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THE GENERA *ANAPTYCHIA* AND *HETERODERMIA* IN EAST AFRICA

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Introduction

Most genera in the Physciaceae have the upper cortex of the thallus composed of hyphae arranged anticlinally. *Anaptychia* and *Heterodermia* are distinguished from them by the periclinal arrangement of their cortical hyphae. Widespread in the temperate regions of the world, *Anaptychia* is represented in East Africa by one species, newly described below, from the mountains of Ethiopia. The mainly tropical genus *Heterodermia*, comprising about 70 species, is represented in East Africa by 25 (including one doubtfully); one of these species is newly described below.

Materials

The following account is based on collections made by the authors as follows: Uganda (T.D.V.S. 1969, 1970, 1971), Southern Ethiopia (H.K. 1972), Kenya (T.D.V.S. and H.K. 1972, 1973, 1974), and Northern Tanzania (T.D.V.S. and H.K. 1974). In addition to specimens in institutional herbaria we have been permitted to examine material collected in recent years by the following botanists: Burnet (Tanzania, Uganda), Lye (Uganda), Manum (Uganda), Nordal (Tanzania), Pentecost (Uganda), Pócs (Tanzania), Ryvarden (Tanzania), Tapper (Ethiopia), Thompson (Uganda) and Winnem (Ethiopia). In the individual sections on the species discussed below we have cited under 'Specimens Examined' the specimens from East Africa collected by these botanists and ourselves, except when they were too numerous to be listed individually. Only the collecting number is given for our specimens; for the others the collector's name is attached to the number.

Holotypes of the two new species described below are deposited in BM and isotypes in O.

Systematics

Poelt (1965) drew attention to differences between spores in some of the species traditionally included in *Anaptychia*. Consequently he divided the genus into two, *Anaptychia* Körb. em. Poelt and *Heterodermia* Trevis. em. Poelt, and typified *Heterodermia* on *H. speciosa* (Wulf.) Trevis. *Anaptychia* contains species producing relatively thin walled spores whose surface is sculptured with minute spines or ridges; *Heterodermia* contains species with thick walled spores whose surface is smooth. Culberson (1966), Awasthi (1973), and others have followed Poelt's arrangement, but Rose and James (1974) rejected the validity of Poelt's revival of *Heterodermia* Trevis. because Kurokawa (1962) had previously lectotypified

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Heterodermia by *Anaptychia ciliaris* (L.) Körb. However, since Trevisan ('1868', 1869) did not include this species in *Heterodermia*, the inadvertent use of it as a lectotype for that genus can be disregarded under Art. 8. Kurokawa (1973) regarded *Anaptychia* as a single genus comprising two subgenera, *Anaptychia* and *Heterodermia* (Trevis.) Kurok.

We follow Poelt's concept of *Anaptychia* and *Heterodermia* because the type of spore provides a character based on propagative organs, to which special taxonomic value is commonly attached, and a character that is relatively unchanging throughout the various species within the genera defined by it. An additional advantage is that spore type is a character clearly recognisable with the aid of equipment ordinarily available to botanists, namely, the light-microscope.

Kurokawa has published two systematic arrangements of the species of *Anaptychia* s. lat. They differ fundamentally. In the first he defined the main divisions by spore characters (Kurokawa, 1962) and in the second by thalline characters (Kurokawa, 1973). The first did not satisfy its author; the second seems less satisfactory to us. For convenience here, therefore, we have arranged the species below in alphabetical order. All descriptions of species are based on personal study of specimens, and the characters of each are described on a uniform plan to aid comparison.

Morphology

In view of the thorough account of the morphology given by Kurokawa (1962, 1973) we shall confine our discussion here mainly to those features that are important for the determination of specimens. But in some cases our taxonomic concepts differ from those of Kurokawa, and then our discussion of the morphological or chemical characters concerns the definition of species.

Thallus

In the one species of *Anaptychia* represented in East Africa the thallus is an irregularly straggling mat loosely attached to the substrate. The upper cortex, as in some other species of *Anaptychia*, is overlaid by a thin layer of hyphae. They lie periclinally, as do those in the cortex itself (Kurokawa, 1973). The thalline cortex and rhizines are tomentose, a character found in some other species of *Anaptychia* but not in *Heterodermia*. The upper cortex is of uneven thickness, sending extensions down through the medulla which appear on the lower surface as vein-like ridges.

In *Heterodermia* three main forms of thallus may be observed. In most species a rosette-shaped thallus develops from the lobes growing out radially and contiguously, attached along their length to the substrate. A second type of thallus is seen in *H. leucomela* and its allies, *H. loriformis*, *H. lutescens*, *H. usambarensis* and *H. vulgaris*. In these species the thallus is composed of a mat or cushion of disjunct, more or less ribbon-like lobes, loosely attached to the substrate or standing away from it with the rhizines attached to other lobes or spreading unattached. The third main group comprises *H. podocarpa*, *H. hypochraea* and *H. comosa*. The first two of these have convex lobes ascending peripherally; the lobes of *H. comosa* are usually almost plane, but they are normally ascending.

The lobes themselves are linear, or linear-cuneate (longly wedge-shaped), or, in *Heterodermia comosa*, spathulate or paddle-shaped. Their branching is initially dichotomous, but the ultimate form of the branching varies. In some species, notably the *H. leucomela* group, two equal lobes grow on from the apex of each lobe; but in most species the main lobe grows out radially, and the branches formed dichotomously at its apex become short lateral lobes. An intermediate condition is sometimes seen, notably in *H. dactyliza*, when several long but unequal lobes grow out from the main lobe in a digitate arrangement.

A pruina is sometimes formed on the upper surface of the lobes in both genera, especially near their apices. Intermediate states between abundant pruina and its complete absence are common. It has little taxonomic significance.

The upper cortex may be of even thickness, forming a fairly uniform layer, or it may be uneven (as in the *Anaptychia* species described below), interrupting the algal layer with extensions down through it into the medulla. These extensions may appear as vein-like ridges on the lower surface of the lobe. While the difference between an even and an uneven upper cortex is not always clear, in that there are intermediate states difficult to classify (for example, in *Heterodermia albicans* and *H. antillarum*), it is worth noting that most species with a lower cortex have an even upper cortex, and most species without a lower cortex have an uneven upper cortex. It appears that an uneven upper cortex, when well developed with hyaline extensions to the lower surface of the medulla, may give rigidity to lobes that otherwise lack it owing to the absence of a lower cortex.

Soralia, Isidia and Squamules

The new species of *Anaptychia* described below has soralia mainly at the apices of the lobes but also further back. They are usually on the under side but not invariably so. The soredia are coarsely granular.

In *Heterodermia* also the soralia are mainly on the under side of the lobes near the apex. The apex often becomes recurved to form a labriform soralium, for example, in *H. japonica* and *H. obscurata*. In some species the soralia form at the tips of the short lateral lobes, which may remain so short as to give the appearance of a sorediate, undulate margin to the main lobes, as, for example, in *H. albicans*. Occasionally soralia form on the lamina far back from the apex, especially on the under side. This is to be seen especially in the *H. leucomela* group. Capitate soralia on pedicels arising from the lamina as may be seen in *Physcia* and *Pyxine* probably do not occur in *Anaptychia* or *Heterodermia*; certainly they are absent from any species dealt with here.

The type of soredia, ranging from farinose to coarsely granular, varies rather indefinitely from one species to another, whether in response to genetic or environmental factors is not clear. Culberson (1966) reported that in North and South Carolina, U.S.A., *Heterodermia pseudospeciosa* had coarse soredia, while in *H. tremulans* they were fine. (In the present paper *H. tremulans* is reduced to synonymy with *H. speciosa*.) We have noted the same difference in the holotypes of these species, and the African material confirms it (though *H. pseudospeciosa* is rare in our area).

Isidia are corticate all over, but squamules are generally non-corticate on the lower side, even in species that have a cortex on the under side of the lobes. Squamules sometimes dissolve into soredia at their apices, and in occasional specimens of *Heterodermia isidiophora* soredia are produced together with isidia.

Species Counterparts

As in other genera the concept of species pairs (Du Rietz, 1924; Poelt, 1970) applies to *Anaptychia* and *Heterodermia* (Kurokawa, 1973). For example, *A. ethiopica*, described below, appears to be a sorediate counterpart of *A. ciliaris*. In *Heterodermia* the existence of several different kinds of vegetative propagula increases the number of possible counterparts, so that not merely pairs but triads and even tetrads are possible. Table 1 shows some counterparts of this kind among species recorded for our area.

TABLE 1. *Species counterparts in East African representatives of* Anaptychia *and* Heterodermia

No vegetative propagula	Soredia	Isidia	Squamules
A. ciliaris[1]	A. ethiopica		
H. tropica[2]	H. albicans	H. antillarum	
H. dactyliza	H. chilensis[3]		
H. diademata	H. speciosa	H. isidiophora	H. lepidota
H. flabellata	H. obscurata		
H. hypoleuca			H. microphylla
	H. japonica[4]		H. appendiculata

[1] Not in East Africa.
[2] Counterpart *fide* Kurokawa (1973); not in East Africa.
[3] Doubtfully in East Africa.
[4] Chemotype containing norstictic acid.

Apothecia and Spores

In these two genera the apothecium has a thalline exciple, and if the thallus bears soredia, isidia, or squamules these also develop on the thalline exciple when it is sufficiently mature. If the thallus has pigmented hyphae on its under side, the inner surface of the thalline exciple usually bears the same pigment, especially on its marginal squamules.

The difference between the spores in *Anaptychia* and *Heterodermia* has been noted above. In addition many species of *Heterodermia* have spores with small locules, or sporoblastidia, at the poles (Kurokawa, 1962). These often appear to communicate with the main locules. None of the *Heterodermia* species that are corticate below have sporoblastidia in the majority of their spores; most of those that are non-corticate below have them in all their mature spores. Sporoblastidia are sometimes to be seen in a few spores of species that generally lack them, for example, *H. hypoleuca* and *H. diademata*; the former species occasionally produces considerable numbers of spores with sporoblastidia (see under *H. hypoleuca* for further discussion).

The size of spores in a species is traditionally expressed as lying within a range of lengths and breadths. This is convenient in practice, but it conceals the great variation that may exist between different specimens of the same species. We have therefore measured the lengths of a considerable number of spores in this study and subjected the results to statistical analysis. The measurements show that the lengths of spores in a single apothecium are consistent with a normal distribution, 95% of them falling within plus or minus twice the standard deviation about the mean. In a single plant different apothecia usually produce spores of similar average mean length, but sometimes statistically significant differences are found. However, different plants of the same species commonly produce spores with considerable differences in their mean lengths.

In the determination of specimens common sense dictates a reasonable use of spore size as a character to be considered, but when this character is used at least partly to define species a critical examination of its validity is necessary. For instance, Kurokawa (1962) differentiated *Anaptychia pseudospeciosa* var. *tremulans* from *A. speciosa* partly on the size of the spores. This question is discussed further under *Heterodermia speciosa* below, where we largely confirm Kurokawa's observations but interpret them differently. Here it is appropriate to record some measurements made on the spores of *H. diademata* from various localities to indicate the kind of range that may be expected. This species was chosen because it is common, usually fertile, and can be determined without doubt. Table 2 shows the size of spores in one apothecium from each of seven specimens.

TABLE 2. Heterodermia diademata: *mean lengths of spores in seven specimens*

Specimen	No. of spores	Mean length of spores (μm)	Standard deviation
K 53/9	50	26·8	2·0
AMB 217	50	27·2	2·0
2K 19/4	50	27·4	1·9
E 22/51	50	28·1	2·2
T 3/48	50	28·5	2·3
Manum s.n.	50	35·8	2·1
2U 44/54	50	38·6	2·6
Total	350	30·3	4·9

The two plants with larger spores were growing on the west side of Mt Elgon in Uganda, where rain is almost perennial and heavy. A more exact comparison between the mean lengths of the spores from some of those specimens appears in Table 3. It shows that differences of this kind can be statistically significant yet have no taxonomic meaning. Such variations may be due entirely to environmental factors.

TABLE 3. Heterodermia diademata: *differences between lengths of spores, with standard errors of differences*

Pairs of specimens	Difference (μm)	S.E. of difference	P
K 53/9 and 2K 19/4	0·6	0·39	>0·05
2K 19/4 and T 3/48	1·1	0·42	<0·05
T 3/48 and Manum s.n.	7·3	0·45	<0·001
Manum s.n. and 2U 44/54	2·8	0·47	<0·001

Rhizines and Cilia

Both rhizines and cilia arise only from the cortex in these two genera. Their differentiation is somewhat arbitrary, but the term cilia is restricted to those fibrillary structures that arise from the upper cortex and obviously have no part in fixing the thallus to the substrate. They occur always in *Heterodermia comosa*, usually in *H. loriformis*, and one or two are occasionally seen in other species. Rhizines grow from the corticate margins of the lobes and from the cortex on the under side in those species that have one. Generally they serve to fix the thallus to the substrate, but sometimes they make no contact with it, being intertwined with other rhizines or simply lying free. They vary from white to black and from simple to densely branched, but the variations seem to have no taxonomic significance. We have therefore not described them below except for the two new species.

Chemistry

All the material referred to in this paper, including type specimens when of sufficient size, has been subjected to thin-layer chromatography (T.L.C.) by means of the techniques described by Culberson and Kristinsson (1970) and Culberson (1972). When type specimens have been tested the fact is noted under each species.

All species of the genus *Heterodermia* produce atranorin in both the cortex and the medulla as judged by a positive K reaction. Of medullary substances various triterpenes are common, notably zeorin, which is in all species. In contrast to the chemical properties of the genus *Pyxine* (Swinscow and Krog, 1975) the triterpene patterns in *Heterodermia* have little value in the determination of species.

The depsidones norstictic acid and salazinic acid are produced in some species, singly or in combination. Their taxonomic significance varies from one species to another. Sometimes they represent a valid specific character in association with distinct morphological characters, as for instance in *Heterodermia pseudospeciosa*; in other cases they represent a chemical race, as in *H. japonica*. Traces of connorstictic or consalazinic acids are found in most species producing depsidones.

In *Heterodermia albicans* and *H. antillarum* an undetermined substance occurs together with salazinic acid. The two substances have similar R_F values in all three of the commonly used solvent systems, so the presence of the unknown substance is best detected by the change in colour produced by treatment with dilute sulphuric acid and heat. Salazinic acid spots will commonly have an orange colour, while the spots caused by a combination of salazinic acid and the unknown substance have a pure red colour.

Pigments are important in the definition of species in *Heterodermia*. They occur on the under side of the thallus in some species without a lower cortex, and may be of two different types. They are produced either in the outer layer of the medulla proper, as in *H. casarettiana* and *H. lutescens*, in which species they react K−, or in the arachnoid hyphae (sometimes in patches) overlying the medulla, as in *H. obscurata* and *H. vulgaris*, in which species they react K+ purple. No further attempt at distinguishing the pigments has been made in this study, but lists of different pigments in different species can be found in Kurokawa (1973).

Though the pigments may appear to be accorded undue taxonomic importance in the present work in comparison with that of other medullary substances, two reasons may be adduced for that. Firstly, in a regional study we consider it best to follow established practice in the evaluation of this particular character. Secondly, the species distinguished most obviously by pigments have additional morphological or distributional characters separating them.

The single species of *Anaptychia* in East Africa has no cortical or medullary substances.

Key to Anaptychia and Heterodermia in East Africa

1 Upper surface of lobes covered with short tomentum; atranorin and zeorin absent ....**Anaptychia**
Upper surface of lobes lacking tomentum (may be glabrous or pruinose); atranorin and zeorin present...**Heterodermia**

Key to Heterodermia Species in East Africa

1 Under side corticate...2
Under side non-corticate...8

2 (1a). Soralia, isidia, and squamules absent........................**9. H. diademata**
Soralia, isidia, or squamules present...3

3 (2b). Soralia present, isidia and squamules absent...................................4
Soralia absent, isidia or squamules present...6

4 (3a). Soralia apical on main lobes and on short lateral lobes, in delimited areas, ± labriform; salazinic acid absent...5
Soralia ± linear and continuous along margins of lobes, not apical; salazinic acid present..**1. H. albicans**

5 (4a). Soredia farinose; norstictic acid absent........................**24. H. speciosa**
Soredia subgranular to granular; norstictic acid present............................
23. H. pseudospeciosa

6 (3b) Lobes bearing cylindrical isidia, sometimes mixed with granular or flattened isidia 7
Lobes bearing entire or dissected squamules........................**15. H. lepidota**

7 (6a) Thallus thick, upper cortex 50–150 μm thick, even; medulla lacking salazinic acid (common in East Africa)........................**13. H. isidiophora**
Thallus thin, upper cortex 10–60 μm thick, somewhat uneven; medulla containing salazinic acid (rare in East Africa)..........................**2. H. antillarum**

8 (1b) Branching dichotomous, with two equal lobes, uncinate when young, arising from apex of each mature lobe (*H. leucomela* group)....................9
Branching sympodial, with short lateral lobes, not uncinate, on radially extending main lobes...13

9 (8a) Lobes with red, yellow, or brown pigment on under side.....................10
Lobes lacking pigment on under side.............................**16. H. leucomela**

10 (9a) Pigment K+ purple...11
Pigment K−..12

11 (10a) Pigment deep red; cilia absent from upper side of lobes...**26. H. vulgaris**
Pigment ochraceous to orange; cilia often present on upper side of lobes.........
17. H. loriformis

12 (10b) Pigment brown or reddish brown, in hyphae overlying medulla on under side of lobes...**25. H. usambarensis**
Pigment yellow to pale orange to pink, in medullary hyphae on under side of lobes...**18. H. lutescens**

13 (8b) Lobes bearing squamules...14
Lobes lacking squamules (or isidia)..15

14 (13a) Thallus containing norstictic acid; spores *c.* 37–50 μm long, containing sporoblastidia...**3. H. appendiculata**
Thallus lacking depsidones; spores *c.* 25–35 μm long, lacking sporoblastidia......
20. H. microphylla

15 (13b) Lobes paddle-shaped or spathulate, bearing white cilia on upper surface...
6. H. comosa
Lobes linear or linear-cuneate, lacking cilia on upper surface.....................16

16 (15b) Lobes bearing soralia...17
Lobes lacking soralia..20

17 (16a) Lobes with yellow or ochraceous pigment, sometimes patchy, on under side..18
Lobes lacking yellow or ochraceous pigment...19

18 (17a) Pigment K+ purple...**21. H. obscurata**
Pigment K−...**4. H. casarettiana**

19 (17b) Lobes stiff; branching mainly digitate; upper cortex forming thick border to under side; usually saxicolous (not yet correctly recorded for Africa)...**5. H. chilensis**
Lobes softer; main lobes with short lateral branches; upper cortex forming no or thin border to under side; usually corticolous..............**14. H. japonica**

20 (16b) Lobes with yellow or ochraceous pigment on under side.................21
Lobes lacking yellow or ochraceous pigment...22

21 (20a) Thallus attached at base of lobes to substrate; apothecia subapical to apical, longly stipitate; usually on twigs, small branches, and bamboo joints...
11. H. hypochraea

Thallus attached to substrate along the lobes except at apices; apothecia laminal to subapical, adnate to shortly stipitate; on larger branches and trunks of trees..**10. H. flabellata**

22 (20b) Lobes stiff; branching ± digitate; upper cortex forming thick border to under side; usually saxicolous..**8. H. dactyliza**
Lobes softer; main lobes with short lateral branches; upper cortex forming no or very thin border to under side; usually corticolous..........................23

23 (22b) Apothecia apical or subapical, longly stipitate; lobes ± ascending at apices 24
Apothecia laminal to subapical, adnate to shortly stipitate; lobes ± adnate at apices 25

24 (23a) Thallus compact, attached at base of lobes to substrate; usually on twigs, small branches, and bamboo joints..............................**22. H. podocarpa**
Thallus spreading irregularly, attached to substrate along the lobes except at apices; usually among bryophytes on rock or bark............**7. H. congoensis**

25 (23b) Spores 25–35 μm long, none or few with sporoblastidia.......................
12. H. hypoleuca
Spores 35–45 μm long, all mature spores with sporoblastidia.......................
19. H. magellanica

Anaptychia Körb. em. Poelt

Anaptychia ethiopica Swinsc. & Krog sp. nov.

PLATE 1

Thallus fuscus ad murinus aut incanus, substrato laxe affixus. Lobi disjuncti, lineares ad lineariter cuneati, lobis lateralibus longisque brevibus, tomentosi. Cortex superior inequaliter incrassatus; cortex inferior nullus. Soralia praecipue apicales vel subapicales, aliquando in lamina; soredia granulosa. Rhizinae fuscae vel nigrescentes, vix ramosae, tomentosae. Apothecia et pycnidia ignota.

Holotypus: Ethiopia, Begemder Province, Buahit, on moss, *Tapper* 260, 23 June 1971 (BM); isotypus O.

Thallus brown to grey, loosely attached to substrate, forming an irregular mat. Lobes disjunct, linear to linear-cuneate, with long and short lateral lobes, tomentose; upper cortex uneven, here and there forming vein-like ridges on lower surface of medulla; under side non-corticate, pale. Soralia mainly apical and subapical, occasionally laminal; soredia granular. Rhizines brown to black, scarcely branched, tomentose. Apothecia and pycnidia unknown. T.L.C.: no lichen substances.

In general habit this species resembles some forms of *Anaptychia ciliaris* (L.) Körb., especially those growing on exposed rocks. In fact it may be regarded as the sorediate counterpart of that species. The colour is usually a greyish brown, sometimes with a pinkish tinge and tending towards black at times. The tomentum is on nearly all the lobes, giving many of them a hoary appearance. The medulla on the under side varies from white to pale brown, is bounded by thick corticate margins, and is here and there veined by ridges growing down from the under side of the

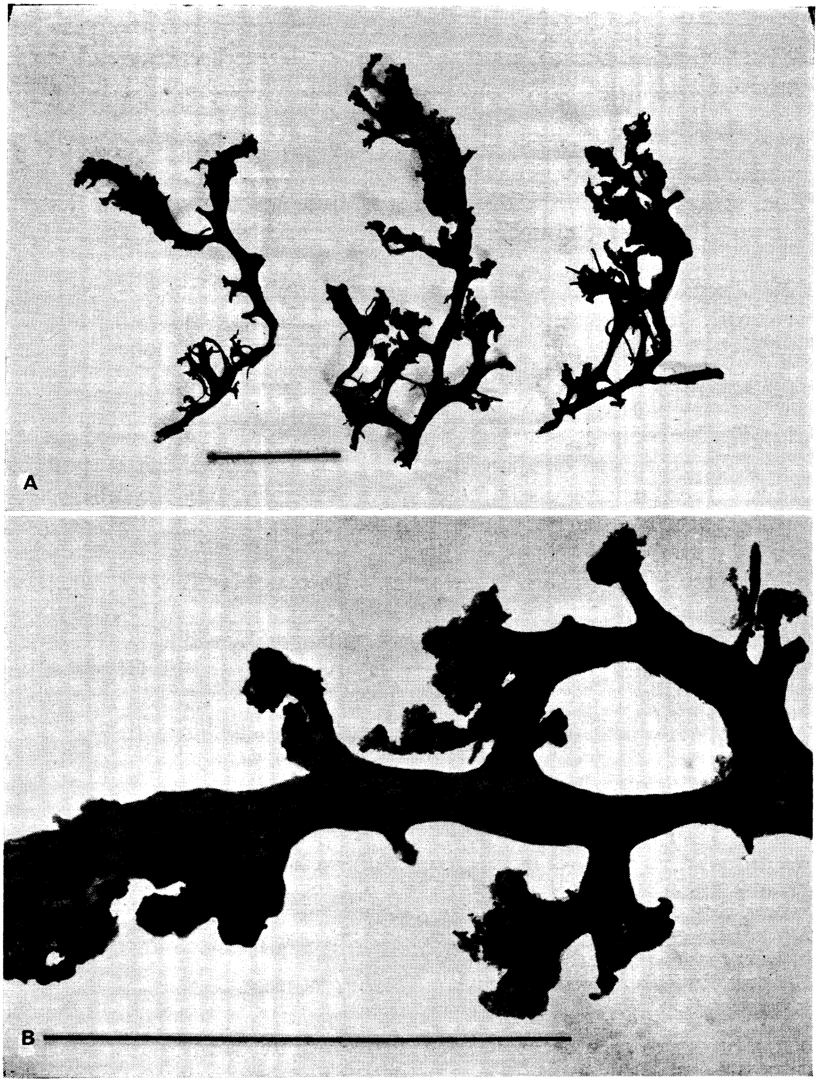

PLATE 1. A. *Anaptychia ethiopica* Swinsc. & Krog, part of holotype, general appearance of lobes. B. *A. ethiopica*, part of holotype, soralia on lobe apices. Scales = 1 cm.

cortex. The soralia sometimes form on the under side of the lobes near their apices and become labriform; on other lobes they appear at the tip or on the upper surface of the apex; yet again they occasionally form further back on the lamina. They are excavate in form but may be filled and overflowing with soredia. These are finely to coarsely granular.

The thickness of the lobes is about 150–300 μm, each lobe showing great variation in different parts. Several layers or zones may be distinguished in the cortex. The outermost consists of a thin irregular layer of colourless hyphae. It overlies a brown pigmented zone, about 5–15 μm thick, of the main cortex. The projecting hyphae forming the tomentum cover the surface both above and below the thallus wherever cortex is present; they are 10–30 μm long, and their walls are irregularly verrucose. The cortex, consisting of densely packed hyphae orientated more or less parallel with the surface, extends round the sides of the lobes to the under side in many places, and where it penetrates the medulla to form ridges on the underside it breaks up the medulla into locules. The algal cells lie in these locules among loosely arranged medullary hyphae. Arachnoid medullary fibres compose most of the under side of the thallus.

Known so far only from the mountains of Ethiopia at altitudes over 3500 m, this species grows over bryophytes, heather stems, mossy rocks, and dead plant remains.

Specimens Examined

Ethiopia: Begemder Province, Buahit, *Tapper* 260 (holotype), *Tapper* 241 (BM); Sankaber Camp, *Tapper* 164a, b (BM). Bale Province, Araenna, Mt Orobo, *Tapper* 772 (BM); 1–2 km WNW of Tullu Deemtu, *Tapper* 784a (BM).

Heterodermia Trevis. —. Poelt

1. Heterodermia albicans (Pers.) Swinsc. & Krog comb. nov.

Parmelia albicans Pers., *Annln Wetter. Ges.* **2:** 17 (1811); type:—St. Domingo (L—holotype !).—*Physcia albicans* (Pers.) Thoms., *Beih. Nova Hedwigia* **7:** 88 (1963). Non *Anaptychia albicans* Kurok., *Beih. Nova Hedwigia* **6:** 80 (1962).

Parmelia domingensis Ach., nom. nov., *Syn. Lich.*: 212 (1814).—*Anaptychia domingensis* (Ach.) Massal., *Mem. Lich.*: 39 (1853).

Physcia ravenelii Tuck., *Syn. N. Amer. Lich.* **1:** 68 (1882); type:—S[outh] C[arolina] Sullivan's Island, *Ravenel* 203 (BM—isotype !).—*Anaptychia ravenelii* (Tuck.) Zahlbr., *Cat. Lich. Univ.* **7:** 737 (1931).

Lobes slightly disjunct, adjacent, more or less plane, not ascending, with short lateral lobes, often giving a crenate margin to main lobes; upper cortex somewhat uneven; lower cortex present. Soralia extended along margins and round apices of lateral lobes, but generally absent from apices of main lobes, producing finely granular soredia. Apothecia laminal, adnate to substipitate; margin of thalline exciple sorediate. Spores 24–35 × 11–15 μm (mean length of 50 in holotype, 26·1 μm, S.D. 1·9), without sporoblastidia. TLC (holotype): Atranorin, zeorin, salazinic acid, unknown substance.

This species is close to *Heterodermia pseudospeciosa* but is distinguished from it by having continuous soralia along the margins rather than localized labriform soralia, and by the chemistry. The chemistry of *H. albicans* is identical to that of *H. antillarum*.

In East Africa *Heterodermia albicans* is scattered and possibly overlooked. It grows both on rock and on tree trunks.

Specimens Examined

Ethiopia: Sidamo Province, E shore of Lake Awasa, *Winnem* 415/8, 442/9 (O). **Kenya:** Eastern Province, Machakos Districk, lava flow 5 km NW of Kibwezi, 2K 22/8, 3K 23/30. Coast Province, Taita District, Taita Hills, near Wundanyi, 2K 24/105.

2. Heterodermia antillarum (Vain.) Swinsc. & Krog comb. nov.

Anaptychia granulifera (Ach.) Vain. var. *antillarum* Vain., *Suomal. Tiedeakat. Toim.*, ser. A, **6:** 63 (1914); type:—Indias occ., Guadalupa, Camp-Jacob, alt. 500–800 m, sur les *Inga laurifolia*, *Duss* 459 pr. p. (TUR, Hb. Vainio 07737—lectotype !).—*Anaptychia tropica* Kurok. var. *antillarum* (Vain.) Kurok., *Beih. Nova Hedwigia* **6:** 36 (1962).—*Anaptychia antillarum* (Vain.) Kurok., *J. Hattori bot. Lab.* **37:** 596 (1973).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex somewhat uneven; lower cortex present. Isidia cylindrical to flattened, simple or branched, marginal and laminal. Apothecia adnate to substipitate; margin of thalline exciple isidiate. Spores (holotype) 23–30 × 12–18 μm (mean length of 50, 26·8 μm, S.D. 1·9). TLC (holotype): Atranorin, zeorin, salazinic acid, undetermined substance.

The isidia in this species differ from those in *Heterodermia isidiophora* by being more flattened. See under *H. lepidota* for comparison with that species.

Physcia speciosa f. *isidiophora* Nyl., Antilles, *Husnot*, 1868 (H, Hb. Nylander 32514 !) is in fact *H. antillarum.* So also are Welwitsch Lich. Angol. 97 and 104 (BM).

The American species *Heterodermia granulifera* (Ach.) Massal. also contains salazinic acid, but it lacks the characteristic undetermined substance found in *H. antillarum.* Kurokawa (1962) implied that the spores of these two species differ in size. *H. granulifera* rarely fruits, but examination of an apothecium kindly supplied by Dr M. E. Hale (*Hale* 11519, US) showed that the range of size of 30 spores (all available) was 21–32 × 10–15 μm, mean length 27·3 μm (S.D. 2·7). These measurements do not differ significantly from those recorded above for spores in the *H. antillarum* holotype.

The one specimen from our area had the characteristic chemistry, but the upper cortex was more even than in the holotype. It was on *Ficus* by a lake at 1700 m altitude.

Specimen Examined

Ethiopia: Sidamo Province, E shore of Lake Awasa, *Winnem* 415/7 (O).

3. Heterodermia appendiculata (Kurok.) Swinsc. & Krog comb. nov.

Anaptychia appendiculata Kurok., *Beih. Nova Hedwigia* **6:** 61 (1962); type:—Ivory Coast, cercle of Man, Mont Tonkoui, 'Rocher au Sacrifices,' alt. *c.* 1100 m, *Santesson* 10645a, 14 August 1954 (UPS—holotype !).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side non-corticate, white to pale brown. Squamules mainly marginal, a few laminal, dissected. Apothecia laminal, adnate to substipitate; margin of thalline exciple squamulose, the squamules becoming long and deeply dissected. Spores 37–53 × 18–25 μm (mean length of 50, 44·7 μm, S.D. 3·6), with sporoblastidia. TLC (holotype): Atranorin, zeorin, norstictic acid. (Kurokawa (1962) reported only atranorin and zeorin, but norstictic acid is plentiful.)

The other species in East Africa that bears squamules and is non-corticate below is *Heterodermia microphylla.* It normally lacks norstictic acid (though Kurokawa (1962) has reported a strain with norstictic and salazinic acids), and fertile specimens have spores without sporoblastidia.

The one collection of *Heterodermia appendiculata* so far in our area, cited below, was from bryophytes on bark. It is sterile.

Specimen Examined

Tanzania: Tanga Province, Lushoto District, Usambara Mountains, Magamba, *Ryvarden* 10917B (O).

4. Heterodermia casarettiana (Massal.) Trevis.

Atti Soc. ital. Sci. nat. **11:** 624 ((1868) 1869).—*Anaptychia casarettiana* Massal., *Mem. Lich.*: 39 (1853); type:—Brazil, *Casaretto* (VER—holotype, not seen; P. M. Jørgensen (personal communication) has examined this specimen and found that it agrees with the description given by Kurokawa (1962), who had not seen it).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side non-corticate, white to blackish violet suffused with yellow pigment, K−. Soralia apical, labriform. Apothecia laminal, adnate to substipitate; margin of thalline exciple sorediate. Spores 32–48 × 18–25 μm, with sporoblastidia. TLC: Atranorin, zeorin, norstictic acid, salazinic acid, pigment.

This species is very close to depsidone-containing strains of *Heterodermia japonica* but is distinguished from them by its yellow pigment. This is deposited in the lower layers of the medulla, not in a superimposed layer of hyphae as in *H. obscurata*.

Our one collection is exceptionally well developed and abundant, though it is not fruiting; the yellow pigment is profuse. It was growing among grass and bryophytes on an earth bank by a track in an open situation at 2100 m altitude.

Specimen Examined

Uganda: Kigezi District, Rubanda County, 10 km W of Burimbe, 3U 49/4.

5. Heterodermia chilensis (Kurok.) Swinsc. & Krog comb. nov.

Anaptychia chilensis Kurok., *Beih. Nova Hedwigia* **6:** 65 (1962); type:—Chile, Valparaiso, Alto del Puerto, *Santesson* 2919, 14 August 1940 (S—holotype !).

Lobes linear, disjunct, plane to somewhat involute laterally, not ascending, mainly digitately branched but with a few short lateral branches; upper cortex uneven; under side non-corticate, white, with thick corticate margins. Soralia apical, labriform. Apothecia laminal, adnate to substipitate; margin of thalline exciple pruinose. Spores (holotype) 28–39 × 18–22 μm (mean length of 50, 30·1 μm, S.D. 3·3), notably broad in relation to length (possibly abnormal), a few with small sporoblastidia (in 5 out of 50 spores). TLC (holotype): Atranorin, zeorin.

The occurrence of this species in Africa needs confirmation. All specimens assigned to it that we have examined belong to other species or are so fragmentary as to be of doubtful determination. We have seen no specimen assigned to this species and recorded from East Africa, but Kurokawa (1973) cites a record from Kenya.

For *Anaptychia chilensis* var. *austroafricana* Kurok. see under *Heterodermia japonica*.

6. Heterodermia comosa (Eschw.) Follm. & Redón

Willdenowia **6:** 446 (1972).—*Parmelia comosa* Eschw. in Martius, *Icon. Pl. Cryptog.* **1:** 26 (1828); type:—Brazil (not seen).—*Anaptychia comosa* (Eschw.) Massal., *Mem. Lich.*: 39 (1853).

Lobes linear-spathulate or paddle-shaped, with short or long lateral lobes; upper cortex uneven and forming vein-like ridges on under side; under side non-corticate, white, with pale ochraceous pink pigment, K−. Cilia on upper side numerous, laminal, white. Soralia on under side of lobes, subapical or apical, irregularly orbicular. Apothecia more or less apical; margin of thalline exciple crenulate. Spores 30–35 × 13–16 μm (Kurokawa, 1962), with sporoblastidia. TLC: Atranorin, zeorin, pigment.

The only other species in East Africa with cilia growing from the upper cortex is *Heterodermia loriformis*, and that has linear lobes like those of *H. leucomela* and an orange pigment, K+ purple, on the under side.

Heterodermia comosa has a strong preference for twigs, but it also grows on the smooth bark of small branches and trunks of trees and shrubs. It tolerates sunny or partially shady sites, and our records are from 1000 to 2500 m altitude.

Specimens Examined

Ethiopia: Shewa Province, Wondo Gennet Agricultural and Handicraft School, E 5/53. Sidamo Province, 12 km S of Kibre Mengist, E 13/26, *Winnem* 504/5 (O), 544/6 (O); E shore of Lake Awasa, *Winnem* 414/8 (O); Wondo Gennet, 20 km S of Shashemenne, *Winnem* 427/28 (O); W of Dilla, *Winnem* 470/17 (O); Yirga Alem, *Winnem* 476/18, 19, 477/13 (O); 12 km S of Kibre Mengist, *Winnem* 504/5 (O), 544/6 (O); NW of Kibre Mengist, *Winnem* 587/15 (O); between Kibre Mengist and Wadera, *Winnem* 595/11 (O); Wadera Mission Station, *Winnem* 597/7 (O). Arussi, between Shashemenne and Kofele, E 27/20. **Kenya:** Eastern Province, Marsabit District, Marsabit, NW side of Lake Paradise, *Lye* L 649 (Hb. Lye); Machakos District, 01 Doinyo Sapuk, 2K 4/124. Central Province, Kiambu District, escarpment E of Rift Valley 35 km NW of Nairobi, K 15/122; Limuru, *Burnet* AMB 57 (BM). **Uganda:** West Mengo District, Kyadondo County, 1–2 km N of Kawanda Agricultural Research Station, *Lye* L 199 (MAK); Busiro County, 15 km SW of Kampala, 3U 8/5a. Masaka District, Kalungu County, 0·5 km S of Masaka-West Mengo border, *Lye* L 525, 526 (MAK). Ankole District, Bunyanguru County, W edge of Kalinzu Forest 10 km S of Kisenyi, 2U 9/6; Isingiro County, Kantsyore Island, *Burnet* AMB 191f, 192, 197 (BM). Kigezi District, Bufumbira County, 6 km N of Hamurwa, 3U 35/2.

7. Heterodermia congoensis (Kurok.) Swinsc. & Krog comb. nov.

Anaptychia congoensis Kurok., *Beih. Nova Hedwigia* **6:** 72 (1962); type:—[Zaire], Ituri, *Humbert* (not seen).

Lobes delicate and disjunct, more or less convex, ascending, with short or long lateral lobes; upper cortex uneven; under side non-corticate, white. Marginal squamules on some lobes. Apothecia apical or subapical, stipitate; margin of thalline exciple with squamules. Spores 30–40 × 18–20 μm, with sporoblastidia. TLC: Atranorin, zeorin.

It has not proved possible to see the holotype (REN), and our material has been determined by reference to two fertile specimens from Rhodesia, Zimbabwe, *Höeg*, 3 April 1930 (LD), det. Kurokawa 1969.

This species, as Kurokawa (1962) has noted, is very close in external appearance to *Heterodermia hypoleuca*; in fact plants without apothecia can hardly be distinguished with certainty from small forms of the latter common and polymorphic species. But the lobes are more delicate than in most *Heterodermia* species, and erect squamules often arise from their margins. Occasionally these squamules dissolve into granular soredia. The lower surface sometimes shows vein-like ridges formed by the upper cortex. They are present in both specimens from Rhodesia referred to above and can be seen here and there in our material.

The two collections cited below, both fertile, were from mossy rocks at 1400–1800 m altitude. 2U 42/1 was on boulders at the edge of a village street on the slopes of Mt Elgon.

Specimens Examined

Uganda: Toro District, Burahya County, 2–3 km N of Kichwamba, *Lye* L 194. Bugisu District, North Bugisu County, Bumagabula, 2U 42/1.

8. Heterodermia dactyliza (Nyl.) Swinsc. & Krog comb. nov.

Physcia speciosa Fr. var. *dactyliza* Nyl., *Syn. Lich.* **1:** 417 (1860); type:—Brasilia, *Weddell*, 1844 (PC—isotype !).—*Anaptychia dactyliza* (Nyl.) Zahlbr. in Skottsb., *Nat. Hist. Juan Fernandez* **2:** 403 (1924).

Anaptychia speciosa var. *lineariloba* Müll. Arg., *Bot. Jb.* **15:** 508 (1893); type:—[Tanzania], bei westl. Njansagebiet, Kanesse, *Stuhlmann* 952 (G—holotype ! BM—isotype !).

Lobes disjunct, somewhat convex, not ascending but loosely attached to substrate, mainly digitately branched but with a few short lateral branches; upper cortex uneven; under side non-corticate, white, with thick corticate margins. Isidia and soralia absent. Apothecia laminal or marginal, substipitate or stipitate on a lobule; margin of thalline exciple crenulate. Spores (isotype, PC) 33–40 × 15–20 μm, with small simple sporoblastidia. TLC (isotype, PC): Atranorin, zeorin.

In this species the cortex at the margin of the lobes is thick and curved down to give a smooth, rounded edge to the lobe, as also in *Heterodermia chilensis.* The thallus seems to be generally on rock, and it stands away from the substrate on its rhizines. *H. hypoleuca* can also grow on rock, though usually corticolous. Its lobes are more closely adjacent to each other, more adnate to the substrate, and lack the thick corticate borders on the under side; if spores are present they differentiate it from *H. dactyliza.*

Our specimen was from a fully exposed, slightly inclined sheet of acidic rock at 1300 m altitude; Dale's was also on rock, at 2400 m.

Specimens Examined

Uganda: Bunyoro District, Bugangaizi County, 18 km NE of Kakumiro, 3U 67/6. Kigezi District, Kinkizi County, Mafuga, *Dale* L 28 (BM).

9. Heterodermia diademata (Tayl.) Awas.

Geophytology **3:** 113 (1973).—*Parmelia diademata* Tayl., *Hook. J. Bot.* **6:** 165 (1847); type:—Nepal, *Wallich* (not seen).—*Anaptychia diademata* (Tayl.) Kurok., *Beih. Nova Hedwigia* **6:** 28 (1962).

Physcia speciosa f. *cinerascens* Nyl., *Syn. Lich.* **1:** 417 (1860); type:—Ethiopia, Schimper iter abyss. 417 (BM—isotype !).

Physcia speciosa var. *cinerascens* f. *brachyloba* Müll. Arg., *Flora, Jena* **73:** 340 (1890); type:—India orientalis, Khasia Hills, *Griffith et al.* s.n. et d. (G—lectotype !).

Anaptychia albopruinosa Kurok., *Beih. Nova Hedwigia* **6:** 32 (1962); type:—Kenya, Mt Elgon, 3300 m, *Hedberg* 248, 3 March 1948 (UPS—holotype !).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; lower cortex present. Isidia and soralia absent. Apothecia laminal, adnate to substipitate; margin of thalline exciple crenulate to squamulose. Spores 25–35 (–40) × 12–17 μm (see also Table 2). TLC: Atranorin, zeorin.

Anaptychia albopruinosa is simply a pruinose form, and transitional degrees of pruinosity are common.

Widespread throughout the tropics, *Heterodermia diademata* is common in East Africa on the trunks and branches of trees, and is to be found also on sheltered rocks. It tolerates artificial habitats such as parks, street avenues, and trees on cultivated land, and it ranges in altitude from 1000 to over 3500 m, where frost at night is common. It does not grow in very dry bushland or subdesert. Its localities in East Africa are too numerous to list individually.

10. Heterodermia flabellata (Fée) Awas.

Geophytology **3:** 113 (1973).—*Parmelia flabellata* Fée, *Suppl. Ess. Crypt. Ecorc. Exot. Offic.*: 122 (1837); type:—[South America], ad corticem Cinchonae lancifoliae (G—lectotype !).—*Anaptychia flabellata* (Fée) Massal, *Mem. Lich.*: 41 (1853).

Anaptychia hypoleuca var. *fulvescens* Vain., *Philipp. J. Sci.*, sect. C, **8:** 106 (1913); type:—Philippines, Benguet, Luzon, *Merrill* 7935, May 1911 (BM—isotype !).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex uneven; under side non-corticate, with ochraceous orange hyphae, K+ purple, overlying medulla. Isidia and soralia absent. Apothecia laminal, adnate to stipitate; margin of thalline exciple crenulate to squamulose, inner surface of squamules pigmented. Spores (holotype) 30–37 × 12–18 μm (mean length of 29, 33·3 μm, S.D. 1·97), with sporoblastidia. TLC: Atranorin, zeorin, pigments.

Heterodermia flabellata is recorded from elsewhere in Africa (Kurokawa, 1962), the specimen cited below from our area is sparse and questionable. It has smaller spores than those of the holotype. The mean length of 100 from two ascocarps was 27·1 μm (S.D. 2·1). The pigmented layer of hyphae on the under side is well developed. The specimen may be a form of *H. hypochraea.*

Heterodermia dendritica (Pers.) Poelt, as interpreted by Kurokawa (1962), resembles this species in having an ochraceous, K+ purple, pigment on the under side, but differs from it in producing norstictic and salazinic acids. An examination of the type specimens has shown that this view of the species presents some problems. The holotype in PC (!) and the isotypes in G (!) and H (!) all lack the ochraceous pigment. Kurokawa (1962) himself noted the lack of this pigment 'in the type'. On TLC the holotype and one isotype (G) were found also to lack norstictic and salazinic acids; the other isotype (H) was too scanty to test by TLC, but a minute fragment reacted K+ yellow, not red. Moreover, several lobes in the holotype have some soralia-like regions below their apices, though it is uncertain whether these represent incipient labriform soralia or are abnormalities. The isotypes lack them. The upper cortex of these specimens is even. This is a somewhat questionable character, but in addition to their lack of pigment it does further differentiate them from *H. flabellata*.

The specimen cited below was growing on twigs of a shrub on a lava flow at 1000 m altitude.

Specimen Examined

Kenya: Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, 3K 23/152 (determination doubtful: see above).

11. Heterodermia hypochraea (Vain.) Swinsc. & Krog comb. nov.

Anaptychia hypochraea Vain., *Bot. Mag., Tokyo* **35:** 59 (1921); type:—Japan, Prov. Inaba, Mt Sensoku, *Yasuda* 151, 25 September 1915 (TUR, Hb. Vainio 07958—holotype !).

Lobes slightly disjunct, convex, ascending, with short lateral branches; upper cortex uneven; under side non-corticate, with ochraceous pigmented hyphae, K+ purple, overlying medulla. Isidia and soralia absent. Apothecia apical or subapical stipitate; margin of thalline exciple squamulose, inner surface of squamules pigmented. Spores 35–45 × 14–22 μm, with sporoblastidia. TLC (holotype): Atranorin, zeorin, two pigments.

The habitat at both of the localities listed below was the upper joints and twigs of bamboo in montane forest at 2300–2500 m altitude.

Specimens Examined

Uganda: Toro District, Busongora County, Ruwenzori, 10 km NW of Kilembe, 2U 12/46a. Kigezi District, Bufumbira County, 1 km E of Kanaba Gap, 3U 57/1.

12. Heterodermia hypoleuca (Ach.) Trevis.

Atti Soc. ital. Sci. nat. **11:** 615 ((1868) 1869).—*Parmelia speciosa* b. *hypoleuca* Ach., *Syn. Lich.*: 211 (1814); type:—Amer. bor., *Mühlenburg* 33–2 (H—holotype !).—*Anaptychia hypoleuca* (Ach.) Massal., *Atti I. R. Ist. Veneto*, ser. 3, **5:** 249 (1860).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex uneven; under side non-corticate, white. Isidia and soralia absent. Apothecia adnate to substipitate; margin of thalline exciple crenulate. Spores (holotype) 23–30 (–36) × 11–16 μm (mean length of 34, 27·4 μm, S.D. 2·62), nearly all without sporoblastidia, but one healthy spore showing a single sporoblastidium at each end. TLC: Atranorin, zeorin.

Apart from the spores *Heterodermia hypoleuca* comes very close to *H. magellanica.* Chemically there are no differences. Consequently specimens lacking spores cannot be assigned with certainty to one or other species, and statements about geographical distribution need to be based on fertile specimens. Such records as exist at present indicate that *H. hypoleuca* is mainly distributed in the northern hemisphere and *H. magellanica* in the southern, but both cross the equator to some extent. Only fertile specimens are cited below in the list of localities.

The mean lengths of the spores in the holotype of *Heterodermia hypoleuca* and of four East African specimens are recorded in Table 4. They are consistently shorter than those of *H. magellanica* (see Table 12). An occasional spore with one or two simple sporoblastidia is to be found in most specimens of *H. hypoleuca,* but two of our 22 East African fertile specimens have numerous spores with sporoblastidia.

TABLE 4. Heterodermia hypoleuca, *mean lengths of spores in holotype and four East African specimens*

Specimen	Number of spores	Mean length of spores	Standard deviation
Holotype	34	27·4	2·62
U 9/34	50	29·3	2·83
K 1/501	50	30·7	2·36
K 54/36*	69	29·1	2·33
2K 25/7*	84	29·0	1·96

* Specimens with sporoblastidia: see Table 5.

A count of 152 spores in one apothecium of K 54/36 gave 58 (38%) with sporoblastidia and of 181 spores in one apothecium of 2K 25/7 gave 59 (33%). Some of the spores from the latter specimen are depicted in Fig. 1. Spores from an East

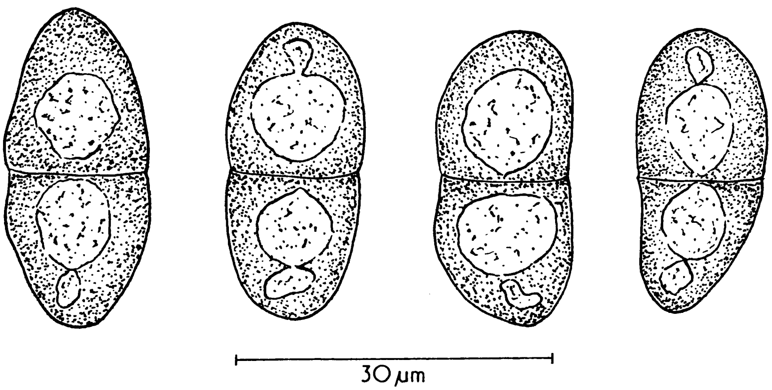

FIG. 1. *Heterodermia hypoleuca*, spores with sporoblastidia (2K 25/7).

African specimen of *Heterodermia magellanica* are shown in Fig. 3. Spores from two other apothecia in these two specimens of *H. hypoleuca* were measured to compare the mean length of those without sporoblastidia and those with them. Table 5 shows there is no significant difference between the mean lengths of spores with and without sporoblastidia.

TABLE 5. Heterodermia hypoleuca, *comparison between spores with and without sporoblastidia in two specimens from Kenya; measurements in µm*

Specimen	Spores without sporoblastidia			Spores with sporoblastidia			Mean difference in length	S.E. of difference
	No.	Mean	S.D.	No.	Mean	S.D.		
K 54/36	48	29·3	2·29	21	28·6	2·34	0·74	0·61
2K 25/7	50	27·2	1·94	34	26·4	1·91	0·72	0·43

A specimen collected in Kenya at Embu (K 53/113) and not at present determined has a yellowish pigment on the under side, K+ crimson in patches, yet in its thallus, apothecia, spores, and chemistry it otherwise resembles *Heterodermia hypoleuca*. It differs from *H. flabellata* in lacking sporoblastidia.

Kurokawa (1962) reports the existence of a rare strain of *Heterodermia hypoleuca* containing norstictic and salazinic acids. In view of the close similarities between this species and *H. magellanica* it is interesting to note that the latter species also has a depsidone-producing strain.

Heterodermia hypoleuca is widespread in East Africa and commoner than the following records suggest. It grows in open woodland and parkland, including artificial habitats such as Nairobi Arboretum, and is to be found on twigs as well as, more generally, on the boles and larger branches of trees among mosses or on the bare wood. Our records lie between 1000 and 2400 m altitude.

Specimens Examined

Ethiopia: Shewa Province, Wondo Gennet Agricultural and Handicraft School, E 5/75. Sidamo Province, 6 km N of Wadera, E 10/9; Wondo Gennet, 20 km S of Shashemenne, *Winnem* 428/8 (O); between Shashemenne and Malge Wondo, *Winnem* 490/4 (O); Hagere Selam Mission Station, *Winnem* 591/3 (O). Gemu Gofa Province, Arba Minch, E 25/6. **Kenya:** Central Province, Kirinyaga District, Mt Kenya, 2 km NW of Irangi Forest Station, K 48/55, 145; by Thiba Fishing Camp, K 52/114. Eastern Province, Embu District, Embu, K 53/11; Meru District, Mt Kenya E side, 3K 15/3; Machakos District, Ol Doinyo Sapuk, 2K 4/121; Mua Hills, K 5/14; Kilima Kiu, K 54/36. Rift Valley Province, Kajiado District, Ngong Hills, K 2/12; Chyulu Hills, K 39/6, 105. Nairobi Province, Nairobi Arboretum, K 1/8, 501. Coast Province, Taita District, Taita Hills, above Wundanyi, 2K 25/7. **Tanzania:** Eastern Province, Morogoro District, Uluguru Mountains, above Morogoro, *T. Pócs et al.* 6713/C; Mamiwa Range N of Kilosa, *Pócs & Mabberley* 6740/N.

13. Heterodermia isidiophora (Vain.) Awas.

Geophytology **3:** 114 (1973).—*Anaptychia isidiophora* Vain., *Cat. Afr. Pl. Coll. Welwitsch* **2:** 409 (1901); type:—Angola, Pungo Andongo (2400 ad 3800 ped. s.m.). Ad rupes perpendiculares juxta rivulos ad Barranco da Pedra Songue frequenter, at raro fructificans, *Welwitsch* 96, 1857 (LISU—holotype ! BM, TUR—isotypes !).—Non *Physcia speciosa* f. *isidiophora* Nyl., *Syn. Lich.* **1:** 417 (1860).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; lower cortex present. Isidia cylindrical, simply branched or coralloid, marginal and laminal. Apothecia adnate to substipitate; margin of thalline exciple isidiate. Spores (holotype) 21–31 × 12–17 μm (mean length of 50, 25·2 μm, s.d. 2·0). TLC (holotype): Atranorin, zeorin.

Physcia speciosa f. *isidiophora* Nyl. has been cited as the basionym of this species (Kurokawa, 1962), but in fact Nylander (1860) did not publish a diagnosis of that forma; and the specimen cited by Kurokawa (1962) as its holotype (Hb. Nylander 32514 in H !) belongs to *Heterodermia antillarum* (TLC: atranorin, zeorin, salazinic acid, undetermined substance). Nylander (1863) subsequently listed **Physcia domingensis* (Ach.) Nyl. f. *isidiophora*, again without any description except the word 'sterilis'. He assigned to this taxon a specimen collected in Bogota, *Lindig* 2534 (H !), which does belong to *H. isidiophora*. Hue (1892) referred back to Nylander (1863) and included *Physcia domingensis* f. *isidiophora* without description. The first description of the taxon (and it was as a species) thus came from Vainio (*loc. cit. supra*), who based it on Welwitsch Lich. Angol. 96, and he stated that the *Physcia domingensis* f. *isidiophora* listed by Hue (1892) belonged to the same species.

Though the isidia are normally cylindrical in *Heterodermia isidiophora*, a few flattened and squamulose are often seen, especially if the plant has been growing in a damp or shady place. But the isidia are distinct from the squamules characteristic of *H. lepidota*. *H. antillarum* contains salazinic acid. *H. microphylla* lacks a lower cortex.

A widespread tropical species, *Heterodermia isidiophora* is common throughout East Africa. Though usually on the trunks and large branches of trees, it also grows on rocks in sheltered places. It favours open woodland and wayside trees, and tolerates town avenues and parks. Our records are too numerous to list individually; in altitude they range from 1400 to 2750 m.

14. Heterodermia japonica (Sato) Swinsc. & Krog comb. nov.

Anaptychia dendritica (Pers.) Vain. var. *japonica* Sato, *J. Jap. Bot.* **12:** 427 (1936); type:—Formosa (not seen).—*Anaptychia japonica* (Sato) Kurok., *Beih. Nova Hedwigia* **6:** 58 (1962).

Anaptychia japonica (Sato) Kurok. var. *reagens* Kurok., *J. Jap. Bot.* **35:** 354 (1960); type:—Japan, Honshu, Prov. Sagami, Mt Kintoki, Hakone, *Kurokawa* 58064, 26 April 1958 (TNS—holotype !).

Anaptychia chilensis Kurok. var. *austroafricana* Kurok., *J. Hattori bot. Lab.* **37:** 600 (1973); type:—Basutoland, Div. Leribe, Buthabuthe, *Kofler*, 24 March 1963 (LD).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side non-corticate, white to blackish violet. Soralia apical, labriform. Apothecia laminal, adnate to substipitate; margin of thalline exciple sorediate. Spores 35–45 × 15–22 μm, with sporoblastidia. TLC: Atranorin, zeorin; holotype of *Anaptychia japonica* var. *reagens* Kurok., atranorin, zeorin, norstictic acid; holotype of *A. chilensis* var. *austroafricana* Kurok., atranorin, zeorin, norstictic acid, salazinic acid.

Our African depsidone-containing plants are chemically identical with the holotype of *Anaptychia japonica* var. *reagens*. There is no morphological, ecological, or topographical difference between plants with and without norstictic acid. Consequently we regard the depsidone-containing plants as simply representing a strain of the species.

The chemical strains of this species without depsidones and with norstictic acid (but without salazinic acid) are common throughout East Africa on trunks and branches of moderately shaded trees. Our records range from 1800 to 3400 m altitude and are too numerous to list individually. The salazinic-acid-containing strain has not yet been found in East Africa.

15. Heterodermia lepidota Swinsc. & Krog sp. nov.

PLATE 2

Thallus albidus. Lobi lineariter cuneati, lobis lateralibus brevibus, squamulis numerosis, versum thalli peripheriam praecipue marginalibus, versum centrum dense ad laminam. Cortex superior aequaliter incrassatus, cortex inferior praesens. Rhizinae praecipue nigrescentes, vix ramosae. Apothecia adnata ad substipitata; margo excipuli thallini crenulata ad squamulosa. Sporae 24–33 × 12–17 μm, sporoblastidiis destitutae.

Holotypus: Uganda, Karamoja District, Matheniko County, Mt Moroto, near Sogolomon, 2°30′N, 34°45′E, 2500 m altitude, *Swinscow* 2U 36/12, June 1970; isotypi O, MAK.

Lobes linear to linear-cuneate, slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side with cortex, white to dark brown. Squamules numerous, marginal and laminal, dissected, non-corticate below. Rhizines mainly black, pale at periphery of thallus, scarcely branched. Apothecia adnate to substipitate, laminal; margin of thalline exciple crenulate to squamulose, inner surface of squamules non-corticate. Spores 24–33 × 12–17 μm

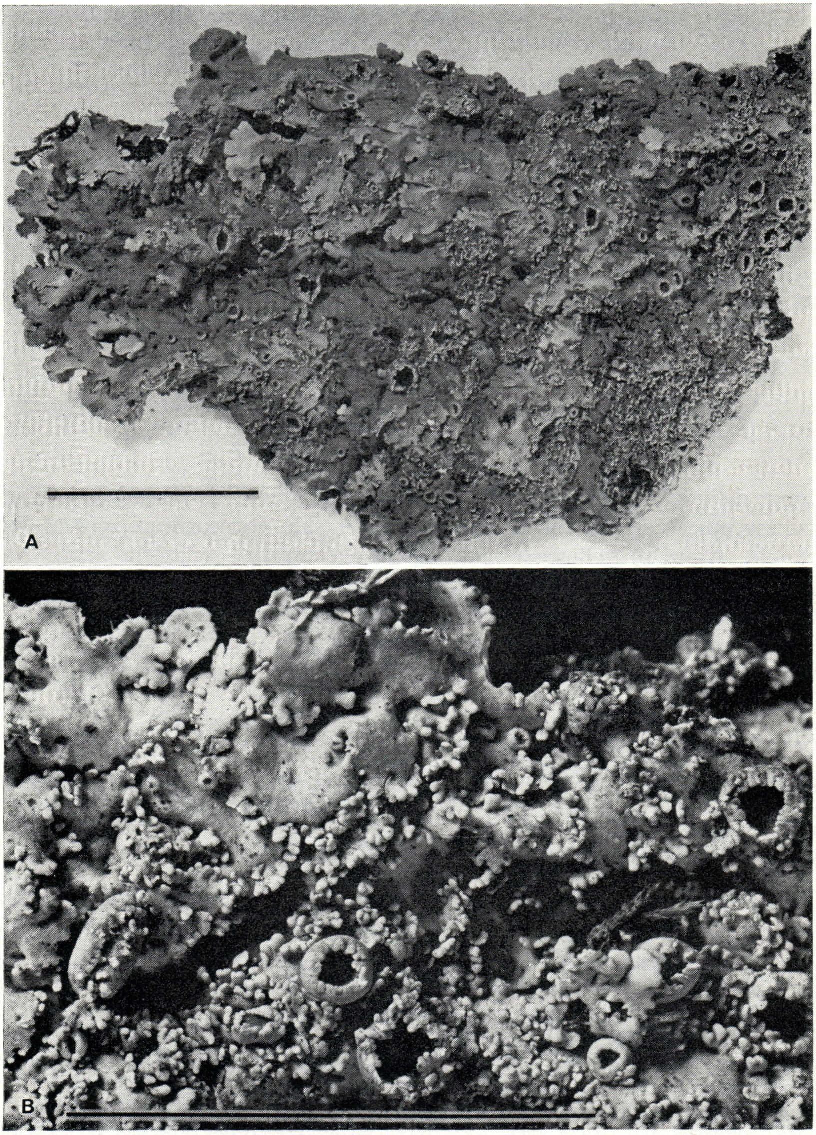

PLATE 2. A. *Heterodermia lepidota* Swinsc. & Krog, part of holotype, general appearance of thallus. B. *H. lepidota*, part of holotype, squamules and apothecia. Scales = 1 cm.

(mean of 50, 28·7 μm, S.D. 2·0), without sporoblastidia. TLC (all specimens): Atranorin, zeorin.

The numerous squamules of *Heterodermia lepidota* distinguish it from the isidiate species *H. isidiophora*, *H. antillarum*, and the American *H. granulifera* (Ach.) W. Culb. The latter two species also contain depsidones. *H. dissecta* (Kurok.) Awas. (TNS—holotype !) contains dissectic acid and is somewhat more isidiate than *H. lepidota*. *H. microphylla* lacks a lower cortex.

The records of this species are all from woodland in partial shade at 2000–3000 m altitude. The plant grows on the trunks and branches of large trees, on the bare wood or on bryophytes covering it.

Specimens Examined

Ethiopia: Shewa Province, Wondo Gennet Agricultural and Handicraft School, E 5/61. Sidamo Province, E shore of Lake Awasa, E 6/19. **Kenya:** Rift Valley Province, Uasin Gishu District, 5 km NW of Timboroa summit, 2K 19/139. Eastern Province, Meru District, Mt Kenya, Themwe, 3K 16/63, 264; Machakos District, Mua Hills, 3K 2/1. **Uganda:** Karamoja District, Matheniko County, Mt Moroto, near Sogolomon, 2U 36/12 (holotype). Toro District, Busongora County, 10 km NW of Kilembe, 2U 12/13. Kigezi District, Bufumbira County, Muhavura N side, U 16/15, 19a, 3U 60/3.

16. Heterodermia leucomela* (L.) Poelt

Nova Hedwigia **9:** 31 (1965).—*Lichen leucomelos* L., *Sp. Plant.*, ed. 2, **2:** 1613 (1763); type:—Amer. (LINN [in BM]—holotype !).—*Anaptychia leucomela* (L.) Massal., *Mem. Lich.*: 35 (1853).

Lobes disjunct, up to about 1·5 mm wide, dichotomously branched, branches remaining apical; upper cortex uneven; under side non-corticate, pulverulent to arachnoid, white to yellowish pink (from decomposed salazinic acid). Soralia common subapically on under side of lobes. Apothecia laminal or subapical to apical, stipitate; margin of thalline exciple crenulate to squamulose. Spores 35–52 × 18–25 μm, with sporoblastidia. TLC (holotype, by P. W. James): Atranorin, zeorin, two other triterpenes, salazinic acid, consalazinic acid, purple pigment.

Subsp. boryi (Fée) Swinsc. & Krog comb. nov.

Borrera boryi Fée, *Ess. Cryptog. Ecorc. Exot. Offic.*: Introd. XCVI et tab. II, fig. 23 (1824); type:—Ile Bourbon, *Fée* s.n. et d. (PC—syntype !).—*Anaptychia boryi* (Fée) Massal., *Mem. Lich.*: 41 (1853).

Anaptychia neoleucomelaena Kurok., *J. Jap. Bot.* **36:** 51 (1961).

Differs from ssp. *leucomela* in usually having narrower lobes, more circinately revolute tips to the distal lobes, an arachnoid more often than pulverulent under

* The specific epithet has often been written as *leucomelaena*, but we agree with Culberson (1966) that *leucomela* is to be preferred. The *leucomelos* of Linnaeus (*loc. cit.*) is probably a misprint for *leucomelas*, the Greek for white-black. The feminine of *melas* is *melaena*. Hence with feminine generic names some authors wrote *leucomelaena*. But under the *International Code of Botanical Nomenclature, 1969*, Recommendation 23 B, botanists are enjoined to use Latin terminations insofar as possible. In accordance with this recommendation the masculine form is *leucomelus* and the feminine *leucomela*. The latter was used in the combination *Parmelia leucomela* Ach., *Meth. Lich*: 256 (1803). We are grateful to Professor G. Degelius for discussion of some aspects of this question but of course accept full responsibility for the opinion given here.

side, a lower frequency of soralia and a higher frequency of apothecia, and in lacking depsidones. TLC (syntype, PC): Atranorin, zeorin.

The two taxa that we treat here as subspecies were accepted as distinct species by Kurokawa (1961). Other authors have regarded ssp. *boryi* (under various synonyms) as identical with *Heterodermia leucomela*, or as a variety of it, or as a form (see Kurokawa, 1962, 1973). These divergent opinions reflect the morphological and chemical diversity commonly found in the plants. Firstly, for instance, though the lobe apices of *H. leucomela* ssp. *leucomela* and ssp. *boryi* look clearly distinct when characteristically developed (Fig. 2), they are often intermediate in form; and,

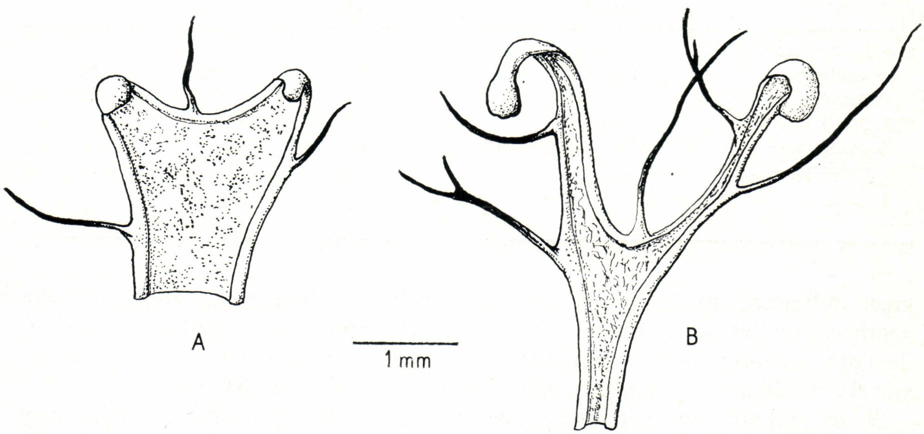

FIG. 2. *Heterodermia leucomela* ssp. *leucomela* (A) and ssp. *boryi* (B), differences between lobe apices in well developed specimens (3K 23/26 and 2K 8/21 respectively).

though the lobes of ssp. *leucomela* are generally broader in proportion to their length than those of ssp. *boryi*, the proportions in some plants are reversed. Secondly, the type and amount of depsidones produced vary in different plants. Most of our depsidone-producing plants contain abundant salazinic acid, and some have a trace of norstictic acid also. Some have merely a trace of salazinic acid, and two (*Tapper* 202, *Winnem* 507/6) have only norstictic acid. Thirdly, the chemistry is not precisely correlated with the morphology in that some ssp. *leucomela*-like plants lack depsidone and some ssp. *boryi*-like plants contain it. In fact the holotype of *H. leucomela* is morphologically close to ssp. *boryi*. In addition some plants of *H. leucomela* from South America contain, like the holotype, a purple pigment which as well as being readily detectable on TLC gives, in a few specimens, a faintly visible tint to the lobes (P. W. James, personal communication). It seems to be present mainly in the rhizines but in some specimens has spread also to the thallus. However, the taxonomically important substances are the depsidones, and our analysis is based on their presence or absence.

The question first examined here is whether we have only a single species showing continuous variation from one extreme to another and comprising two chemical strains—with and without depsidone—or whether more than one taxon should be admitted. Our study is based on 140 specimens. These are the total collected by ourselves and other collectors listed above in this paper. The only selection they have undergone is by the exclusion of a few depauperate or juvenile specimens.

In Table 6 the 140 specimens are arranged by morphotype, chemotype, and presence of apothecia and soralia. (The existence of intermediate forms of lobe makes the decision on which morphotype a plant should be assigned to questionable in a few cases.) If the 140 were all of a single species it is unlikely that there would be

TABLE 6. *Specimens of* Heterodermia leucomela *arranged by morphotype, chemotype, and presence or absence of apothecia and soralia*

Morphotype and chemotype	With apothecia	Without apothecia	With soralia	Without soralia	Total
ssp. leucomela					
depsidone +	13	37	34	16	50
depsidone −	3	1	0	4	4
ssp. boryi					
depsidone −	26	48	23	51	74
depsidone +	1	11	5	7	12
Total	43	97	62	78	140

great differences in the frequency with which one character is associated with another. In other words, the production of soralia might be expected to be independent of morphotype and chemistry, the chemotype to be independent of morphotype, and the production of apothecia to be independent of these characters.

Plants of both the main morphotypes, irrespective of chemical strain, may produce soralia or apothecia or both, but do not always do so. Before these relationships are examined it should be noted that there is a common preference in the field to collect fruiting plants. Those in our sample therefore cannot be accepted as a random sample of the population from which they were collected. Two consequences follow. Firstly, no estimate of the true frequency of fruiting in these morphotypes can be hazarded. Secondly, since Table 7 shows that there is an inverse relationship

TABLE 7. *Specimens of* Heterodermia leucomela, *both subspecies, arranged by presence of apothecia and soralia*

	With soralia	Without soralia	Total
With apothecia	8	35	43
Without apothecia	54	43	97
Total	62	78	140

$\chi^2 = 16{\cdot}59$. $P \ll 0{\cdot}001$.

between presence of apothecia and presence of soralia, any study of the frequency of soralia should be restricted to non-fruiting plants. Soralia were present in 19% of fruiting plants and in 56% of non-fruiting plants, a statistically highly significant difference.

When non-fruiting specimens are examined the following high correlations are found:

(1) Between production of depsidone and presence of soralia. Of 49 specimens lacking depsidone 37% had soralia compared with 75% of 48 specimens producing depsidone (Table 8).

TABLE 8. *Non-fruiting specimens of* Heterodermia leucomela, *both subspecies, arranged by chemotype and presence of soralia*

Chemotype	With soralia	Without soralia	Total
Depsidone −	18	31	49
Depsidone +	36	12	48
Total	54	43	97

$\chi^2 = 14{\cdot}39$. $P \leqslant 0{\cdot}001$.

(2) Between ssp. *leucomela*-like morphology and presence of soralia. Of 38 specimens morphologically ssp. *leucomela* 84% had soralia compared with 37% of 59 specimens morphologically ssp. *boryi* (Table 9).

TABLE 9. *Non-fruiting specimens of* Heterodermia leucomela, *both subspecies, arranged by morphotype and presence of soralia*

Morphotype	With soralia	Without soralia	Total
ssp. leucomela	32	6	38
ssp. boryi	22	37	59
Total	54	43	97

χ^2 (with Yates's correction) $= 18{\cdot}76$. $P \leqslant 0{\cdot}001$.

(3) Between ssp. *leucomela*-like morphology and production of depsidone. Of 38 specimens morphologically ssp. *leucomela* 97% contained depsidone compared with 19% of 59 specimens morphologically ssp. *boryi* (Table 10).

TABLE 10. *Non-fruiting specimens of* Heterodermia leucomela, *both subspecies, arranged by morphotype and chemotype*

Morphotype	Depsidone −	Depsidone +	Total
ssp. leucomela	1	37	38
ssp. boryi	48	11	59
Total	49	48	97

χ^2 (with Yates's correction) $= 54{\cdot}2$. $P \leqslant 0{\cdot}001$.

However, it is clear from these three Tables that, though most of the pairs of characters analysed in them are strongly associated, none are exclusively so. The strongest association is between chemistry and morphology (Table 10).

On these data, therefore, we accept the existence of at least two taxa, but two questions follow. What is the status of these taxa? And are there more than two?

On the first question it is worth noting that such data as exist suggest that the depsidone-containing and depsidone-lacking plants are not entirely sympatric. The depsidone-containing plants are the only ones so far recorded in Europe and the temperate regions of North America, for instance. In parts of the tropics the depsidone-lacking plants seem to be commoner; in East Africa they certainly are, though the actual distribution of the chemotypes does not differ significantly.

Thus to the correlated morphological and chemical data suggesting the existence of two taxa may be added geographical differences. But despite that there seems to be too much overlapping of characters to regard these taxa as separate species. As Tables 8–10 show, there is no single character by whose presence or absence it is possible to determine a specimen with certainty. The two taxa are separated in effect by frequency distributions of characters. In these circumstances to accept the status of species for them would seem to be inappropriate.

The status of form has been very variously applied, sometimes as a non-taxonomic category to denote a purely phenotypic modification of environmental origin. As a taxonomic category it commonly marks a rather small difference from the main form of the species and is restricted to a single or few linked characters (Du Rietz, 1930). The boundary between the form and the variety is indefinite, but the variety is commonly used for local facies of a species, morphologically distinct and occupying a restricted geographical area. The emphasis (Davis and Heywood, 1963) is on the small scale and more localized range of the variety in contrast to 'the large-scale, regional basis of the subspecies'. In the present case no single character or group of clearly defined characters unequivocally separates the two taxa. Nor does one or other of these taxa form a more or less distinct *or* local facies of the other. They intergrade in a number of ways, and their distributions overlap without being identical.

The choice of subspecies to mark the difference between them seems most appropriate despite the lack of substantial geographical separation, because the two differ in a number of characters but are not sufficiently differentiated to be regarded as separate species (Du Rietz, 1930). In fact these two subspecies belong to that category sometimes thought of as representing a species observed in the course of evolving into two. They are clearly not a sorediate-esorediate pair in the sense of Du Rietz (1924) and Poelt (1970), in that other differences than the frequency of soralia production divide them.

Finally, the question whether there are more than two taxa is prompted by the data set out in Table 6. This shows that of 54 specimens with ssp. *leucomela* morphology 4 (7%) were depsidone-negative, while of 86 specimens with ssp. *boryi* morphology 12 (14%) were depsidone-positive. These aberrant specimens could be regarded either as representing chemical strains of the subspecies or as being morphological variants with normal chemistry. The numbers are unfortunately too small for any certain conclusions to be drawn, but the following facts are worth noting. Of the 4 plants of morphologically determined depsidone-negative ssp. *leucomela* 3 produced apothecia and none produced soralia. These figures are contrary to the trend for ssp. *leucomela* and concordant with that for ssp. *boryi*. Conversely, of the 12 plants of morphologically determined ssp. *boryi* that are depsidone-positive only one produced apothecia and as many as five produced soralia. These figures are contrary to the trend for ssp. *boryi* and concordant with that for ssp. *leucomela*. At present all that can be said on those data is that the chemistry may correctly denote the subspecies and the morphology be abnormal. Consequently, in view of these uncertainties we believe the best course here is not to create taxa subordinate to the two subspecies, and in assigning aberrant plants to one or other we give primacy to chemical criteria, while recognizing that the decision is arbitrary.

Both subspecies of *Heterodermia leucomela* are widespread in East Africa except in desert and subdesert areas. Our 140 records are too numerous to list individually but far too few to give a real idea of the ubiquity of these subspecies. There is no significant difference in the geographical distribution or altitude of the two subspecies; both are found up to about 3500 m. The ssp. *boryi* is the commoner of the two throughout the area. They occupy a great variety of habitats: mossy rocks, earth banks, and the trunks, branches, and twigs of trees and shrubs. In general they prefer some shade.

17. Heterodermia loriformis (Kurok.) Swinsc. & Krog comb. nov.

Anaptychia loriformis Kurok., *Beih. Nova Hedwigia* **6:** 81 (1962); type—East Africa, West Usambara, *Brunnthaler* (not seen).

Lobes disjunct, dichotomously branched, branches remaining apical; upper cortex uneven, forming vein-like ridges on under side; under side non-corticate, with ochraceous orange to brick red pigment in hyphae overlying medulla, K+ purple. Cilia on upper side sparse to numerous, laminal, white. Isidia and soralia absent. Apothecia apical or subapical; margin of thalline exciple squamulose to linear-lobate, often bearing ribbon-like extensions resembling small thalline lobes, inner surface pigmented. Spores 32–50 × 16–22 μm (mean length of 50, 42 μm, S.D. 3·8). TLC: Atranorin, zeorin, pigment.

Kurokawa kindly confirmed the determination of our material.

This is a much more robust species than *Heterodermia vulgaris*, the only other species in East Africa with ribbon-like lobes bearing a K+ purple pigment on the under side. Moreover, the colour of the pigment is different.

The species grows on the twigs and branches of exposed shrubs and trees at 1000–1900 m altitude. It was abundant and fertile at the three localities listed below.

Specimens Examined

Kenya: Rift Valley Province, Kajiado District, Chyulu Hills, K 39/7, 106. Eastern Province, Machakos District, Kilima Kiu, K 54/2, 26, 42, 43; lava flow 5 km NW of Kibwezi, K 20/12, 131, 2K 22/17, 136, 3K 23/22, 24, 149, 151.

18. Heterodermia lutescens (Kurok.) Follm.

Philippia **2:** 73 (1974).—*Anaptychia lutescens* Kurok., *J. Jap. Bot.* **36:** 54 (1961); type:—Mexico, Monte Ovando, Chiapas, *Matuda* 46, 25 March 1932 (TNS—holotype !).

Lobes disjunct, dichotomously branched, branches remaining apical; upper cortex uneven; under side non-corticate, with pigment in lower layers of medulla, the pigment pale yellow, sometimes becoming orange pink or pink with age, K−. Soralia often present subapically on under side of lobes. Apothecia adnate to substipitate, subapical; margin of thalline exciple crenulate. Spores (Kurokawa, 1962)

36–43 × 20–21 μm, with sporoblastidia. TLC (holotype): Atranorin, zeorin, pigments.

The type specimen has some minute squamules and cylindrical lobules or isidia scattered here and there over the lobes; they are mainly lateral, occasionally laminal. They seem not to be a characteristic feature of the species. None of the African specimens has them.

The pigmentation in this species is somewhat variable, and in contrast to that of *Heterodermia loriformis*, *H. usambarensis* and *H. vulgaris* is within the basal layers of the medulla, not in hyphae superimposed on it. The colour varies from pale yellow through sulphur yellow and shades of pale orange to pink. Some specimens retain their yellow colour; others have lobes showing a variety of colours in different parts of the thallus; others again are entirely pink. The pigment was pale yellow in one of the Uganda specimens when it was collected in 1968 (*Lye* L 6); by 1975 it had become pink except subapically, where it remained yellow.

Apothecia are rare and have not been seen in African specimens.

The species is widespread in the tropics generally but appears to be rare in East Africa, though perhaps overlooked owing to the pale colour of the pigment in some plants when fresh. It grows on trees and shrubs in sheltered places. Our records are all from about 1700–1800 m altitude.

Specimens Examined

Tanzania: Northern Province, Moshi District, Mwika, *Sitari* 287a (TUR). Southern Highlands Province, Iringa District, Image Mountain 1750 m, *I. N. Bjørnstad* 786 (O). **Uganda:** Ankole District, Igara County, Lubare Ridge 10 km S of Rubirizi, 2U 3/11. Bugisu District, Manjiya County, near Bukalasi, *Lye* L 6.

19. Heterodermia magellanica (Zahlbr.) Swinsc. & Krog comb. nov.

Anaptychia magellanica Zahlbr., *K. svenska VetenskAkad. Handl.* 57: 54 (1917); type:—Magellans Sund, Isla Felix, *C. Skottsberg*, 24 May 1908 (UPS—holotype !, S—isotype !).

Anaptychia dactyliza f. *pectinata* Zahlbr. in Skottsb., *Nat. Hist. Juan Fernandez* 2: 403 (1924); type:—Juan Fernandez, Masatierra, Cerro de la Damajuana, *C. & I. Skottsberg* 138, 29 January 1917 (UPS—holotype !).—*A. pectinata* (Zahlbr.) Sant., *Ark. Bot.* 31A (7): 14 (1944).—*A. magellanica* var. *pectinata* (Zahlbr.) Kurok., *Beih. Nova Hedwigia* 6: 67 (1962).

Anaptychia magellanica var. *africana* Kurok., *J. Hattori bot. Lab.* 37: 604 (1973).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex uneven; under side non-corticate, white. Isidia and soralia absent. Apothecia laminal, adnate to substipitate; margin of thalline exciple crenulate. Spores 35–45 (–49) × 15–25 μm, with sporoblastidia. TLC (holotype): Atranorin, zeorin; also chemical strain producing depsidones.

As Kurokawa (1962) pointed out, the holotype of *Anaptychia magellanica* Zahlbr. is an abnormal form of this species, consisting largely of subascending lacinules. Normal forms are probably distinguishable only by the spores from *Heterodermia hypoleuca*. Table 11 shows the mean length of spores in several specimens, including type specimens, of *H. magellanica*. For the appearance of spores in this species see Fig. 3, and to compare their length with that of *H. hypoleuca* spores see Table 4.

Kurokawa (1973) described *Anaptychia magellanica* var. *africana* as differing from var. *magellanica* in containing norstictic and salazinic acids, and regarded it as 'endemic to southern Africa'. Of the 13 specimens of this species cited below three

TABLE 11. Heterodermia magellanica, *mean lengths of spores in type and other specimens*

Specimen	Number of spores	Mean length of spores	Standard deviation
H. magellanica isotype (S)	50	41·9	3·1
A. dactyliza var. pectinata holotype (UPS)	38	40·0	3·3
Santesson 6009 (S)	50	41·4	3·0
Lich. austro-amer. 401 (S)	50	40·3	4·2
E 30/32	42	40·4	5·5

contain norstictic but not salazinic acid. Like some other species of this genus *Heterodermia magellanica* evidently exists in more than one chemical strain.

Old trees in montane forest provide the favourite habitat in East Africa for this species. Our few records suggest a preference for partial shade on mossy tree trunks. The altitudes at which specimens have been collected range from 1800 to 3000 m.

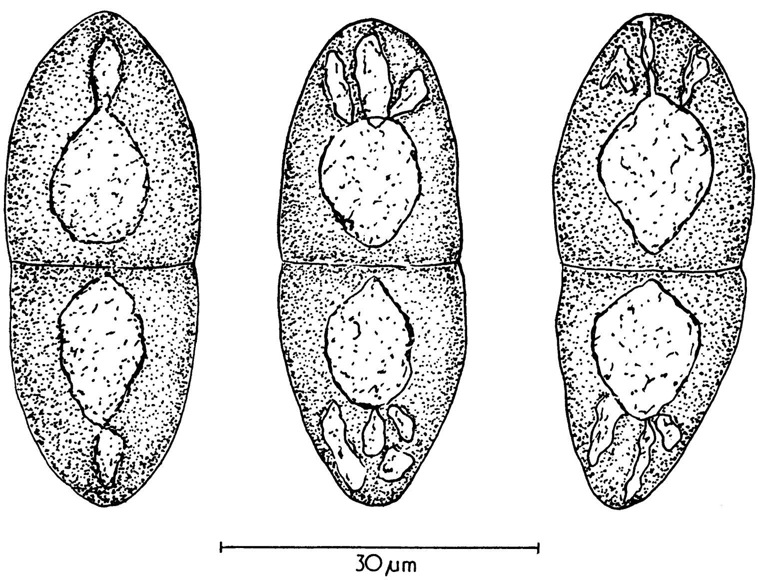

FIG. 3. *Heterodermia magellanica*, spores, with large sporoblastidia (K 48/151).

Specimens Examined

Ethiopia: Shewa Province, Addis Ababa, *Crees* 4/93 (BM); Wondo Gennet Agricultural and Handicraft School, E 5/59. Sidamo Province, 40 km N of Kibre Mengist, *Winnem* 531/3 (O); Hagere Selam, E 17/7, *Winnem* 584/3 (O). Arussi Province, E of Asella, E 30/32, 37, E 31/27, *Winnem* 750/7, 751/24 (O). **Kenya:** Central Province, Kirinyaga District, Mt Kenya, 2 km NW of Irangi Forest Station, K 48/151*; Nyandarua District, Aberdare Mountains, near Karuru-Gura waterfalls, 3K 32/136.* Eastern Province, Machakos District, Ol Doinyo Sapuk, 2K 3/115.*

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20. Heterodermia microphylla (Kurok.) ~~Swinsc. & Krog comb. nov.~~

Anaptychia hypoleuca (Ach.) Massal. var. *microphylla* Kurok., *J. Jap. Bot.* **34:** 123 (1959); type:—Japan, Honshu, Prov. Shinano, Sakakita-mura, Higashi-Chikumagun, on rocks, *Yamazaki*, 28 July 1953 (TNS—holotype !).—*Anaptychia microphylla* (Kurok.) Kurok., *Beih. Nova Hedwigia* **6:** 44 (1962).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex uneven; under side non-corticate, pale. Squamules marginal and laminal, dissected, sometimes becoming sorediate. Apothecia laminal, adnate to substipitate; margin of thalline exciple squamulose or squamulose-sorediate. Spores 25–35 (–37) × 12–18 μm, without sporoblastidia. TLC (holotype): Atranorin, zeorin.

As in *Heterodermia hypoleuca*, to which this species is allied, occasional spores contain sporoblastidia. Kurokawa (1962) reports that this species occasionally produces norstictic and salazinic acids. None of our specimens contains depsidones. See under *H. appendiculata* for differentiation from that species.

In East Africa this species prefers the trunks of trees in sheltered but open woodland. It has also been collected from old wayside trees, which may be the remains of natural forest, and once on rocks (2K 29/105).

Specimens Examined

Ethiopia: Sidamo Province, Dilla, *Winnem* 471/2 (O); Yirga Alem, *Winnem* 477/14 (O); Wondo Gennet, *Winnem* 494/9 (O). **Kenya:** Rift Valley Province, Elgeyo Marakwet District, Sogotio Forest 8 km N of Chebiemit, 2K 10/115; Nakuru District, River Karati near Enashe Ngai, 3K 19/104. Central Province, Nyeri District, Mt Kenya, bridge where Naro Moru track crosses Naro Moru River, K 32/37; Kirinyaga District, Mt Kenya, by Thiba Fishing Camp, K 52/18. Eastern Province, Meru District, Mt Kenya E side, 3K 15/23; Machakos District, Ol Doinyo Sapuk, 2K 3/110; Mutondoni, 3K 3/10, 119. Coast Province, Taita District, Taita Hills E of Mwanda summit, 2K 29/105, 2K 30/105.

21. Heterodermia obscurata (Nyl.) Trevis.

Nuovo G. bot. ital. **1:** 114 (1869).—*Physcia obscurata* Nyl., *Annls Sci. nat., Bot., ser.* 4, **19:** 310 (1863); type:—Colombia, *Lindig* 704 (not seen).—*Anaptychia obscurata* (Nyl.) Vain., *Acta Soc. Fauna Flora fenn.* **7:** 137 (1890).

Anaptychia adamesii Dodge, *Ann. Mo. bot. Gdn* **40:** 400 (1953); type:—Sierra Leone, *Adames & Deighton* M4752 (could not be traced in BM).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex uneven; under side non-corticate, with ochraceous orange hyphae overlying medulla, K+ purple. Soralia labriform on recurved apices of lobes. Apothecia laminal, adnate to substipitate; Margin of thalline exciple crenulate to sorediate. Spores 25–35 × 15–18 μm, with sporoblastidia. TLC: Atranorin, zeorin, pigments.

Of the 24 specimens cited below two are fertile, both from Uganda (U 22/1 and *Lye* L 698). A count of 50 spores in each gave a mean length of 29·0 μm (S.D. 2·4) in U 22/1 and 30·6 μm (S.D. 3·3) in *Lye* L 698.

* Norstictic acid strain.

Heterodermia dendritica var. *propagulifera* (Vain.) Poelt comes near this species according to Kurokawa (1962) and Culberson (1966), but is said to differ from it in producing norstictic and salazinic acids. However, both the holotype (!) in TUR and the isotype (!) in BM of *H. dendritica* var. *propagulifera* are devoid of pigment on the under side, and the holotype does not contain norstictic acid or salazinic acid (isotype not tested). These specimens appear to be indistinguishable from *H. japonica.*

In East Africa *Heterodermia obscurata* grows on sheltered mossy trees and rocks, usually in partial shade. Our records range in altitude from 1100 to 3000 m.

Specimens Examined

Ethiopia: Shewa Province, Wondo Gennet Agricultural and Handicraft School, E 5/57. Sidamo Province, 12 km S of Kibre Mengist, E 13/29; W of Dilla, E 19/25, *Winnem* 470/18 (O); Yirga Alem, Sidamo Provincial Hospital, E 20/35, *Winnem* 477/15 (O). Gemu Gofa Province, Gidole, E 26/34, *Winnem* 641/11 (O). Arussi Province, E of Asella, E 31 /25.**Kenya:** Eastern Province, Meru District, near Chogoria, 3K 7/10. **Tanzania:** Northern Province, Arusha District, Arusha National Park, by Seneto Pool, T 8/104; Moshi District, Marangu, *Burnet* AMB 121 (BM). **Uganda:** Karamoja District, Matheniko County, 5 km E of Moroto in Lya Valley, *Lye* L 249 (MAK). West Mengo District, Kyadondo County, Kampala, Makerere Hill, *Burnet* AMB 232 (BM); Busiro County, Entebbe Botanical Garden, U 10/2; 15 km SW of Kampala, 3U 8/12 (BM). Masaka District, Kyotera County, Katera, *Lye* L 698 (Hb. Lye); Mawogola County, near Sembabule, *Thompson* U 19 (MAK); Bukoto County, 1 km E of Buyaga, *Lye* L 542 (MAK). Ankole District, Igara County, Lubare Ridge, 2U 3/4, 8 (MAK), *Lye* L 400 (MAK). Kigezi District, Bufumbira County, near Gakeri, U 21/5; near Kirwa, SW of Lake Mutanda, U 22/1.

22. Heterodermia podocarpa (Bél.) Awas.

Geophytology **3:** 114 (1973).—*Parmelia podocarpa* Bél., *Voy. Ind. Orient. Bot.*, II, Crypt.: 122, Pl. e, Fig. 1 (1840); type:—Bourbon (not seen). *Anaptychia podocarpa* (Bél.) Massal., *Atti I. R. Ist. Veneto*, ser. 3, **5:** 249 (1860).

Anaptychia podocarpa (Bél.) Awas. var. *stellata* Vain., *Acta Soc. Fauna Flora fenn.* **7:** 131 (1890); type:—Brazil, Minas Geraës, Sitio, Vainio Lich. Brasil. exs. 1080 (BM—isotype !).—*Anaptychia stellata* (Vain.) Kurok., *Beih. Nova Hedwigia* **6:** 90 (1962).

Anaptychia podocarpa var. *conferta* Vain., *Suomal. Tiedeakat. Toim.*, ser. A, **6** (7): 61 (1914); type:—Guadalupa, ad corticem Callandrae petiolaris prope Bains-Jaunes, 900 m s.m., *Duss* 1163 (TUR, Hb. Vainio 07939—holotype !).

Lobes disjunct to imbricate, convex, ascending, with short or long lateral lobes; upper cortex uneven; under side non-corticate, white. Isidia and soralia absent. Apothecia apical or subapical, stipitate; margin of thalline exciple squamulose. Spores 40–51 × 18–25 μm (mean length of 50, 43·9 μm, S.D., 2·5) with sporoblastidia. TLC: Atranorin, zeorin; also chemical strains producing norstictic acid (holotype of *Anaptychia podocarpa* var. *conferta*) and norstictic and salazinic acids (East African specimens cited below).

Kurokawa (1962) considered that the red colour in the illustration of the type specimen of *Parmelia podocarpa* accompanying the type description by Bélanger (*loc. cit.*) indicated decomposed salazinic acid. He had not seen the actual specimen. *Anaptychia podocarpa* var. *stellata* is simply a depsidone-deficient strain of the species. It is the commoner of the two in East Africa.

This is mainly a species of twigs and small branches. It is nearly always to be found on the upper joints and branches of bamboo in montane forest, though it also grows on the twigs of lowland shrubs. Our records range in altitude from 450 to 3400 m.

Specimens Examined

Ethiopia: Shewa Province, Suba, *Tapper* 541a (BM). Sidamo Province, Hagere Selam Mission Station, *Winnem* 578/8, 10 (O). Gemu Gofa Province, Gidole, E 26/33. **Kenya:** Rift Valley Province, Elgeyo Marakwet District, Cherangani Hills 10 km S of Labot, 2K 8/22, 156; Uasin Gishu District, 5 km NW of Timboroa summit, 2K 19/3, 136; Kajiado District, Ngong Hills, near summit at S end, K 2/10, K 45/139. Central Province, Nyeri District, Mt Kenya W side, *c.* 3000 m, K 13/17, 20, 24b, 124, 2K 33/19; Aberdare Mountains E of Lesatima 3000–3400 m, K 26/117, K 35/107. Eastern Province, Machakos District, lava flow 5 km NW of Kibwezi, K 20/12b, 134, 2K 22/134, 3K 23/18. Coast Province, Kwale District, Shimba Hills, K 43/106. **Uganda:** Masaka District, Bukoto County, Jubiya Forest, 3U 28/15*, 3U 32/1*; N edge of Malabigambo Forest, 3U 25/6*.

23. Heterodermia pseudospeciosa (Kurok.) Culb.

Bryologist **69:** 484 (1966).—*Anaptychia pseudospeciosa* Kurok., *J. Jap. Bot.* **34:** 176 (1959); type:—Japan, Honshu, Prov. Idzu, Suishochi, Amagi Pass, 20 August 1956, *Asahina* (TNS—holotype !).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side corticate. Soralia apical on main and lateral lobes, labriform, producing granular soredia. Apothecia laminal, adnate to substipitate; margin of thalline exciple sorediate. Spores 25–35 × 12–18 μm, without sporoblastidia. TLC: Atranorin, zeorin, norstictic acid.

The holotype contains norstictic acid but not salazinic acid. This finding agrees with what Culberson (1966) reported for the plants in North and South Carolina, U.S.A., and with the chemistry of our African plants.

In East Africa *Heterodermia pseudospeciosa* seems to be a rare saxicolous species. The two localities where we have collected it were rocks near a river at 2100 m altitude on the east side of Mt Kenya and rocks in a river south of the mountain at 1400 m.

Specimens Examined

Kenya: Eastern Province, Embu District, River Thuchi S of Chuka, 3K 17/1, 107, 108 109; Meru District, Mt Kenya, E side, 3K 16/265.

24. Heterodermia speciosa (Wulf.) Trevis.

Atti. Soc. ital. Sci. nat. **11:** 614 ((1868) 1869).—*Lichen speciosus* Wulf. in Jacq., *Coll. Bot.* **3:** 119 (1789); type:—Carinthia (not seen).—*Anaptychia speciosa* (Wulf.) Massal., *Mem. Lich.*: 36 (1853).

Physcia hypoleuca Nyl. var. *tremulans* Müll. Arg., *Flora, Jena* **63:** 277 (1880); type:—Prope Petropoli Brasiliae supra muscos, *Deventer* 28 (G—holotype !).—*Anaptychia pseudospeciosa* Kurok. var. *tremulans* (Müll. Arg.) Kurok., *Beih. Nova Hedwigia* **6:** 26 (1962).—*Heterodermia tremulans* (Müll. Arg.) Culb., *Bryologist* **69:** 485 (1966).

Lobes slightly disjunct or adjacent, more or less plane, not ascending, with short lateral lobes; upper cortex even; under side corticate. Soralia apical on main and lateral lobes, labriform, producing farinose soredia. Apothecia laminal, adnate to

* Containing norstictic and salazinic acids.

substipitate; margin of thalline exciple sorediate. Spores (20–) 25–35 (–37) × 12–18 µm, without sporoblastidia. TLC: Atranorin, zeorin.

Kurokawa (1962) differentiated *Anaptychia pseudospeciosa* var. *tremulans* from *A. speciosa* by 'size of spores and the sorediate margin of the apothecia'. Fruiting specimens are rare, as would be expected of a sorediate species, but we have collected eight in East Africa, and examined a further one from this area and one from South Africa. We have also examined eight from Europe (counting different specimens under a single number in an exsiccata as one). Measurements of the spores of all these specimens, sometimes from more than one apothecium of each, are set out in Table 12, which gives mean lengths and standard deviations.

TABLE 12. *Length of spores in µm from specimens of* Heterodermia speciosa *outside Europe and within Europe*

Specimen	Number of spores	Mean length	Standard deviation
Outside Europe			
2U 7/4	50	26·4	2·0
3K 21/6	50	26·9	2·6
K 17/1	50	27·1	2·9
Winnem 158/4	50	27·4	2·4
Hoëg 31/7, 1929 (TRH)[1]	65	27·4	2·1
2K 31/1	50	27·9	2·1
U 22/2	50	28·1	2·4
3K 17/1	17	28·5	2·1
2U 17/20[2]	50	29·2	2·2
3K 3/120	50	31·7	2·4
2U 17/20[3]	50	32·1	2·6
Within Europe			
Vězda 795 (BM)[4]	50	30·1	2·5
Körber 56 (BM)[5]	50	30·2	3·1
Funck (BM)[6]	50	30·7	3·6
Algarve 35 (BM)[7]	50	30·9	2·4
Vězda 795 (LD)	50	31·1	2·2
Anzi Lang. 56 (O)[8]	50	31·1	2·8
Salzburg (O)[9]	50	31·2	2·8
Anzi Lang. 57 (BM)[10]	50	31·5	2·6
Arnold 1611 (BM)[11]	50	31·5	2·9
Anzi Lang. 56 (O)[12]	50	32·5	2·4
Arnold 1611 (O)[13]	40	33·5	3·1
Anzi Lang. 56 (O)[14]	50	33·7	2·8
Arnold 1611 (O)[15]	50	33·8	3·2
Total	1172	29·9	3·4

[1]From South Africa. [2]One apothecium. [3]A second apothecium. [4]From Yugoslavia. [5]From Germany. [6]From Germany. [7]From Portugal. [8]From Italy; one apothecium. [9]From Germany; collector unstated. [10]From Italy. [11]From Germany. [12]From Italy; a second apothecium. [13]From Germany; one apothecium. [14]From Italy; a third apothecium. [15]From Germany; a second apothecium.

These results show a total range of mean length of 7·4 µm, from 26·4 to 33·8 µm. If these spores are regarded as coming from a single population with normal distribution, whose mean is 29·9 μm and standard deviation 3·4 (Table 12), the range in which 95% would be expected to fall is 23·1 to 36·7 μm. The theoretical expectation is fulfilled in that 1122 spores (95·7%) lie within the range. Since a range of approximately 7 μm about a mean is perfectly acceptable in a single species of this genus (as of many other genera), the figures are compatible in that respect with the view taken here that all these plants belong to one species. And this receives further support from the examination of the spores of *Heterodermia diademata* discussed above in the general part of this paper under 'Morphology'. In that clearly identifiable species the range of spore lengths in seven specimens (Table 2) was considerably greater than in those reported here for *H. speciosa* (Table 12).

But our figures do confirm the observation (Kurokawa, 1962) that 'Spores of *A. speciosa* are usually longer than 30 μm' (by *A. speciosa* Kurokawa was referring to what we regard simply as European specimens of this species). Table 12 shows that the European specimens have spores that are slightly longer than all the African specimens except two. The explanation of this small disparity, we suggest, lies in the environment in which the plants were growing. The warm temperate climate of southern central Europe and its Atlantic coast, with warm summers and cold winters, is very different indeed from that of the tropics, even the cool tropical places at high altitudes. Differences in the rate and degree of ascocarp maturation could have their effects on the size of the spores.

As regards soredia on the apothecial margin, it would certainly be remarkable if a sorediate species failed to produce them, and in fact they do occur, though the apothecia must have attained a certain maturity before they appear. They are well developed, for instance, on Anzi Lang. 56 and Arnold Lich. exs. 1611 in O, from Italy and Germany respectively. But our studies do give some confirmation of Kurokawa's observation that soredia are characteristic of *Anaptychia pseudospeciosa* var. *tremulans* and not of *A. speciosa*, for they are commoner and generally more abundant on the African specimens (though *Winnem* 158/4 is an exception, having apothecia of the 'European' type with hardly any soredia on well developed exciples). Again the environment probably accounts for these differences by its effect on the rate at which apothecia mature or on the continuity of their growth.

Though Kurokawa (1962) mentions that the laciniae are linear-elongate in *Anaptychia speciosa* but short and flexuose in *A. pseudospeciosa* var. *tremulans*, our African specimens show no difference in this respect from the European.

Culberson (1966) differentiated *Heterodermia tremulans* (i.e., *H. speciosa* in this paper) from *H. pseudospeciosa* in the Carolinas by several characters. In particular, his *H. tremulans* had fine, very abundant soredia; large soralia; white or pale rhizines (dark in *H. pseudospeciosa*); a corticolous as opposed to saxicolous mode of growth; and a different geographical distribution. The difference in the soredia is to be seen in the type specimens of *H. pseudospeciosa* and *H. tremulans*, and also in the African material, though it is not very clear-cut. On the other hand neither those type specimens nor the African material show the differences he found in the soralia and rhizines in the Carolina plants. But the rock habitat of the Carolinas *H. pseudospeciosa* is confirmed in East Africa—where admittedly we have only two collections. Both were on rock. So also was the holotype. However, *H. speciosa* does also occur on rock, though it is much more often corticolous. Finally there is the chemical difference in that *H. speciosa* does not produce depsidones whereas *H. pseudospeciosa* produces norstictic acid.

In East Africa *Heterodermia speciosa* is common throughout the area on sheltered tree trunks in natural and artificial habitats; it occasionally grows on rock. Our records range in altitude from 1100 to 3600 m, and are too numerous to list individually.

25. Heterodermia usambarensis (Kurok.) Swinsc. & Krog comb. nov.

Anaptychia usambarensis Kurok., *Beih. Nova Hedwigia* **6:** 82 (1962); type:—D.O. Afr. [Tanzania], Usambara, *Holst* 2646 pr. p. (G—holotype !).

Lobes disjunct, dichotomously branched, branches remaining apical; upper cortex uneven, forming vein-like ridges below; under side non-corticate, with tufts of brownish red hyphae, K−, overlying the medulla. Isidia and soralia absent. Apothecia subapical or apical, stipitate; margin of thalline exciple squamulose, with squamules pigmented on inner side. Spores 40–50 × 20–25 μm, with sporoblastidia. TLC (holotype): Atranorin, zeorin, UV+ substance, pigments. (The UV+ substance does not cause fluorescence of the thallus in UV light.)

In Africa this species is known so far only from the type locality. In the type specimen the pigmented hyphae are restricted to small scattered tufts.

26. Heterodermia vulgaris (Vain.) Follm. & Redón

Willdenowia **6:** 447 (1972).—*Anaptychia leucomelaena* (L.) Massal. var. *vulgaris* Vain., *Acta Soc. Fauna Flora fenn.* **7:** 128 (1890); type:—Brazil, Minas Geraës, *Lafayette*, Vainio Lich. Bras. exs. 227 (BM—isotype !).—*Anaptychia vulgaris* (Vain.) Kurok., *Beih. Nova Hedwigia* **6:** 81 (1962).

Lobes disjunct, dichotomously branched, branches remaining apical; upper cortex uneven; under side non-corticate, with layer of crimson red hyphae, K+ purple, overlying medulla. Soralia often present subapically on under side of lobes. Apothecia subapical or apical, stipitate; margin of thalline exciple squamulose, with red hyphae, K+ purple, on inner side. Spores 40–50 × 18–25 μm, with sporoblastidia. TLC (isotype): Atranorin, zeorin, pigments.

This species grows on tree trunks and branches and on rocks in earth banks, tolerating artificial habitats such as a garden (*Burnet* AMB 222) and a neglected coffee plantation (3U 8/13). Generally it prefers shade and humidity. Our records range in altitude from 1100 to 2200 m.

Specimens Examined

Ethiopia: Sidamo Province, 12 km S of Kibre Mengist, E 13/30, *Winnem* 504/6 (O); near small river W of Dilla, E 19/26, *Winnem* 470/19 (O); Yirga Alem, *Winnem* 477/11 (O). **Kenya:** Central Province, Nyeri District, Mt Kenya, where Naro Moru track crosses Naro Moru River, K 32/6, 123. **Uganda:** West Mengo District, Busiro County, 15 km SW of Kampala, 3U 8/13. Kigezi District, Ndorwa County, Kabale, *Burnet* AMB 222 (BM); Kinkizi County, Chelima Forest Reserve, *Burnet* AMB 231; Bufumbira County, near Gakeri, U 21/4. **Tanzania:** Northern Province, Moshi District, Marangu, *Burnet* AMB 139c (BM).

Summary

One species of *Anaptychia* and 25 species of *Heterodermia* are recorded (including one doubtfully) for East Africa. The *Anaptychia* species is newly described as *A.*

ethiopica Swinsc. & Krog. The 25 species of *Heterodermia* include one newly described as *H. lepidota* Swinsc. & Krog.

Anaptychia domingensis (Ach.) Massal. and *A. ravenelii* (Tuck.) Zahlbr. are reduced to synonymy with *Heterodermia albicans* (Pers.) Swinsc. & Krog; *A. albopruinosa* Kurok. to synonymy with *H. diademata* (Tayl.) Awas.; *A. stellata* (Vain.) Kurok. to synonymy with *H. podocarpa* (Bél.) Awas.; and *H. tremulans* (Müll. Arg.) Culb. to synonymy with *H. speciosa* (Wulf.) Trevis. *Anaptychia boryi* (Fée) Massal. is changed in status to *Heterodermia leucomela* ssp. *boryi* (Fée) Swinsc. & Krog.

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