AGAURIA AND AGARISTA:

An example of tropical transatlantic affinity

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ABSTRACT. Anatomical and morphological studies in the Andromedeae (which includes the Gaultherieae) show that there are two groups of genera within this tribe of the Ericaceae: the *Lyonia* group, made up of *Lyonia*, *Craibiodendron*, *Agauria*, *Arcterica* and *Pieris*; and the *Gaultheria* group, which includes *Gaultheria*, *Leucothoë*, *Zenobia*, *Diplycosia*, *Pernettyopsis* and *Tepuia*. *Oxydendrum*, *Andromeda* and *Chamaedaphne* are isolated genera. Section *Agastia* of *Leucothoë* has been wrongly placed in *Leucothoë*; it is restored to generic rank as *Agarista*, which is placed in the *Lyonia* group. It is shown that *Agauria* and *Agarista* are two very closely related genera, more closely related to one another than to other genera. Both are tropical montane plants, and together form a distribution pattern spanning the South Atlantic: *Agauria* is found in Africa, Madagascar and the Mascarenes; *Agarista* is mainly S American. The significance of this distribution pattern is discussed, and it is concluded that continental drift in the early part of the Cretaceous is the most likely cause of the American–African distribution pattern. Owing to the geologically transient nature of their montane habitats, the details of their present-day distribution throw little light on the events causing the initial sundering of the range of *Agauria* and *Agarista*; other, more recent, causes are operative at the level of the details of the present-day distribution.

INTRODUCTION

During the course of examination of some generic and tribal limits in the Ericaceae (Stevens, 1969), the generic limits in part of the Andromedeae were found to be awry. As a result of this, a particularly interesting and unusual distribution pattern had been obscured. There is a close relationship between *Agarista*, previously included in *Leucothoë*, found predominantly in S America, and *Agauria*, from Africa, Madagascar and the Mascarenes.

It is essential for the interpretation of any distribution pattern that the relationships of the plants concerned be correctly established; this problem is particularly acute here since *Agarista* has been included in *Leucothoë*, which belongs to a different group of genera from *Agauria*, *Agarista* and their relatives. The first section of the taxonomic part of this paper is devoted to establishing the main generic groupings of the Andromedeae as a background for the ensuing taxonomic and phytogeographic discussion. In section 1b reasons are given for removing *Agarista* from *Leucothoë*, and in section 1c the close similarity between *Agauria* and *Agarista* is shown. Finally, in section 1d, the relationship of this pair of genera to the rest of the group to which they belong is discussed. The second part of the paper is a discussion on the significance of the distribution pattern observed.

The anatomy of over 175 species of the Andromedeae has been examined. Leaves and portions of stem have been boiled up in water to resuscitate them; the stem has been sectioned at nodal and internodal regions, the leaf at different levels of the petiole and lamina. The epidermis from both sides of the leaf, calyx and corolla has been examined. In addition, details of indumentum and gross morphology have been studied and particular attention has been paid to seed type. Of the genera particularly under discussion, 23 out of 42 species of *Leucothoë* (including 15 of the 34 species

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now placed in *Agarista*) have been examined anatomically; the gross morphology only of some other species of *Agarista* has been studied. The nomenclature of *Leucothoë* follows Sleumer (1959). Only one species of *Agauria*, with eight varieties, is recognised by the latest monographer of the genus (Sleumer, 1938); material from all over its range has been examined.

1. Taxonomic Considerations

1a. Generic groupings in the Andromedeae.

The Andromedeae as recognised here include the Gaultherieae (see below) and so has limits similar to the Andromedeae of Hooker (1876) rather than Drude (1897). *Orphanidesia*, *Epigaea* (both members of the Rhododendroideae), *Enkianthus*, *Cassiope* and *Harrimanella* are not closely related to the other Andromedeae (Stevens, 1969, 1970) and so will not be discussed further.

The Lyonia group of genera comprises *Lyonia*, *Craibiodendron* (including *Nuihonia*), *Pieris*, *Agauria*, *Arcterica* and, as will be shown, *Agarista*. The similarities between the members of this group have previously been unrecognised because characters such as placental position, stamen appendages and various details of lamina anatomy have been misinterpreted. There has been a tendency to consider the presence or absence of stamen appendages and the position of the placenta as diagnostic characters; taxa differing in such characters could not be closely related. The re-evaluation of these characters, together with the use of new characters from anatomy, testa and stamen, have been of great help in clarifying relationships in this part of the Ericaceae,

Matthews & Knox (1928) showed that there were all intermediates between the paired appendages occurring on the filament and those at the anther-filament junction; these appendages are called spurs. Loss of spurs has occurred independently several times even within *Lyonia*; the presence of spurs varies infra-specifically in *L. villosa* and *L. ovalifolia*. The same variability is shown by the spurs of some of the Vaccinieae. Awns are apparently terminal on the anther; there are often two on each theca, but only one in *Andromeda* and a few species of *Gaultheria* and *Leucothoë*. There do not seem to be plants with appendages in a position intermediate between awns and spurs. Although genera like *Agauria*, *Lyonia*, *Chamaedaphne* and *Oxydendrum* may have two pairs of minute projections at the top of their anthers, these do not seem to be comparable to the large awns found in *Gaultheria*, *Leucothoë*, etc. Awns and spurs are visible before the dehiscence of the anther but these small projections seem to be formed after, and as a result of, dehiscence. Although more detailed studies are needed, there can be no doubt that stamen appendages in the two groups of genera mentioned below are different: one group has awns, the other has spurs.

Hooker (1876) had a fairly good idea of the Lyonia group: *Agarista*, *Agauria* and *Lyonia* together formed a sub-group of the Andromedeae since they all had dorsally muticous anthers. Hooker noticed a connection between these genera and *Pieris*, but since he over-weighted the presence of appendages on the stamen he placed *Pieris* with *Zenobia*, *Andromeda* and *Enkianthus*. All these genera have dorsally aristate anthers, the aristae being on the anther or filament (these "aristae" included both awns and spurs);

included in *Pieris* were all those species of *Lyonia* which had anther appendages.

Niedenzu (1890), as a result of his anatomical studies on the Andromedeae, placed *Agauria*, *Agarista* and *Leucothoë* in a subtribe, the Leucothoinae, in which the hairs had a well developed stalk with elongated cells; the other subtribe, the Pierinae, had hairs with a shorter stalk. Niedenzu recognised the Leucothoinae even though he noticed that *Leucothoë* itself had the same stomatal type as *Gaultheria*. *Gaultheria* was placed in the Gaultherieae, which was characterised by the frequent presence of fibres in the mesophyll, the so-called "spicular cells"; there was also often a hypodermis.

Drude (1897) failed to recognise the Lyonia group of genera. *Agarista* was included as a section in *Leucothoë*, *Pieris* and *Zenobia* were included in *Andromeda*, and *Chamaedaphne* in *Lyonia*. He recognised the Gaultherieae as a tribe.

No subsequent classifications of the family have recognised a group of genera centred on *Lyonia*, although *Gaultheria*, *Pernettyopsis*, *Pernettya* and *Diplycosia* are recognised as a separate tribe, the Gaultherieae.

THE LYONIA GROUP. The *Lyonia* group of genera usually has biseriate hairs, although the heads are scale-like in *Lyonia* section *Lyonia*. Bracteoles are paired and usually at the base of the pedicel. The stamens usually have slender, geniculate filaments and short, rather broad anthers with a white deposit of dissolution tissue at the anther-filament junction; appendages, where present, are spurs (fig. 1g). The style is quite often swollen. The cells of the testa have rather thin walls and are nearly always much elongated (fig. 2f). The foliar stomata are anomocytic; lignification of the epidermis occurs in at least some species of all genera. This lignification is best developed on the inner periclinal walls, especially those of the abaxial epidermis and at the edge of the leaf. A few species have a hypodermis; fibres in the mesophyll are found only rarely. Bands of fibres are found in the secondary phloem. No other type of lignified cells or pattern of arrangement of such cells has been seen. These bands of fibres have been seen in all genera apart from *Arcterica*, but since most of the material examined has been herbarium material, the observation of this character has been difficult. Pith types are variable within the group, although they are almost constant at the generic level. Chromosome numbers are known from 6 species of three genera, *Lyonia*, *Agarista* and *Pieris*; they are all $x = 12$.

THE GAULTHERIA GROUP. The *Gaultheria* group of genera consists of *Leucothoë*, *Zenobia*, *Gaultheria* (including *Pernettya* and *Chiogenes*), *Pernettyopsis*, *Diplycosia* and probably *Tepuia*, although no material of the last-named genus has been seen. Here the multicellular hairs are always multiseriate. Bracteoles are usually paired and are often borne at the top of the pedicel. The stamens often have stouter filaments which are never geniculate, although those of *Diplycosia* may be bent (fig. 1j). Anther awns are found in *Gaultheria*, *Leucothoë* and *Zenobia*; dissolution tissue is found in these three genera. In the other three genera of the group, as well as a few species of *Gaultheria*, the anther thecae are prolonged into terminal tubules. The cells of the testa are variable in shape and thickness, but they are often little elongated in *Gaultheria*, *Leucothoë* and *Zenobia*. The "fruits" of *Pernettyopsis*,

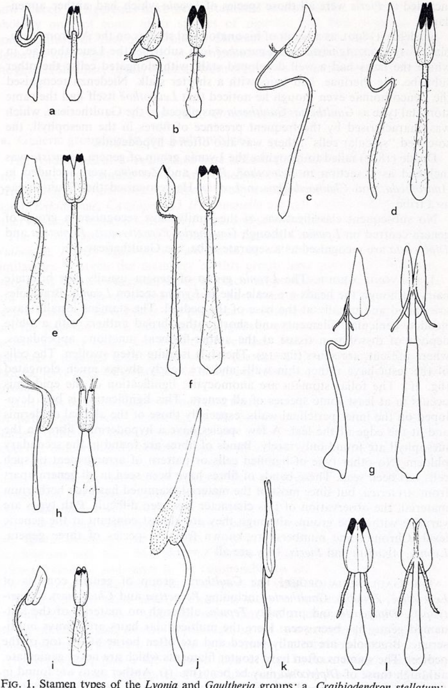

FIG. 1. Stamen types of the *Lyonia* and *Gaultheria* groups: a, *Craibiodendron stellatum*; b, *Lyonia compta*; c, *L. foliosa*; d, *L. macrocalyx*; e, *Agauria salicifolia*; f, *Leucothoë* (= *Agarista*) *populifolia*; g, *Pieris phillyriifolia*; h, *Leucothoë griffithiana*; i, *L. grayana*; j, *Diplycosia microphylla*; k, *Chamaedaphne calyculata*; l, *Arcterica nana*. All x 10 apart from j and l, which are x 20.

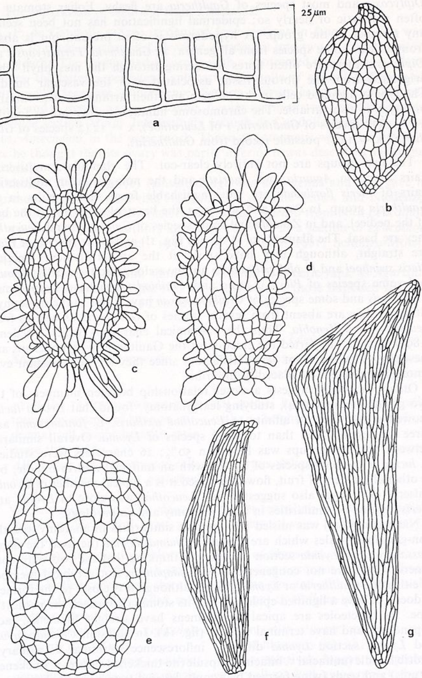

FIG. 2. Seed and epidermis of *Agarista*, *Agauria* and *Leucothoë*: a, *Agarista organensis*, divided epidermis; b, *Leucothoe keiskei*, seed x 50; c, *L. griffithiana*, x 31; d, *L. davisiae*, x 50; e, *L. fontanesiana*, x 50; f, *Agauria salicifolia* var. *buxifolia*, x 31; g, *Agarista mexicana*, x 50.

Diplycosia and most species of *Gaultheria* are fleshy. Foliar stomata are often paracytic or nearly so; epidermal lignification has not been seen in any member of the group. A hypodermis is often present, but is absent from at least some species from all genera; in *Gaultheria, Pernettyopsis* and *Diplycosia* there are often fibres wandering through the mesophyll which originated from the fibrous tissue associated with the vascular bundles. The type of lignified cells in the phloem and their arrangement is variable; pith type is also variable. The chromosome numbers known are as follows: x = 11 (10 species of *Gaultheria*, 1 of *Leucothoë*), x = 12 (2 species of *Gaultheria*), x = 13 (1 possible record from *Gaultheria*).

The two groups are not entirely clear-cut. The glandular, multiseriate hairs found in *Agauria* and *Agarista* and the non-glandular multiseriate hairs of *Pieris floribunda* are indistinguishable from similar hairs in the *Gaultheria* group. In *Pieris* and *Arcterica*, the bracteoles are not at the base of the pedicel, and in *Zenobia* and some species of *Gaultheria* and *Leucothoë* they are basal. The filaments of *Arcterica* (fig. 1l) and some species of *Pieris* are straight, although they have spurs at the anther-filament junction. *Pieris swinhoei* and *P. phillyriifolia* do not have elongated testa cells. *Agauria* and some species of *Pieris*, *Lyonia* and *Craibiodendron* have hypodermes; *P. cubensis* and some species of *Craibiodendron* have fibres in the mesophyll, although they are absent from several species of *Gaultheria* as well as from *Leucothoë* and *Zenobia*. Thus the anatomical characters which Niedenzu (1890) thought supported the erection of the Gaultherieae (hypodermis and mesophyll fibres) are not very satisfactory since they are not constant even amongst the genera he placed in the tribe.

Other work also suggests a closer relationship between members of the two groups. Lems (1964), studying leaf anatomy, found that *Lyonia lucida* showed greater overall affinity to *Leucothoë axillaris*, *L. fontanesiana* and three species of *Pieris* than to other species of *Lyonia*. Overall similarity between the two groups was less than 50%; 26 characters were studied. *L. lucida* is the only species of *Lyonia* with an unifacial midrib bundle, but in other characters of fruit, flower and seed it is a typical member of *Lyonia*. Palser (1951, 1952) also suggested that *Leucothoë* was close to *Lyonia* and *Pieris* because of similarities in floral anatomy and embryology.

Niedenzu (1890) was misled by apparent similarities in anatomy and the non-glandular scales which are found in *Chamaedaphne* (he used the name *Cassandra*) and *Lyonia* section *Lyonia* into thinking that the two were congeneric. They are not congeneric; *Chamaedaphne* is not a typical member of either the *Gaultheria* or *Lyonia* groups, although it is closer to the former. It does not have a lignified epidermis and its stomata approach the paracytic type. Its bracteoles are apical; its stamens have straight filaments, lack appendages and have terminal tubules (fig. 1k). In addition *Chamaedaphne* and *Lyonia* section *Lyonia* differ in inflorescence (terminal v. axillary), midrib bundle (unifacial v. bifacial), capsule (no thickened sutures v. thickened sutures) and seeds (wing formed by a multi-layered testa v. no such wing).

Both *Andromeda* and *Oxydendrum*, the two genera of the Andromedeae which have not yet been discussed, are isolated from the rest of the tribe in characters of vegetative and floral anatomy, inflorescence, flower and embryology. *Andromeda* has a partially lignified epidermis, but its other characters are not those of the *Lyonia* group.

1b. The separation of *Agarista* from *Leucothoë*.

A. P. de Candolle (1839) recognised four sections in *Leucothoë*. He was the first to place *Agarista* in *Leucothoë*, dividing it into two sections, *Agastia* and *Agauria*. The former had a corolla with a contracted mouth and axillary racemes, the latter a persistent, sub-carnose corolla of a similar shape and a supposedly terminal inflorescence. Section *Euleucothoë* had a cylindrical corolla and a dense, axillary raceme. *Lyonia mariana* was also included as *Leucothoë* section *Maria*. Interestingly enough de Candolle described a new genus, *Amechania*, in the same work. This is synonymous with *Agarista*, but since he thought that its ovary was partly inferior it was described under the Vaccinieae.

Although Hooker (1876) reinstated *Agarista* as a genus and also gave it its present limits by removing *Agauria* as a separate genus, and Niedenzu (1890) found anatomical characters separating *Agarista* from both *Leucothoë* and *Agauria*, all recent authors have kept *Agarista* as a section of *Leucothoë* (e.g. Drude, 1897; Sleumer, 1936 & 1959; Wood, 1961; Schultze-Motel, 1964).

Leucothoë section *Agastia* should be restored to generic rank as *Agarista*. The characters separating the two are listed below; those italicised suggest that *Agarista* belongs to the *Lyonia* group of genera.

	Agarista	*Leucothoë*
1.	*Stomata always anomocytic*	Most species with paracytic stomata, all with many paracytic configurations.
2.	13 of the 15 species whose anatomy was examined have an epidermal cell height:breadth ratio more than 1 (fig. 2a).	All species have low epidermal cells with a height:breadth ratio of c. 0·5.
3.	*All species have epidermal cells with lignified inner periclinal walls.*	Epidermis unlignified.
4	Veinlet reticulum very dense, higher order lateral veins prominent.	Veinlet reticulum less dense, higher order lateral veins less prominent.
5.	Bands of fibres in the phloem.	Bands of fibres not seen.
6.	Pith is *Calluna*-type, with small, thick-walled cells round the outside and large, thin-walled cells in the centre.	Pith is homogeneous (all cells about the same size and with the same wall thickness) or *Calluna*-type.
7.	*Stamens with slender, geniculate filaments* (fig. 1f).	Stamens with stouter, more or less straight filaments (fig. 1h, i).
8.	*Anthers rather short, without appendages, although they may be slightly bifidly apiculate.*	Anthers relatively longer, all species with well-marked awns, apart from *L. davisiae* and *L. grayana.*
9.	*Top part of the style swollen.*	Top part of the style not swollen.
10.	*Cells of the testa much elongated* (fig. 2f, g); no species having winged seeds.	Cells of the testa not much elongated (fig. 2b–e); most species having winged seeds.

There are other characters which might be investigated. The leaves of *Leucothoë* definitely have convolute vernation; this also seems to be so in *Agarista* (*Leucothoë populifolia*), so far as could be seen from the dissection of young shoots of herbarium material. Some of the S American species which have very revolute leaves when mature may have revolute vernation.

Lems (1964) found that the vein endings of *Agarista* (he cites the species he studied as *L. acuminata* and *L. mexicana*) were much shorter than in *Leucothoë* sensu stricto. He also quantified the vein reticulum density and found that in *Agarista* (*Leucothoë acuminata*) the vein lengths per unit area were 60–100 cm/cm^2 of leaf; comparable figures for *L. axillaris* were 45–58 cm/cm^2. These two species live in the same habitat. Two other species of *Leucothoë* had less than 60 cm/cm^2 of leaf; *A. mexicana* had an even denser reticulum than *Agarista* (*Leucothoë acuminata*).

In view of the numerous and important differences between *Leucothoë sensu stricto* and *Leucothoë* section *Agastia*, the latter is restored to generic rank as *Agarista*. *Agarista* is a member of the *Lyonia* group of genera, rather than the *Gaultheria* group to which *Leucothoë* belongs. New combinations in *Agarista* will not be made here, since the author does not have sufficient knowledge of specific limits within the genus. Fortunately, most species already have combinations in *Agarista*.

1c. The relationship between *Agauria* and *Agarista*.

Madagascar species now placed in the genus *Agauria* were included in *Agarista* without comment in the original description of the latter genus by D. Don (1834). A. P. de Candolle (1839) was the first to recognise the two as separate entities, although both were included in *Leucothoë* as sections and the characters used to separate them were not good ones: there is no difference in corolla shape or inflorescence position. Most authors have followed Hooker (1876) in maintaining *Agauria* as a genus, although the characters originally used to separate it from *Agarista* were poor. *Agauria* was described as having a cylindrical corolla, ventricose at the base, anthers with two tubules and oblique pores, basal placentae, and a central column not persisting in fruit; *Agarista* as having a conical-tubular or urceolate corolla, anthers with short tubules and large pores, the placenta central in the loculus and the central column persisting in fruit. The persistence or otherwise of the central column is directly dependent on the position of the placenta, since the placenta is attached near where the style joins the central column. If the placenta is basal there can be no central column (fig. 3d).

Detailed studies have confirmed the close relationship of the two genera. Both have most of the characters of the *Lyonia* group in common, although neither genus has spurred anthers, and the style of *Agauria* is not prominently swollen. Other important similarities are listed below.

1. They agree in most details of habit, indumentum and inflorescence. Their glandular hairs have multiseriate stalks with small glandular heads (fig. 3a, b). Both genera have predominantly axillary inflorescences, although a few collections of *Agarista* have been seen with terminal inflorescences. This is an unusual condition, as it is in *Agauria*.
2. Both genera have a very dense veinlet reticulum, with the higher order lateral veins relatively prominent.

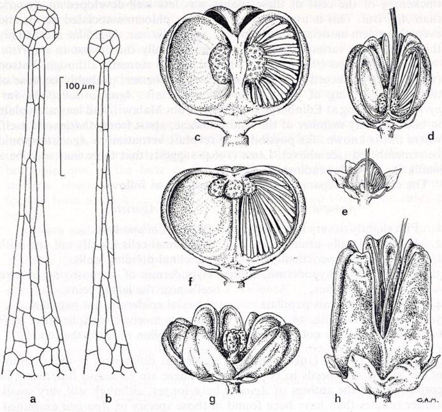

FIG. 3. Hairs and capsules of *Agauria* and *Agarista*: a, *Agarista serrulata*, hair from abaxial surface of calyx; b, *Agauria salicifolia* var. *pyrifolia*, stem hair; c, *Agarista oleifolia*, capsule with two valves removed, x 6; d, *Agauria salicifolia* var. *pyrifolia*, capsule with one valve removed, x 6; e, *A. salicifolia* var. *pyrifolia*, L.S. young ovary x 6; f, *Agarista revoluta*, capsule with two valves removed, x 6; g, *A. oleifolia*, old capsule, x 4; h, *Agauria salicifolia* var. *acutissima*, capsule x 6.

3. Both genera have some species with tall epidermal cells which are divided irregularly by periclinal cross walls (fig. 2a). As mentioned above, tall epidermal cells are the rule in *Agarista*; dividing walls are also frequent. As Niedenzu (1890) noted, tall epidermal cells with periclinal dividing walls are found in *Agauria buxifolia* (= *A. salicifolia* var. *buxifolia*). The collections of this variety examined have the largest epidermal cell height:breadth ratio in the genus (c. 1·0–1·5; in other varieties usually less than 1), and it is the only variety in which cross walls have been seen. *Agarista serrulata* and *A. ericoides* also have low epidermal cells, although in herbarium material the danger of incomplete resuscitation leading to an underestimate of the height-breadth ratio must be remembered. Niedenzu (1890) suggested that *A. serrulata* (as well as *A. nummularioides*, which has not been studied) approached *Leucothoë* because of its low epidermal cells, but this seems to be the only similarity between the two.

4. Both genera have an unifacial midrib bundle, usually with very prominently developed bundle-associated fibres. Niedenzu (1890) noted that the

thickening of the cells of these tissues was less well-developed in *Agauria* than *Agarista*. This is usually not true of the phloem-associated fibres, and even the xylem-associated fibres in *A. salicifolia* var. *buxifolia* are heavily thickened. This variety of *Agauria* is anatomically the closest to *Agarista*.

Agauria and *Agarista* both have abaxial corolla stomata, although Watson (1965) failed to record these stomata from the former, probably because of the dense covering of papillae on the epidermis. *Agauria salicifolia* var. *pyrifolia*, growing at Edinburgh (originally from Malawi), had leaves revolute in bud, the only member of the Andromedeae, apart from *Andromeda* itself, where this is known; the possibility of revolute vernation in *Agarista* should be remembered (see above). Lems (1964) suggests that there may also be a similarity in veinlet endings.

The characters separating the two genera are as follows:

	Agauria	*Agarista*
1.	Pith slightly to very heterogenous.	Pith of *Calluna*-type.
2.	Epidermal cells usually not tall, rarely divided periclinally.	Epidermal cells usually tall and with periclinal dividing walls.
3.	Single-layered hypodermis, more or less continuous.	Hypodermis of at most one or two cells near the larger veins.
4.	Abaxial epidermis papillate.	Abaxial epidermis not papillate.
5.	Placenta basal (fig. 3d, e).	Placenta more or less apical (fig. 3c, f)
6.	Style apparently not swollen.	Style swollen towards the top.

According to Cox (1948) there are significant differences in the anatomy of the xylem; this needs to be confirmed. There are no major differences in corolla shape; the anthers of *Agauria* have longer, although still very small, anther tubules than have been found in those species of *Agarista* examined. The capsule of *Agauria* is relatively rather longer than that of *Agarista*.

As can be seen, the differences between the two genera are not great; all the characters listed above show infra-generic variation elsewhere in the Ericaceae, even within other genera of the *Lyonia* group. However, since their occurrence in those two genera is highly correlated, *Agauria* and *Agarista* can be maintained as separate, but apparently very closely related, genera.

1d. The relationship of *Agauria* and *Agarista* to other members of the *Lyonia* group.

Agauria and *Agarista* both have stamens without spurs, and in this they are similar to *Craibiodendron*, *Lyonia* section *Lyonia* and some other species of *Lyonia* (fig. 1a, d). However, they differ from *Craibiodendron* in their usually racemose inflorescence (paniculate in *Craibiodendron*), urceolate/tubular and not more or less campanulate corolla, as well as in seed type. The seeds of *Craibiodendron* have prominent flat wings on one side, unique in the Ericaceae. The midrib bundle of *Craibiodendron* is bifacial, and some species have a hypodermis.

Most species in the other sections of *Lyonia* apart from section *Lyonia* have stamen spurs. All species of *Lyonia*, apart from *L. lucida*, have bifacial vascular bundles; all members of the genus have capsules with thickened sutures. Some members of *Lyonia* sections *Lyonia* and *Pieridopsis* have a hypodermis; *Lyonia* section *Lyonia* often has rather tall epidermal cells (height:breadth ratio c. 1·0) whilst *L. rubrovenia* (section *Pieridopsis*) has epidermal cells with a ratio of 1·5; there are no periclinal walls irregularly dividing these cells. Some members of *Lyonia* section *Pieridopsis*, e.g. *L. macrocalyx*, *L. rubrovenia* and *L. doyonensis*, have scattered papillae on their abaxial epidermis; these papillae are not nearly so dense as those of *Agauria*, where they are found on almost all the cells of the abaxial epidermis apart from the guard cells.

Although *Arcterica* and all members of *Pieris* examined (apart from *P. cubensis*) have unifacial midrib bundles they differ from *Agauria* and *Agarista* in having often straight filaments, stamens always with spurs (fig. 1g, l), bracteoles not at the base of the pedicel, and in the absence of corolla stomata. *Arcterica* also has whorled leaves and a seed which has a wing formed from a locally several-layered testa; it has no stomata on calyx or corolla.

Agauria and *Agarista* differ from all other members of the *Lyonia* group in their glandular hairs which have multiseriate stalks. The swollen style of *Agarista* finds its closest parallel in some species of *Lyonia* and *Pieris*, whilst the basal placenta of *Agauria* is almost unique in the group, although it is also found in *Pieris phillyriifolia* and *P. swinhoei* (*P. cubensis* may also have a basal placenta, but the material seen was too young).

Venation density and type of vein ending, as well as floral anatomical studies, may provide additional information to help in the elucidation of the relationships within the *Lyonia* group, but the evidence available shows that *Agauria* and *Agarista* have some similarity with several genera of this group. They are perhaps most similar to *Lyonia*, rather less so to *Pieris*. Most of their distinguishing characters are to be found in at least some species of the former genus.

2. The phytogeographical significance

Agauria and *Agarista* show one of the rare distribution patterns among angiosperms; tropical transatlantic (fig. 4). Additional examples of plants with this sort of distribution pattern are given by Hawkes & Smith (1965), Hepper (1965), Iltis (1967) and Fryxell (1969). Several other examples are known from animal groups as diverse as triclads (*Turbellaria*), trematodes, *Ostracoda* (crustaceans), *Dermaptera* (earwigs) and fish; more examples are coming to light.

Agauria, although it has a considerable number of localities on the African mainland, is most variable on Madagascar (Sleumer, 1938). It prefers montane localities and this may partly explain its scattered distribution on a continent where large mountain systems are absent from the tropical belt. *Agauria* is found on four islands off the African mainland; Fernando Po, in the Bight of Biafra, where it reaches 2800 m; Madagascar, where it grows from 700–2600 m; Reunion, where it grows mostly above 1000 m, and finally Mauritius, which reaches only 827 m, and where it does not seem to be very plentiful. On mainland Africa *Agauria* is rarely found below 1200 m, reaching 3500 m on the Cameroon mountains, 3350 m on Mt. Elgon, and 3100 m on Kilimanjaro (above the forest zone).

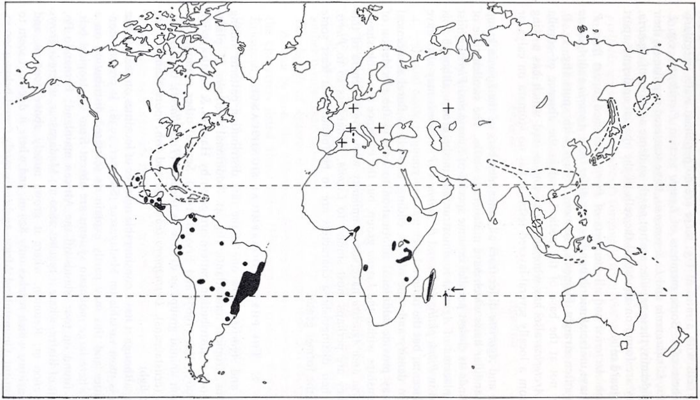

FIG. 4. The distribution of the *Lyonia* group of genera. The black shaded and dotted areas in N and S America represent the distribution of *Agarista*; similarly shown is the range of *Agauria* in Africa, Madagascar and the Mascarene Islands (partly after Sleumer, 1938). The areas enclosed by dotted lines indicate the distributions of other genera of the *Lyonia* group: in SE Asia, *Pieris*, *Lyonia* and *Craibiodendron*; in Japan, *Pieris*, *Lyonia*, *Arcterica*; in Kamchatka, *Arcterica*; in N and C America and the W Indies, *Pieris* and *Lyonia*. The localities of some fossil leaves which have been compared to *Agarista* are indicated with crosses

In the New World, *Agarista* is very similar. It too is most diverse in the east of its range, in the maritime states of Brazil. 25 of the 34 species of the genus are found here, including such distinct species as *A. ericoides*, *A. serrulata* and *A. angustissima*. Only one Brazilian species also grows outside the country (*A. eucalyptoides*, in adjacent Uruguay). Most of its stations are from 700–2500 m, although *Agarista* (*Leucothoë duckei*) grows by the Amazon at under 100 m. The altitudinal range of *Agarista* in its other S American localities is about 1800–2400 m. In C America it is found from under 500 m (Mexico) to 2500 m. Its N American stations in Florida to South Carolina are at low elevations on the coastal plain; this is to be expected of a tropical montane group at the edge of its range (Bader, 1960).

Thus *Agauria* and *Agarista* are both essentially tropical montane plants. This is the least well-represented class among the tropical transatlantic disjunct plant groups.

Fossils of *Leucothoë protogaea* are known from several localities in Europe (fig. 4); this species is usually compared with *Agarista oleifolia* and other species of *Agarista*. According to Takhtajan (1969), *L. protogaea* forms 30% of the fossil flora in parts of the Ural mountains. However, illustrations of its leaves are like those of many angiosperms and not like *Agarista* in particular. Identification of these fossils has been on general appearance, a hazardous procedure because of the notorious variability of angiosperm leaves. Ferguson (in litt.) found that fossil material from Germany identified as *Andromeda* (= *Leucothoë*) *protogaea* probably belonged to *Myrica*, both on gross morphology and cuticle characters. *L. balearica*, originally compared to *Agarista* (*Leucothoë populifolia*) (Arènes, 1951, as *L. acuminata*), is now considered to be synonymous with *Myrica arensi* (Arénes & Depape, 1956). Obviously the comparison of such fossil impressions with *Agauria* or *Agarista* cannot be taken seriously at present.

If Tertiary fossil records referable to *Agauria* or *Agarista* are confirmed from the northern temperate regions, explanations of the present-day distribution of these two genera invoking events such as continental drift or long-distance dispersal across the Atlantic will be made redundant. Alternative explanations similar to those suggested by Darlington (1965) would be possible. The plants would migrate south, ascending the mountains to retain a favourable climatic regimen. Persistence in Africa and S America might be due to freedom from competition. Niedenzu (1890) toyed with the idea that *Agauria* and *Agarista* represented parallel developments of a group migrating southwards down opposite sides of the Atlantic. Sleumer (1938) thought that *Agauria* had migrated into Africa from the north in the Tertiary since fossil Andromedeae are found in Europe and four genera grow there at present; these, like *Agauria*, were derivatives of the Tertiary tropical montane flora. Of these genera, *Orphanidesia* is a member of the Rhododendroideae (Watson, Williams & Lance, 1967; Stevens, 1969), *Cassiope* is not a member of the Andromedeae *sensu stricto* and *Andromeda* and *Chamaedaphne* do not belong to the *Lyonia* group of genera.

Long-distance dispersal across the Atlantic would explain the present distribution of *Agauria* and *Agarista*; after the plants crossed the Atlantic some evolution occurred, hence the presence of closely related genera on opposite sides of the Atlantic. Both genera have smallish, spindle-shaped seeds less than 2 mm long which are presumably wind-dispersed. Many genera of the Ericaceae, even the showy-flowered ones, have at least a few self-compatible species. *Agauria* and *Agarista* today inhabit rather open habitats, being plants of the forest margin rather than of the high forest. Thus they have at least some of the characteristics conducive to success in long distance dispersal: means of wide dispersal, self-compatibility and ability to occupy an open habitat (Baker, 1959). However, these Ericaceae are not plants of semi-aquatic successional habitats of high ecological receptivity, as is *Cleome afrospina* and its relatives for which long-distance dispersal is more likely (Iltis, 1967) nor are they plants of open, arid habitats, weedy or strand plants. Although long-distance dispersal is probably not the cause of the disjunction of the two genera, it may explain some of the more isolated localities within the continents they inhabit (see below).

The similarity between *Agauria* and *Agarista* need not imply that they have only recently separated. There are several examples known of hybridisation between species from N America and E Asia; the disjunctions in the ranges of the genera to which these species belong arose at the latest in the Miocene or early Pliocene. There are two example of this in the Ericaceae: *Epigaea repens*, from east N America, crosses with *E. asiatica*, from Japan (Mulligan, 1931); *Rhododendron catawbiense*, from east N America, hybridises with other species of *Rhododendron* section *Hymenanthes* growing in Europe and Asia (Synge & Napier, 1969). Similar examples are found in *Campsis* and *Catalpa* (see Smith, 1941, for references), and possibly in the herbaceous genus *Plantago* (Stebbins & Day, 1967). Evolution in woody genera is often slow compared to that of herbaceous taxa; many of the fossil angiosperms found after the middle Cretaceous can be placed in present-day genera (Takhtajan, 1969).

Thus continental drift is favoured as an explanation of the distribution pattern of *Agauria* and *Agarista*. It can hardly be disputed that at one time Africa and S America were very much closer to one another than they are at present. Evidence for the computer-simulated fit of the continental margins, palaeomagnetism, continuity of orogenic belts, sedimentary and igneous rocks of similar types deposited more or less contemporaneously, and similarities in salt and coal deposits, faunas, floras and glaciations all support this (for a convenient summary, see King, 1967). Continental land-bridges, i.e. isthmian strips of land connecting the continents, are unlikely to have existed because of the nature and extent of these similarities.

It is important to establish the time of separation of S America from Africa, since in the absence of well-authenticated pre-Cretaceous angiosperm fossils the time of separation of these continents has been used as an indirect method of establishing the minimum age of certain angiosperm genera (particularly *Gossypium*, *Bromus* and *Solanum*) which supposedly inhabited these continents before drift (Hawkes & Smith, 1965). Even recent estimates of the time of separation vary widely. Funnell & Gilbert Smith (1968) suggested that the deep water upper Jurassic sediments from the Cape Verde islands mark a stage at which the Atlantic was 1/4 of its present width; opening having started at the end of the Triassic. Valencio & Vicas (1969) using palaeomagnetic data, suggest that separation started in the lower Jurassic. Gilbert Smith & Hallam (1970) suggest a date from the Upper Jurassic to mid-Cretaceous; the Serra Geral volcanic rocks suggested the former date, the sedimentary record the latter. King (1967, p. 63) remarked ". . . at the beginning of the Cretaceous the long-established unity between what are now two continents [S America and Africa] had not been destroyed". He thought that separation must have been achieved soon after the Albian at the latest. Le Pichon (1968), applying sea-floor spreading data to drift, suggested that separation occurred at the Albian–Aptian boundary (120 million years ago); spreading, therefore separation, was rapid for about 30 million years and there were also later spreading episodes. Reyment (1969), using mainly data from ammonite biostratigraphy, concluded that the two continents were in contact between north-east Brazil and the Nigeria–Ivory Coast region as late as the Upper Albian–Lower Turonian, about 110 million years ago. The rifting heralding separation was completed by the early Cretaceous. Although Creer (1965) was inclined to place the break-up in the Permo-Triassic, he later (Creer, in litt.) suggested that "while slight relative movement of the two continents might have occurred in the Jurassic, the major drift episode was at the end of the Cretaceous and in the Tertiary".

Although there is clearly a considerable spread of opinion as to the time of separation of Africa and S America, the early Cretaceous, some 120–140 million years ago, seems a reasonable estimate. A variable which it is difficult to evaluate is the extent to which high, probably volcanic, isles in the opening South Atlantic ocean could have acted as stepping stones; but it seems likely that at least the precursors of *Agauria* and *Agarista* were in existence in the Jurassic. The genera themselves might have differentiated by then, growing on different parts of the super-continent, but this is unprovable at present. This conclusion is similar to that reached by Hawkes & Smith (1965) for the age of *Gossypium*, *Solanum*, etc. However, there is no evidence for the southern origin of the *Lyonia* group; as can be seen from fig. 4, it is predominantly northern, most diverse in SE Asia and to a lesser extent in south east N America. It must have been in the northern hemisphere during at least most of the Tertiary, since both *Lyonia* and *Pieris* are SE Asian–south east N American disjunct genera. Within the *Lyonia* group, *Agauria* and *Agarista* seem to be derived, rather than primitive, genera.

The variability of *Agauria* on Madagascar, and the presence there of *Agauria salicifolia* var. *buxifolia*, the variety anatomically most similar to *Agarista*, might suggest that *Agauria* entered Africa from the east. However, of the six characters separating *Agauria* from *Agarista* (section 1c), three have derived states in *Agauria* (hypodermis present, epidermis papillate, placentae basal), one in *Agarista* (pith *Calluna*-type) and two are uncertain (style type, the height of the epidermal cells may be connected with the presence of a hypodermis). The tendency of the anthers of *Agauria* to have tubules is also a derived character-state. If derived character-states can be used to suggest derived taxa (a reasonable assumption) and derived distribution areas (more disputable), then *Agauria* is derived from *Agarista*, and came from America. *Philippia* (Ericaceae-Ericoideae) also grows on the African mainland, Madagascar and Reunion, but this genus has almost all its relatives on the African continent. Croizat (1952, pp. 161 and 173) suggested that both *Agauria* and *Philippia* entered Africa from the (south) east, from the main centre of angiosperm evolution. The facts mentioned above make this unlikely. Also, the relatively late movement of India northwards in the early part of the Tertiary (le Pichon & Heirtzler, 1968; Davies, 1969; Holloway, 1969) to join Asia where the *Lyonia* group was already presumably to be found makes the entry of ancestral *Agauria/Agarista* into Africa from SE Asia via India, the Seychelles and Magadascar unlikely. The South Atlantic Ocean would already have opened, although not to its full extent, and would have to be crossed.

Most of Africa is a stable, long emergent block, and the area of Madagascar favoured by *Agauria* is on the geologically older part of the island. Whatever the position of Madagascar relative to Africa (see Flowers & Strong, 1969, for a discussion of this point), it has been not far distant from the African mainland for a considerable period, and although at least partly isolated since the Jurassic, it has been emergent for much of this time; it is a continental fragment. Mauritius and Reunion are independent shield volcanoes. Potassium-argon dating of lavas yielded ages of 7·8–6·8 million years for Mauritius and at least 2 million years for Reunion (McDougall & Chamalaun, 1969). Thus there has been considerable time available for the colonisation of these islands, especially Madagascar; remarkable animals have evolved in isolation on all three islands, e.g. lemurs, the dodo and the solitaire. *Agauria* probably arrived in Mauritius and Reunion by long distance dispersal, although these two islands are about 750 km east of Madagascar and are at present in the south-easterly trade wind belt. The relative diversity of *Agauria* on Madagascar may be because this is a relict area for the genus and/or it may have diversified there in isolation. The smaller amount of diversity of *Agauria* on the mainland may be connected with the fact that the surface of Africa was reduced to a peneplain in the early Tertiary; only a small area in the centre remained above 1500 m (Moreau, 1966).

In America the centre of *Agarista* is on the three cratonic areas of the continent (Harrington, 1962). These cratons are stable, positive (emergent) areas which have not been subjected to orogenesis since before the Palaeozoic. In Cretaceous times, Belo Horizonte (Brazil) was apparently mountainland and escaped sedimentary deposition (King, 1967). It was at latitudes similar to those at which it is today, and so would have had a tropical climate. However, this concentration of *Agarista* is likely to be a relatively young centre formed in response to causes acting since the separation of the continents, probable in the Tertiary. There are three reasons for this. (1) This land would probably have had to be continuously above 1500 m or more to satisfy the ecological requirements of the genus, but according to King (1967), by the Oligocene the landscape was one of extreme planation. Even in the Cretaceous the mountains were probably only some 600–700 m high (King, in litt.). (2) *Gaylussacia* is richly developed in the same region as *Agarista*, yet Sleumer (1967a) considers that it is relict there; it is absent from Africa. *Gaultheria* and *Clethra* also occur in Brazil, but not in S Africa. (3) The interior of a large continent would be expected to be arid, as is central Asia today, and so unsuitable for such plants: Belo Horizonte would be in the interior of a combined African–S American continent.

Agarista is poorly represented in the Andes, which are of Miocene and later age, although the Vaccinieae are very diverse there. As with *Gaylussacia*, its stations on the Andes and that by the Amazon are probably fairly recent (see also Sleumer, 1967a). It does not seem to be very successful in these newer habitats; in N America its range is probably limited climatically.

Hence the significance of the centres of diversity of both *Agauria* and *Agarista* is obscure; they both seem to be connected with post-drift events. As van Steenis (1967) showed, plants can disperse from one old almost eroded-away mountain to another younger one, so the age of taxa inhabiting isolated mountains and mountain systems may bear no relation to the age of the physiographic features themselves. The isolated nature of many such features, especially in Africa and S America, would make a certain amount of dispersal between suitable habitats necessary, and this probably was the situation on the pre-drift continents as well.

There are other taxa in the Ericales whose distribution suggests that the formation of the Atlantic may have severed the range of taxa now found on opposite shores. *Clethra* sect. *Cuellaria* grows in S and C America, the Antilles and one species, *C. arborea*, on Madeira (cf. *Bowlesia* and *Homalocarpus* (Umbelliferae) in S America, with a close relative, *Drusa*, in the Canary Islands; Mathias & Constance, 1965). *C. arborea* is placed in a different subsection, *Pseudocuellaria*, to the American plants (Sleumer, 1967b). *Ledothamnus* is found on a few of the Tepuis of the Guiana shield; it is similar in leaf anatomy to the African Ericoideae, although in other characters it is not close (Stevens, 1970). *Vaccinium* section *Neurodesia*, from the Andes and N America, may be close to *Vaccinium* section *Cinctosandra*, from Africa and Madagascar (like *Agauria*, this section is most diverse on Madagascar). These examples need more study, but it is clear that the Ericaceae have still a great deal of interesting information to yield to the phytogeographer.

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