in live new and old world plants of known origin, though plants of unknown origin may be considered. Preserved materials are also solicited. Collectors with plant material for sale or trade please contact: Mark D. Moffler, 2604 E. Yukon St., Tampa, Florida 33604.

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From Dr. Croat: Since my revision of *Anthurium* of Mexico and Central America is now almost finished, duplicates of living plants of some species are available for exchange for South American species, or for sale. See pages 107 and 108 of Volume 2, No. 4 of AROIDE-

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