

ACTA PHYTOGEOGRAPHICA SUECICA

EDIDIT

SVENSKA VÄXTGEOGRAFISKA SÄLLSKAPET

III: 1

LIFE-FORMS OF TERRESTRIAL
FLOWERING PLANTS

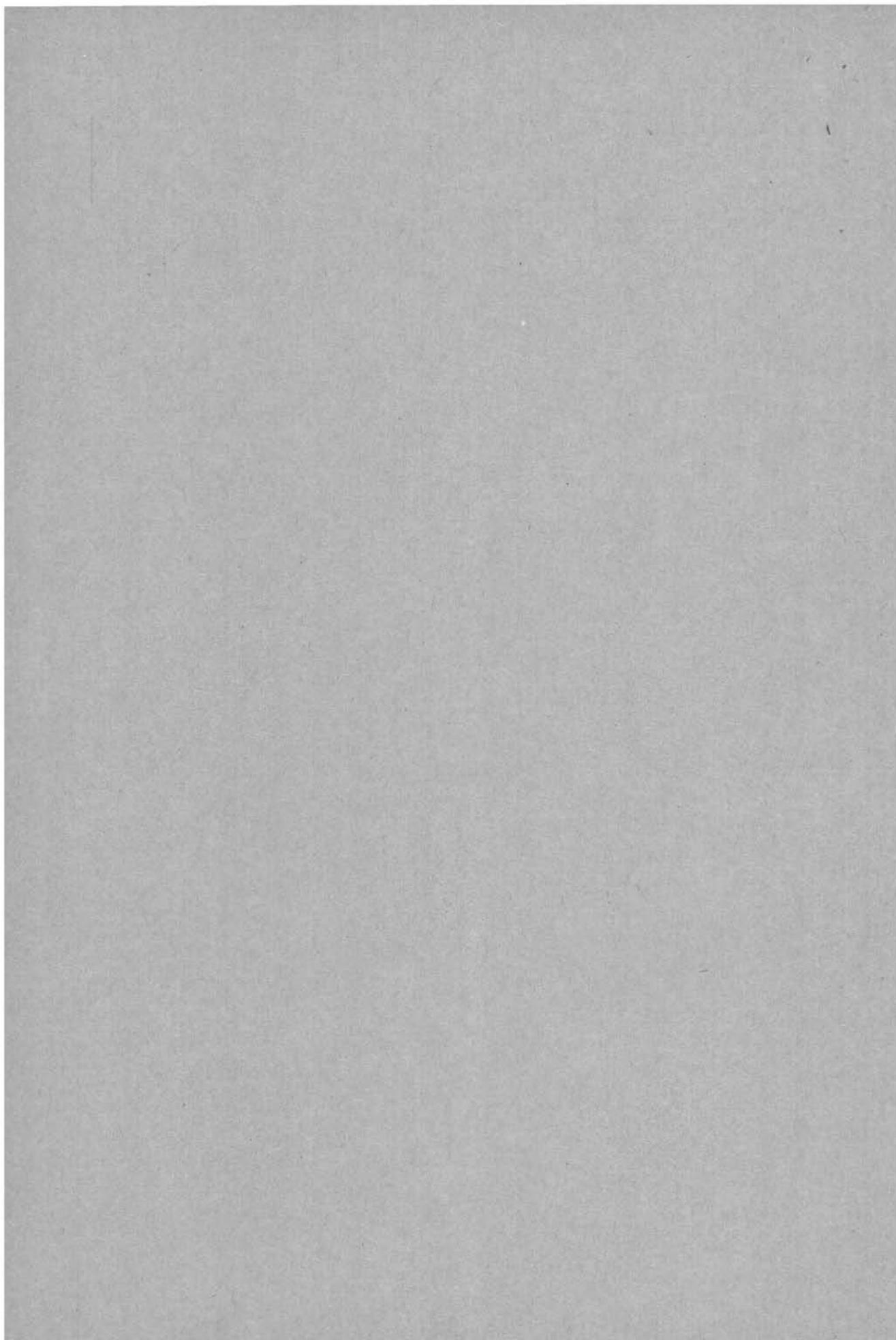
I

BY

G. EINAR DU RIETZ

UPPSALA 1931

ALMQVIST & WIKESELLS BOKTRYCKERI AB



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LIFE-FORMS OF TERRESTRIAL FLOWERING PLANTS

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UPPSALA 1931

ALMQVIST & WIKSELLS BOKTRYCKERI-A. B.

$$n\in \mathbb{N}$$

$$\left(1+\frac{1}{2}\right)^2\approx 1.25$$

$$(\mathcal{X},\mathcal{Y})\in\mathbb{R}^{d_X\times d_Y}$$

$$\mathcal{L}_\text{reg} = \mathcal{L}_\text{reg}^{\text{train}} + \mathcal{L}_\text{reg}^{\text{val}}$$

$$x_1\in \mathbb{R}^d$$

$$\mathcal{A}=\mathcal{A}_1\cup\cdots\cup\mathcal{A}_m$$

$$\mathcal{L}_{\text{reg}} = \mathcal{L}_{\text{reg}}^{\text{train}} + \mathcal{L}_{\text{reg}}^{\text{val}}$$

$$k\in \mathbb{N}$$

$$\mathcal{A}=\mathcal{A}_1\cup\cdots\cup\mathcal{A}_m$$

$$\mathcal{L}_{\text{reg}} = \mathcal{L}_{\text{reg}}^{\text{train}} + \mathcal{L}_{\text{reg}}^{\text{val}}$$

$$\mathcal{E}_1=\left\{ \begin{pmatrix} 1&0\\0&1 \end{pmatrix},\begin{pmatrix} 0&1\\1&0 \end{pmatrix}\right\}$$

$$\mathcal{C}[\cdot]$$

$$\mathcal{A}=\mathcal{A}_1\cup\cdots\cup\mathcal{A}_m$$

$$\mathcal{L}_{\text{reg}} = \mathcal{L}_{\text{reg}}^{\text{train}} + \mathcal{L}_{\text{reg}}^{\text{val}}$$

$$k\in \mathbb{N}$$

$$\mathcal{A}=\mathcal{A}_1\cup\cdots\cup\mathcal{A}_m$$

$$\mathcal{L}_{\text{reg}} = \mathcal{L}_{\text{reg}}^{\text{train}} + \mathcal{L}_{\text{reg}}^{\text{val}}$$

Preface.

This work is the result of studies carried out during the last twelve years. The field-studies have been made partly in various parts of Scandinavia (Sweden and Norway), partly during a year's work in New Zealand and Australia in 1926—1927 as well as during shorter visits to various parts of Central and Western Europe, North America, and Java. The material collected in the field has been worked up in the Plant-Biological Institution of Upsala University. The rich life-form collections of this institution have also been utilized as much as possible. I wish to express my deep gratitude to all those friends in various countries who have supported my work in one way or another — they are too many to be enumerated here.

I have tried to bring the names of the plants mentioned as much as possible into accordance with the following generally known floristic handbooks: For Scandinavia HOLMBERG 1922—1926, and, for the groups not treated there, LINDMAN 1926, for Central Europe HEGI 1908—1931, for the eastern part of North America ROBINSON and FERNALD 1908, for Java KOORDERS 1911—1912, for New South Wales MOORE and BETCHE 1893, for the rest of Australia BENTHAM 1863—1878, and for New Zealand CHEESEMAN 1925. Authors' names have been added to the plant-names only when I have not followed the nomenclature of these handbooks, and when plants from other parts of the world have been occasionally mentioned (except in the case of some generally known species).

The scope of this work has been restricted to terrestrial flowering plants, because the life-forms of the cryptogamic classes and of aquatic flowering plants are so different that they are more conveniently dealt with separately.

Plant-Biological Institution of Upsala University, June 1931.

CHAPTER I.

Life-form Theories and Life-form Systems in Botanical Literature.

1. The Early Period of Purely Physiognomic Life-form Systems (ca. 300 B.C. — 1884).

That the plant-species may be classified not only according to their taxonomical relationship into genera, families etc., but also according to their physiognomic similarity into physiognomic types, has been clear to botanists ever since the childhood of botanical science. An elaborate system of such physiognomic types had been worked out as early as by THÉOPHRASTOS (ca. 300 B.C.) (comp. GAMS 1918 pp. 312—314), and the general physiognomic types known as trees, shrubs, herbs, etc., of course were generally used by the very early botanists. It was, however, ALEXANDER VON HUMBOLDT (1806, comp. WARMING 1908 a pp. 1—3, DU RIETZ 1921 pp. 13, 37—39), who first drew the attention of the botanists to the fact that it could be worth while to work out a system of such purely physiognomic types more purposely, and to the great value of such physiognomic types for the characterization of the vegetation of different regions. In his first fundamental paper on the subject, »Ideen zu einer Physiognomik der Gewächse» (1806), HUMBOLDT described and named 16 »Hauptformen», the number of which was increased to 19 two years afterwards (1808). These 19 »Hauptformen» were named mostly after some characteristic genus or family: »die Palmen, die Bananen-form, die Malvenform, die Form der Mimosen, die Heidekräuter, die Cactusform, die Orchideen, die Form der Casuarinen, die Nadelhölzer, die Pothosgewächse (Arumform), die Lianen, die Aloegewächse, die Grasform, die Farenkräuter, die Liliengewächse, die Weidenform, die Myrtengewächse, die Melastomen- und die Lorbeerform»¹ (comp. DU RIETZ 1921 p. 39). For HUMBOLDT these »Hauptformen» were mainly tools for the description of vegetation physiognomy, and it never occurred to him that there could be anything wrong in letting a family or a larger taxonomical unit form its own »Hauptform» if it was really characterized by a definite physiognomy. The »Hauptformen»-system

¹ In the following treatise all quotations in German and French are presented in the original language, while such in less known languages are translated into English.

was a purely physiognomic one, and no traces of the idea of sorting out »biological» characters from the »morphological» ones are found in the works of HUMBOLDT. The »Hauptformen» according to HUMBOLDT should be based »nicht (wie in den botanischen Systemen aus anderen Beweggründen geschieht) auf die kleinsten Theile der Blüthen und Früchte», but only upon »das, was durch Masse den Totaleindruck einer Gegend individualisiert».

The »Hauptformen» of HUMBOLDT became widely accepted and used especially by botanical travellers during the first half of the last century, often with some minor alterations and complications. Several authors, e.g. S. MEYER (1834), F. J. F. MEYEN (1836) and H. ZOLLINGER (1855) attempted to work out the system somewhat more in detail (comp. DU RIETZ 1921 pp. 41 and 44), but nothing theoretically new was added for more than half a century.

A quite different system of physiognomic plant-types, founded on a more morphological basis, was introduced by A. P. DE CANDOLLE in his »Regni vegetabilis sistema naturale» (1818, comp. also 1827 pp. 232—233). It was based upon the duration of life and the height of the ligneous stem, and contained the following types, marked by certain signs in the taxonomic descriptions (p. 12):

- »1. *Planta monocarpica*, nempe unica vice fructificans, sed cuius duratio est ignota, incerta aut varia.
- 2. *Planta monocarpica annua*, nempe unica vice fructificans, et per annum ad summum vitan totam degens.
- 3. *Planta monocarpica biennis*, nempe unica vice secundo tantum anno fructificans.
- 4. *Planta monocarpica perennis*, nempe per plurimos annos ante florescentiam crescents et post eam moriens.
- 5. *Planta rhizocarpica*, nempe cuius caulis unica vice fructum fert, deinde moritur, et annis sequentibus alii caules fructiferi e radice perenni exsurgunt.
- 6. *Planta caulocarpica*, nempe cuius caules persistunt et plures fructum edunt, sed cuius magnitudo est ignota aut incerta.
- 7. *Planta caulocarpica suffrutex*, nempe fruticosa^{*} et cuius altitudo ad summum pedalis bipedalis.
- 8. *Planta caulocarpica frutex*, nempe fruticosa et cuius altitudo variat, ad 2 ad 10 pedes, et cuius anni ab ipsa trunci basi oriuntur.
- 9. *Planta caulocarpica arbuscula*, nempe fruticosa et cuius altitudo est inter 10 et 25 pedis, et cuius truncus basi denudatur.
- 10. *Planta caulocarpica arbor*, nempe fruticosa et cuius altitudo 25 pedes superat.»

Later on, DE CANDOLLE (1832) introduced the term »polycarpic» plants for the main group formed by his rhizocarpic and caulocarpic plants together.

In his classical work »Das Pflanzenleben der Donauländer» (1863) ANTON KERNER took up the problem of the physiognomic plant-types to a critical revision. His aim was the same as that of HUMBOLDT, namely to establish a system of physiognomic types suitable for the description of vegetation, and the »Grundformen» established by him were theoretically absolutely analogous to the Hauptformen» of HUMBOLDT: »Wenn wir uns die Aufgabe stellen, eine Pflanzenformation zu schildern und zu benennen, so werden wir dabei jedenfalls am zweckmässigsten vorgehen, wenn wir das Einzelne als Ausgangspunkt wählen und uns um die Bausteine umsehen, aus denen sich das ganze grüne Gebäude einer Pflanzenformation aufbaut. Wir werden da vor Allem auf gewisse Grundformen

des Pflanzenreiches hingewiesen, welche gleich beim ersten Anblick eines Landschaftsbildes in die Augen springen, und die ihren eigentümlichen Ausdruck häufig auch auf die ganze Pflanzenformation übertragen. — Diese werden von uns zunächst festgestellt und bezeichnet werden müssen, und wenn wir uns hiebei nicht zu sehr ins Kleinliche verlieren und überdies nur die heimische Pflanzenwelt berücksichtigen, so ergeben sich als derlei Grundformen etwa folgende.» (KERNER 1863 pp. 8—9.) Contrary to HUMBOLDT, however, KERNER found it inconvenient to name these physiognomic types after taxonomical units (comp. KERNER 1863 p. 281), and attempted to choose such names that gave a general idea of the physiognomy without referring to any special family or genus. 12 »Grundformen» were distinguished by KERNER, namely »Bäume, Sträucher, Stauden, Filzpflanzen, Kräuter, Blattpflanzen, Schlinggewächse, Fadenpflanzen, Rohre, Halmgewächse, Schwämme, und Krustenpflanzen» (l. c. p. 9). A rather similar system of simple physiognomic types had been used by HAMPUS VON POST as early as 1851 (comp. DU RIETZ 1921 p. 47), but since this was published in Swedish language, it was certainly not known to KERNER.

A most elaborate system of »Vegetationsformen», constituting an outgrowth of the system of HUMBOLDT and worked out in the same technical style, was published in 1872 in AUGUST GRISEBACH's monumental work »Die Vegetation der Erde»¹. The number of physiognomic types was increased to 54, and a few years later (GRISEBACH 1875) even to 60; they were grouped into 7 main groups: »Holzgewächse, Succulente Gewächse, Schlinggewächse, Epiphyten, Kräuter, Gräser, und Zellenpflanzen».

As an example of the details in this system it may be mentioned that the »Holzgewächse» contained 30 »Vegetationsformen», grouped into 7 intermediate groups, and that one of these, the »Sträucher», consisted of the following »Vegetationsformen»: »Erikenform», »Myrtenform», »Oleanderform», »Proteaceenform», »Sodadaform», »Rhamnusform», and »Dornsträucher». The »Kräuter» were divided into three subordinate groups, »Stengel belaubt», »Stengel nackt», and »Laubrosette ohne Stengel»; the first group contained the »Vegetationsformen» »Stauden und Halbsträucher», »Gnaphaliumform» and »Immortellenform», the second group »Zwiebelgewächse», »Scitamineenform», »Aroideenform» and »Bromlienform», the third group only the »Farnkräuter».

That some of these »Vegetationsformen» coincided with taxonomic groups, was explicitly pointed out by GRISEBACH, and it never occurred to him that the value of a »Vegetationsform» could be affected by such a coincidence.

A system of the same type, entering still more into details but referring only to the subarctic vegetation of Northern Finland, was published in 1881 in the classical work of Swedish plant-sociology, RAGNAR HULT's »Försök till analytisk behandling av växtformationerna». HULT described 43 »vegetation-forms» (swed. vegetationsformer), e.g. »the *Pinus*-form», »the *Abies*-form», »the *Betula*-form», »the *Salix*-form», »the *Erica*-form», »the *Ledum*-form», »the *Oxycoccus*-form», etc. They were grouped into 10 »ground-forms» (Swed. »grundformer»), which were practically the same that had been used for some years in Finland

¹ A second edition was edited in 1884, after GRISEBACH's death.

by J. P. NORRLIN (1870, 1871, etc.; comp. also H. VON POST 1851 and KERNER 1863): coniferous trees, deciduous trees, shrubs, dwarf-shrubs, grasses, herbs, lianes, peat-mosses, other mosses, and lichens. Upon the combinations of those vegetation-forms the »formations« of HULT were founded, and the vegetation-forms were for HULT — just as for HUMBOLDT and other earlier authors — simply the primary units necessary for the description of those physiognomically characterized units of vegetation (= isocoenoses according to the modern terminology of GAMS 1918 and DU RIETZ 1930 a).

2. The Period of the Early Epharmonic Life-form Systems (1884—1905).

The systems mentioned above were all (except that of DE CANDOLLE) built up upon a purely physiognomic basis; the possible importance of the various physiognomic characters for the life of the plant was not taken up to discussion, and the physiognomic types distinguished were meant simply to be the primary units necessary for the description of the physiognomy of a plant-community and of the vegetation of a certain region.

A rather different type of systems developed from the penetration of botanical science with the evolutionistic theories of DARWIN (1859) and his followers. The physiognomy of plants was now more and more looked upon as a direct or indirect product of the environment, and gradually there developed a tendency to a valuation of physiognomic characters according to their supposed importance in the process of natural selection — or for the antiselectionists according to their supposed direct causal relation to the environment. It was probably only due to the personal influence of the strongly antievolutionistic old GRISEBACH, that purely physiognomic systems of »vegetation-forms« remained predominating more than two decades after the publication of »The Origin of Species«. But as early as in 1869 KERNER had published a paper on »Die Abhängigkeit der Pflanzengestalt von Klima und Boden«, and it is significant that when EUGENIUS WARMING published his first contribution to the life-form problem in 1884 (1884 a in Danish, German summary in 1884 b), he considered it rather axiomatic that his system should be founded primarily upon the characters which had the greatest »biological importance«.

This first attempt by WARMING to arrange the higher plants into biological groups was strongly influenced by the morphological school of ALEXANDER BRAUN and TH. IRMISCH (comp. WARMING 1908 a p. 13). It had no connection whatever with the purely physiognomical plant-systems of HUMBOLDT, GRISEBACH etc., and far more formed an outgrowth of the system initiated by DE CANDOLLE in 1818. The plants were classified primarily according to the duration of life, secondarily according to the power of vegetative propagation, thirdly according to the duration of the various shoots, and further according to the hypogeous or epigeous character of the shoots, the evergreen or deciduous habit, etc. The result was the following system (reprinted from WARMING 1884 b):

»I. Hauptgruppe. *Hapaxanthische Pflanzen* (»monokarpische« nach DE CANDOLLE).

- A. Monocyklische (einjährige, annuelle); Sprossbau »monocyklisch«. Gruppe 1.
- B. Dicyklische (zweijährige, biennie); Sprossbau »dicyklisch«. Gruppe 2.
- C. Pleio-polyeyklische (mehrjährige, aber nur einmal fruchtende); Sprossbau »tricyklisch«. Gruppe 3.

II. Hauptgruppe. *Perenne Pflanzen* (»polykarpische« nach DE CANDOLLE).

- A. Arten mit keinem oder äusserst geringem Wanderungsvermögen.

1. Primwurzel durch das ganze Leben der Pflanze bleibend, oder eine bleibende Stamm-Knollenbildung. Einziges Vermehrungsmittel sind die Samen.

- a. Verholzte, lange lebende Sprosse.
Gewöhnliche dikotyle Bäume und Sträucher. Gruppe 4.
- b. Krautartige Pflanzen.
 - * »Vielköpfige Wurzel.« Gruppe 5.
 - α . Begrenzte Sprosse mit monocyklischer Bildung (z. B. *Helianthemum vulgare*, *Lotus corniculatus*, *Agrimonia*-Arten).
 - β . Begrenzte Sprosse mit dicyklischem Bau (z. B. *Hypochoeris maculata*, *Taraxacum officinale*, *Chelidonium majus*, *Armeria vulgaris*).
 - γ . Unbegrenzte Primsprosse und spätere Hauptsprosse, begrenzte laterale Sprosse (z. B. *Plantago media*, *Trifolium pratense*, *T. montanum*).
 - ** Perennirende Knollenbildungen. Gruppe 6.
 - α . Knollenförmige Primwurzel.
 - $\alpha\alpha$. Begrenzte Sprosse (z. B. *Bryonia*, *Phyteuma spicatum*).
 - $\beta\beta$. Unbegrenzte Hauptsprosse (z. B. *Rhodiola rosea*).
 - β . Knollenförmige hypokotyle Stammglieder.
 - $\alpha\alpha$. Begrenzte Sprosse (z. B. *Eranthis hiemalis*, *Umbilicus pendulinus*).
 - $\beta\beta$. Unbegrenzte Sprosse (z. B. *Corydalis cava*).
 - γ . Knollenförmige epikotyle Stamnitheile (z. B. *Tamus*).

2. Die Primwurzel schnell d. h. nach etwa 1—2—3 Jahren absterbend. Von hinten stetig fortschreitende Auflösung des Primsprosses und des folgenden Hauptsprosses. Vermehrung auf vegetativem Wege ist möglich.

- a. Senkrechte oder etwas schräg liegende unterirdische Sprossverbände (Rhizome), dadurch entstanden, dass die unteren Theile der Sprosse (im entwickelten Zustande) mehr als ein Jahr leben. Gruppe 7.

aa. Gewöhnliche Sprossformen.

- α . Kryptogamen (z. B. *Aspidium Filix Mas*).
- β . Phanerogamen mit begrenzten, monocyklisch gebauten Sprossen (z. B. *Cynanchum Vineetoxicum*, *Hieracium umbellatum*, *Sedum Telephium*).
- γ . Phanerogamen mit begrenzten, dicyklisch gebauten Sprossen (z. B. *Leontodon autumnale*, *Spiraea Filipendula*, *S. Ulmaria*, *Cardamine pratensis*, *Primula elatior*).
- δ . Phanerogamen mit unbegrenzten Hauptsprossen und begrenzten floralen Seiten-sprossen (z. B. *Succisa pratensis*, *Geum rivale*, *Hepatica triloba*, *Gentiana Pneumanthe*).

bb. Knollenförmige Sprosse.

[Unterabtheilungen z. Th. wie unter aa.]

cc. Zwiebelförmige Sprosse.

[Unterabtheilungen z. Th. wie unter aa.]

- b. Bleibende Sprossverbände kommen nicht zu Stande, weil jeder Spross monocyklisch ist, also nur ein Jahr lebt, dann aber völlig abstirbt. Gruppe 8.

aa. Die Verjüngungssprosse überwintern als kleine bewurzelte, kurzgliedrige Laubtriebe (z. B. *Samolus Valerandi*).

bb. Die Verjüngungssprosse überwintern als geschlossene Knospen mit einer Nährwurzel versehen (z. B. *Orchis*). [Übergangsform zwischen aa—bb: *Anthriseus silvestris*.]

B. Arten mit einem grösseren, oft bedeutenden Wanderungsvermögen.

1. Oberirdische Wanderer.

a. Mit lange dauernder Primwurzel; wenige Arten (z. B. *Calluna vulgaris*, *Aretostaphylos Uva Ursi*, *Empetrum nigrum*) mit verholzten Sprossen

Gruppe 9.

b. Mit schnell absterbender Primwurzel.

Gruppe 10.

aa. Kryptogamen (z. B. *Polypodium vulgare*).

bb. Phanerogamen.

α. Keine eigentliche Ausläuferbildung; begrenzte Sprosse.

* Monocyklich gebaute Sprosse (z. B. *Asárum europaeum*).

** Sprosse monocyklich oder schwach dieyklich gebaut, aber von 2 bis mehrjähriger Dauer (z. B. *Comarum palustre*, *Menyanthes*, *Iris-Arten*, *Sedum-Arten*).

*** Sprosse dieyklich gebaut; 2- bis mehrjährige Sprossdauer (z. B. *Antennaria dioica*, *Hieracium Pilosella*).

β. Ausläufer neben aufrechten, kurzgliedrigen Sprossen oder Sprosstheilen.

* Begrenzte Sprosse (z. B. *Saxifraga flagellaris*, *Ranunculus repens*, *Rubus saxatilis*, *Fragaria*).

** Unbegrenzte aufrechte, kurzgliedrige Hauptsprosse, Ausläufer von der Blütenbildung begrenzt (z. B. *Potentilla-Arten*).

γ. Unbegrenzte, kriechende Triebe, begrenzte, aufrechte, fruchtende (z. B. *Lycopodium-Arten*, *Linnaea borealis*, *Veronica officinalis*).

2. Unterirdische Wanderer. Primwurzel gewöhnlich schnell absterbend.

a. Wanderung durch horizontal wachsende Sprosse, welche Sprossverbände (Grundachsen) bilden

Gruppe 11.

aa. Alle Achsen unterirdisch, laubblatttragend (z. B. *Pteris aquilina*).

bb. Sprosse mit wandernden, unterirdischen Theilen und senkrechten oberirdischen; alle typisch begrenzt.

α. Das oberirdische Leben einjährig (monocyklicher Bau).

αα. Verzweigung der unterirdischen Sprosstheile stark und unregelmässig (z. B. *Equisetum*, *Phragmites communis* und andere Gramineen, *Lathyrus pratensis*, *Asperula odorata*, *Stachys sylvatica*, *Urtica dioica*).

ββ. Verzweigung der unterirdischen Sprosstheile sparsam, aber äusserst regelmässig durch »Kraftknospen« aus bestimmten Blattachsel-Sympodien.

* Zahl der unterirdisch alljährlich gebildeten Sprossgenerationen nur 1 (z. B. *Polygonatum*, *Anemone nemorosa*, *Epipactis*).

** Zahl der unterirdisch entstehenden Sprossgenerationen mehr als eine, bis viele in jedem Jahre.

Grundstücke eingliedrig (z. B. *Hippuris vulgaris*).

» zweigliedrig (z. B. *Potamogeton*, *Juncus-Arten*).

» mehr- bis vielgliedrig (z. B. *Scirpus-Arten*).

β. Das oberirdische Leben 2- bis mehrjährig.

αα. Dickeyklicher Bau, krautartige Sprosse; die unterirdische Verzweigung unregelmässig (z. B. *Tussilago Farfara*, *Achillea millefolium*, *Aegopodium Podagraria*, *Sium angustifolium*). [Übergangsform zu ββ: *Pyrola rotundifolia*.]

ββ. Das oberirdische Leben 2- bis mehrjährig, verholzte Zweige (z. B. *Myrtillus nigra*, *Vaccinium Vitis idaea*).

cc. Unbegrenzte, unter der Erde wandernde Sprosse; begrenzte senkrechte (z. B. *Adoxa*, *Oxalis*, *Paris*).

b. Wanderung durch horizontal wachsende, unterirdische Sprosse, die aber so schnell sterben, dass nur Sprossverbände von nur ganz kurzer Dauer gebildet werden können [parallel der 8. Gruppe]. Die oberirdischen Sprosstheile von monocyklichem Bau und Dauer.

Gruppe 12.

* Nach dem Tode der Mutterpflanze überwintern die ganzen neuen unterirdischen Sprosse und sterben erst im nächsten Jahre gleichzeitig mit dem Auswachsen zum oberirdischen Sprosstheile ab (z. B. *Oxalis stricta*, *Mentha-Arten*, *Lycopus europaeus*).

- ** Nur der speciell als Achsenorgan ausgebildete Endtheil der unterirdischen Sprosse überwintert und bildet im nächsten Frühlinge neue Sprosse unter gleichzeitigem Absterben (z. B. *Solanum tuberosum*, *Ciræa alpina*, *Trifolium europaea*, *Stachys palustris*, *Epilobium palustre*).
- e. Wurzelwanderer, d. h. Pflanzen, welche durch Sprossbildende Wurzeln überwintern, wandern und sich vermehren. Gruppe 13
 - * Einzige vegetative Vermehrung durch Wurzelbrut; keine Sprossverzweigung (z. B. *Pyrola uniflora*).
 - ** Hauptsächliche Vermehrung durch Wurzelsprosse; sparsame oder jedenfalls für die Wanderung unwesentliche Sprossverzweigung (z. B. *Linaria vulgaris*, *Epilobium angustifolium*, *Convolvulus arvensis*, *Rumex acetosella*).
- 3. Schwimmende Wasserpflanzen. Gruppe 14.
 - a. Rosetteform (z. B. *Stratiotes*, *Hydrocharis*, *Pistia*, *Lemna*).
 - b. Horizontal liegende, gestreckt gliedrige.
 - aa. ohne besondere Winterknospen (z. B. *Hottonia*, *Ceratophyllum*).
 - bb. mit solchen (z. B. *Myriophyllum*, *Utricularia*).*

One year after the paper of WARMING and apparently independently of it there appeared a book by HANNS REITER (1885), »Die Consolidation der Physiognomik», containing the first attempt to a revision of the old physiognomic system of HUMBOLDT and GRISEBACH in the light of the new evolutionistic theories. In the previous year CARL VON NÄGELI (1884) had published his »Mechanisch-physiologische Theorie der Abstammungslehre», introducing the distinction between »Organisationsmerkmale», *i.e.* characters developed independently of the environment by some sort of »Vervollkommenungstrieb», and »Anpassungsmerkmale», *i.e.* characters developed by transformation directly induced by the environment. Though apparently not directly influenced by NÄGELI, REITER proposed, »zur Unterscheidung der Vegetationsformen nur diejenigen Merkmale heranzuziehen, welche, soweit wir heute zu beurtheilen im Stande sind, als das Resultat nachheriger Anpassung erscheinen», *i.e.* only NÄGELI's »Anpassungsmerkmale». To a certain vegetation-form he referred »sämtliche Lebewesen, welche in Bezug auf ihre Lebenstätigkeit und die dazu gehörige Ausrüstung in allen wesentlichen Stücken untereinander übereinstimmen, mögen sie nun nahe verwandt sein oder nicht...» (pp. 5—6). The system of REITER, however, was not so very different from that of GRISEBACH as could have been expected from his theoretical views. His elementary »Vegetationsformen», most of which were identical with those of GRISEBACH, were still founded mainly upon the form and size of the stem and the leaf, and named in the old way after some characteristic genus or family, but they were arranged into higher groups in a more logical way than in the system of GRISEBACH. The system of REITER had the following appearance:

- A. Assimilierende Chlorophyllpflanzen.
- AA. Wurzellose Lagerpflanzen.
 - I. Algen.
 - II. Moose; a. Schorfmoose (Marchantiiform, Cetrarienform); b. Laubmoose (Sphagnumform, Polytrichumform).
- BB. Wurzeltragende Stammpflanzen.
 - I. Landpflanzen.
 - a. Kräuter.

1. Wurzelstockgewächse. α . Stauden (Spiränenform, Gnaphaliumform, Distelform, Melidenform, Chenopodinenform, Lythrumform). β . Gräser (Ruchgrasform, Thyrsaform, Hirseform, Rohrgrasform). γ . Rosetten (Pterisform, Bromelienform, Agavenform, Arumform. — Pisangform, Ingwerform).
2. Zwiebelgewächse.
- b. Holzgewächse.
 1. Kronenträger. α . Sträucher; α' . immergrüne (Oleanderform, Oschurform, Erikenform); β' . periodisch belaubte (Rhamnusform, Sodaform); γ' . Laublose (Spartiumform); δ' . Dorntragende (Tragacanthenform). β . Wipfelbäume. α' . Immergrüne (Lorbeerform, Eukalyptenform, Fichtenform, Mimosenform, Mangroveform). β' . Periodisch belaubte (Buchenform, Sykomorenform). γ . Laublose (Casuarinenform).
 2. Rosettenträger. α . Zwergpalmen. β . Hochpalmen: α' . Schmalspreitige (Dracaeniform, Velliosienform, Aloëform, Pandanusform). β' . Breitspreitige (Balantiumform, Palmenform. — Aralienform).
 3. Büschelträger (Bambusenform).
 - c. Succulenten (Cactusform).
- II. Wasserpflanzen.
 - a. Stabile (Binsenform; Simsenform).
 - b. Fluthende (Elatinenform. Myriophyllum, Nymphaeienform, Castelnavienform).
- III. Luftwurzelgewächse.
- B. Chlorophyll-lose Schmarotzer.
 - I. Haustoriumpflanzen (Neottienform, Orobanchenform).
 - II. Myceliumpflanzen.

It was only a few years after REITER that OSCAR DRUDE (1887) began his long series of important contributions to the problem of »the biological system» of plants. The attitude of DRUDE towards the evolution-problem much approached that of NÄGELI (1884). He believed in the transformation of species by the direct action of the environment (comp. DRUDE 1887 pp. 225—226), but apparently not much in the selection-theory, and he strongly emphasized the difference between the morphological characters (= NÄGELI's »Organisationsmerkmale») and the biological ones (= NÄGELI's »Anpassungsmerkmale»). While the taxonomical plant-system ought to be based upon the former group of characters, the biological system ought to be based only upon the biological characters or the »Vegetationsweise» (DRUDE 1887 p. 486). »Die Vegetationsweise ist ein Character leichterer Art, dessen Correlation zu Klima und Standort direct zu verstehen ist, der in kürzerer Zeiten Abänderungen unterworfen sein kann, der bald aus diesem, bald aus jenem Organ seiner morphologischen Grundlage eine biologische Anpassung neuer Art macht» (l.c. pp. 483—484). The physiognomic system of HUMBOLDT and GRISEBACH was severely criticized by DRUDE (l.c. p. 489), according to whom the mixing of »biological character forms» with »morphological types» in those systems had led to »jener physiognomische Wirrwarr, mit dem weder der classificierende Florist noch der nicht morphologisch denkende Biologe etwas anfangen konnte». For the units in DRUDE's »biological system» the old term »Vegetationsformen» was still used. The following main types were distinguished (l.c. pp. 487—489):

- I. Holzpflanzen mit Belaubung.
 - a. Bäume und Sträucher.
 - b. Lianen.
 - c. Mangroven.
 - d. Holzparasiten.
- II. Blattlose Holzpflanzen.
 - a. Stamm-Succulenten.
 - b. Blattlose Gesträuche.

- III. Halbsträucher.
- IV. Den Holzgewächsen ähnliche, oberirdisch durch viele Vegetationsperioden ausdauernde Kräuter.
 - a. Rosettenträger und Blattsucculenten. b. Epiphyten.
- V. Hapaxanthische oder redivive Gewächse, autotroph und durch Chlorophyll führende Laubblätter assimilierend.
 - 1. Landgewächse.
 - a. Moose. b. Stauden. c. Zwei und Einjährige Kräuter.
 - 2. Süßwassergewächse.
 - 3. Seewassergewächse.
- VI. Autotrophe, ohne Laubblätter assimilierend: Flechten.
- VII. Parasitische und saprophytische Gewächse ohne Chlorophyll.
 - a. Aus Samen keimend: Parasiten, Saprophyten.
 - b. Aus Sporen keimend: Pilze.

The views of DRUDE upon the problem and system of the »Vegetationsformen» were further developed in his treatment of plant-geography in NEUMAYER's »Anleitung zu wissenschaftlichen Beobachtungen auf Reisen» (1888) and in his »Handbuch der Pflanzengeographie» (1890). The main features of his system, however, were kept unchanged in these contributions. The question, »welche Beziehungen in der Harmonie zwischen Bau und Funktion der Organe so sehr die wichtigsten sind, dass sie als Grundlage der Vegetationsklassen gelten können», was answered by DRUDE as follows: »Es scheint, dass das Ausdauern der Organe und die Hilfsmittel gegen Schädigungen während der Ruheperiode die natürlichste Grundlage bleiben.» (DRUDE 1890 p. 69.)

In 1891, ERNST KRAUSE published an important paper on »Die Eintheilung der Pflanzen nach ihrer Dauer», proposing the following system (comp. WARMING 1908 a pp. 18—19, GAMS 1918 p. 322):

- »A. Nur einmal blühende Pflanzen oder Zeitgewächse. Plantae hapaxanthaes. Unterabteilungen s. o.
- B. Mehrmals blühende Pflanzen, ausdauernde oder Dauergewächse, Plantae perennes.
 - I. Alle oberirdischen Langtriebe fehlen oder haben eine kurzbegrenzte Dauer: Triebpflanzen, Plantae turionales sive apobryes.
 - a. Langtriebe fehlen oder sind nicht zu allen Zeiten vorhanden, ihre Lebensdauer beträgt längstens ein Jahr: Stauden, Herbagines sive plantae herbagineae.
 - 1. Oberirdische Organe überhaupt sind nur zu bestimmten Jahreszeiten vorhanden: Zeitsauden, Etesiae (sc. herbagineae sive plantae).
 - 2. Es sind ausdauernde oberirdische Kurztriebe vorhanden, an welchen sich zu allen Jahreszeiten Blätter finden: Dauerstauden, Dietesiae.
 - b. Langtriebe sind zu allen Jahreszeiten vorhanden, in der Regel von mehr als einjähriger Dauer, in der Regel hapaxanth: Büsche, Virgulta s. pl. Virgultosae.
 - II. Perennirende (in der Regel verholzende). Langtriebe vorhanden: Stammmpflanzen, Plantae arbryes.
 - a. Halbsträucher, Suffrutices;
 - b. Sträucher, Frutices;
 - c. Bäume, Arbores.»

This system is of great interest as the first one founded mainly upon one principle, namely the duration of life.

Among the contributions to the system of »vegetation-forms» found in WARMING's »Lagoa Santa» (1892), the most important one is probably the discussion

in pp. 211—213 of the differences between the two types half-shrubs (suffrutes) and dwarf-shrubs (fruticuli), which had usually been confused by earlier authors, even by DRUDE (1890).

In WARMING's »Plantesamfund» (1895) we find for the first time the term life-form [Danish »lifsform», translated to »Lebensform» in the German edition (1896)] used as a substitute for the »Vegetationsform» of the earlier Middle- and North-European authors. The views of WARMING upon the problem of the delimitation of life-forms are best shown by the fact that he (p. 3) puts the life-form of a plant simply as a synonym to its »epharmonie» in the sense of VESQUE (1882).

In 1896, the problem of the »biological system» was taken up again by DBUDE in his »Deutschlands Pflanzengeographie». The »Vegetationsformen» of Central Europe were discussed in great detail, and arranged into an elaborate system forming an outgrowth of the earlier system of DRUDE. In the main group of the »Holzpflanzen» the two groups »Schösslingssträucher» (= KRAUSE's »virgulta») and »Zwerggesträuche» were taken up coordinated with trees and shrubs. The most important improvement was the following detailed system of the main groups of »Halbsträucher, Succulenten und Stauden» (pp. 48—49):

III. Halbsträucher und oberirdisch verholzende Rhizombildner.

a (5). Holzstauden.

VI. Nicht verholzende Stauden.

b. Perenne Stauden (= KRAUSE's »Dauerstauden, Dietesiae»).

6. Rosettenstauden. 7. Polsterbildner (der Dikotyledonen).

8. Blattsucculenten. 9. Kriechstauden.

*

c. Monokotyledone Rasenbildner.

10. Gedrängte Rasenbildner. 11. Ausläufer-Rasenbildner.

d. Redivive Stauden (= KRAUSE's »Zeitstauden, Etesiae»).

12. Erdstauden. 13. Zwiebel- und Knollen-pflanzen. 14. Wurzelsprosser. 15. Farne.

In a paper by F. W. C. ARESCHOUG (1896) we find for the first time the term »Geophyten» or »geophile Pflanzen» as a designation for »solche Pflanzen, welche ihre Erneuerungsknospen unter der Erdoberfläche anlegen, und deren Lichtsprossen also ihre Entwicklung mehr oder weniger vollständig unter der Erde durchmachen» (p. 1). The opposite type ARESCHOUG called »Aërophyten». While according to him annuals and ligneous plants belonged to the aërophytes, biennials and most of the perennial herbaceous plants were referred to the geophytes in his sense. The following main types of perennial herbaceous plants were distinguished and described:

1. Durch Rasen Stämme überwinternde Pflanzen oder Rasenperennen.
2. Durch Brutknospenstämme überwinternde Pflanzen oder Brutknospenperennen.
3. Durch Stengelbasiskomplexe überwinternde Pflanzen oder Stengelbasisperennen.
4. Durch Rosettenstämme überwinternde Pflanzen oder Rosettenperennen.
5. Durch Rhizome überwinternde Pflanzen oder Rhizomperennen.

In 1898, J. A. Z. BRUNDIN published a paper on the shoot-development and hibernation of Swedish herbs, presenting a rather complicated system of types delimited and arranged according to the same points of view as those of WAR-

MING 1884. He maintained the main division of WARMING into hapaxanthos (a term first used by AL. BRAUN) and perennials (or »polycarpic plants» according to DE CANDOLLE), but for the latter group the term pollacanthos, proposed by F. R. KJELLMAN, was now used for the first time in literature. In the hapaxanthos, both the monocyclic and the dicyclic group of WARMING were divided into several subordinate groups. In the pollacanthic group, 28 types were distinguished, founded upon principles similar to those of WARMING but arranged in a rather different way.

In the same year, WARMING presented a system of the types of ligneous plants, printed in the next year (1899) and consisting of the following 8 types: Trees, shrubs, ligneous lianes, stem-succulents, dwarf-shrubs (fruticuli), creeping shrubs, shrubs with underground runners, and half-shrubs (suffrutices). In the last group DRUDE's »Schösslingsträucher» were included, though it was mentioned that they perhaps ought to form a separate group.

The systems of WIESNER (1889 and 1902) and of POUND and CLEMENTS (1898) closely resembled that of DRUDE. This system was further developed by DRUDE in the third edition of NEUMAYER's »Anleitung zu wissenschaftlichen Beobachtungen auf Reisen» (1905). Following WARMING's proposition of 1895, DRUDE now took up the term »Lebensform» as a substitute for his earlier »Vegetationsform». As a supplement to his life-form system, DRUDE gave a special system of the biological leaf-types (DRUDE 1905 p. 353, criticized by WARMING 1908 a p. 17).

3. The Period of Raunkiaer's First Life-form Works (1905—1913).

In the same year as the term »Lebensform» was brought to general international recognition by being accepted also by DRUDE (1905), CHRISTEN RAUNKIAER published the first comprehensive account of a new life-form system destined to become the life-form system of many botanists for a long period of years. This system was briefly presented by RAUNKIAER already in 1903 (printed 1904, in Danish); the first comprehensive account of 1905 was published in French, and an enlarged Danish edition followed in 1907. A special paper on »Life-form Statistics as a Fundament of Biological Plant-geography» was published in 1908 (in Danish and German).

The system of RAUNKIAER differs from all the life-form systems of earlier authors (except that of KRAUSE) by being based mainly upon one single character-complex, namely »the adaptation of the plants to the surviving of the unfavourable season especially with regard to the protection of the surviving buds or shoot-apices» (RAUNKIAER 1908 p. 44). Theoretically, RAUNKIAER defines the life-form as »the sum of the adaptation of the plant to the climate» (l.c. p. 43), but practically he finds it necessary to pick out one of the most fundamental adaptations as a base for the system of life-forms, as only this way makes a statistical treatment of the life-forms possible. RAUNKIAER is one of the first

botanists who have dared to put such a statistical treatment as the aim of the study of life-forms (statistical studies of the distribution of life-form in various Danish plant-communities were published also by WARMING 1906 and 1907); his life-form system is worked out with the definite purpose of enabling him to use the flora as an exact indicator of climate (RAUNKIAER 1907 p. 10). His well-known system has the following composition:

- A. Phanerophytes. Renewal-buds on aerial shoots more than 25 cm above the soil level.
 - I. Megaphanerophytes (above 30 m) and mesophanerophytes (8—30 m).
 - 1. Evergreen megaphanerophytes without bud-scales.
 - 2. » mesophanerophytes » » »
 - 3. » megaphanerophytes with » » »
 - 4. » mesophanerophytes » » »
 - 5. Deciduous megaphanerophytes » » »
 - 6. » mesophanerophytes » » »
 - II. Microphanerophytes (2—8 m).
 - 7. Evergreen microphanerophytes without bud-scales.
 - 8. » » with » » »
 - 9. Deciduous » » » » »
 - III. Nanophanerophytes (below 2 m) and Herbaceous phanerophytes.
 - 10. Evergreen nanophanerophytes without bud-scales.
 - 11. » » with » » »
 - 12. Deciduous » » » » »
 - 13. Herbaceous phanerophytes.
 - IV. (14.) Epiphytic phanerophytes.
 - V. (15.) Succulent-stemmed phanerophytes.
- B. (VI.) Chamaephytes. Renewal-buds on shoots lying on the ground or rising not more than 25 cm above it.
 - 16. Half-shrub chamaephytes (suffrutescent chamaephytes). Aerial shoots orthotropic, more or less erect, not forming cushions.
 - 17. Passive chamaephytes. Aerial shoots orthotropic, but lying down on the ground because of their own weight.
 - 18. Active chamaephytes. Aerial shoots plagiotropic and prostrate.
 - 19. Cushion-plants.
- C. (VII.) Hemicryptophytes. Renewal-buds in the soil surface, protected by the surrounding soil or litter.
 - 20. Proto-hemicryptophytes. Without leaf-rosettes.
 - A. Without runners. B. With runners.
 - 21. Semi-rosette plants. With a basal leaf-rosette and a leafy stem.
 - A. Without runners. B. With runners.
 - 22. Rosette plants. With a basal leaf-rosette and a leafless or nearly leafless stem.
 - A. Sympodial rosette-plants.
 - 1. Without runners. 2. With runners.
 - B. Monopodial rosette-plants.
 - 1. Monopodium with foliage-leaves but no scales.
 - a. Aerial shoots with leaves.
 - b. Aerial shoots without leaves (only with flowers).
 - 2. Without runners. 2. With runners.
 - 2. Monopodium with both scales and foliage-leaves.
 - a. Without runners. b. With runners.
 - 3. Monopodium with scales only.

D. **Cryptophytes.** Renewal-buds buried in the soil or submersed in water.

VIII. **Geophytes.** Buds buried in the soil.

23. Rhizome geophytes.
24. Stem-tuber geophytes.
25. Root-tuber geophytes.
26. Bulb geophytes.
27. Root(-bud) geophytes.

IX. **Helophytes and Hydrophytes.** Buds submersed in water.

28. Helophytes. Vegetative shoots projecting into the air.
29. Hydrophytes. Vegetative shoots submersed in water.

E. (X.) **Therophytes.** Surviving the unfavourable season only as seeds.

Only the 10 main life-form (or life-form classes) are used by RAUNKIAER for statistical purpose. He firmly believes that »the plant climate is characterized by the statistics of life-forms» (1907 p. 124), *i.e.* that the life-forms best adapted to a certain climate will form a higher percentage of the flora than the others. On the basis of extensive statistical investigations of the life-form composition of various floras, resulting in »biological spectra» of the floras concerned, he attempts to define the main plant-climates of the earth according to the percentage of the various life-forms: one »phanerophyte-climate» in the tropics (with mega—nanophanerophytes prevailing in the moister tropical regions, and nanophanerophytes—chamaephytes in the dryer parts) one »therophyte-climate» in the winter rain regions of the subtropics, one »hemicryptophyte-climate» in the greater part of the cold-temperate zones, and one »chamaephyte-climate» in the cold zones.

While the three plant-climates first mentioned were characterized by a larger percentage of phanerophytes, therophytes, and hemicryptophytes respectively than of any other group, the »chamaephyte-climate» was characterized only by a larger percentage of chamaephytes than in »the normal spectrum», *i.e.* a spectrum based upon 400 species taken from an alphabetical index of all known species.

In his monograph of the land-vegetation of the Faeröes, C. H. OSTENFELD (1906, 1908), was the first author to use two parallel and independent life-form systems for the biological analysis of the vegetation: one consisting of the main types of RAUNKIAER, and the other based upon the duration of life, and upon the vegetative propagation and the structure of the shoots. The latter system contained the following units:

- I. Annual (summer-annual) plants.
- II. Hapaxanthic, but not annual plants.

III. Perennial plants.

1. Spot-bound (sedentary) species.
2. Wandering species with epiterranean (above-ground) runners.
3. Wandering species with subterranean shoots: stolons, creeping rhizomes or bud-producing roots.

The life-form system and life-form statistics of RAUNKIAER were criticized by WARMING (1908 a), who at the same time gave a comprehensive account of his own life-form system, differing considerably from that of RAUNKIAER as well as

from his own first sketch of 1884, and of his general theoretical views upon the life-form problem.

WARMING, as well as RAUNKIAER, was a convinced »Neolamarckian«, and like RAUNKIAER he never doubted that the life-form of a plant was the direct product of the action of the environment. He defined the life-form as »the form in which the vegetative body of the plant (*individuum*) is dressed in harmony with the environment, during its life from the cradle to the grave, from the germination of the seed until the ensuing of death» (p. 27). He accepted NÄGELI's old distinction between »Organisationsmerkmale« and »Anpassungsmerkmale«, but replaced these terms with the terms »indifferent« and »epharmonic« characters, and divided the epharmonic characters into one constant and one inconstant group. The life-forms, according to WARMING, should be based only upon the epharmonic characters, in spite of the fact that »the physiognomically most characteristic forms stand in many cases as rather indifferent in biological respect» (p. 50). The aim of his life-forms was thus not to express the physiognomy of vegetation, as was that of the old »vegetation-forms« of HUMBOLDT, GRISEBACH, HULT etc., but simply to express the epharmonic component of the physiognomy.

As to the value of RAUNKIAER's main life-forms as climatic indicators, WARMING was in some cases rather sceptical. He did not believe that hemicyclopediae and cryptophytes were climatic types, but was far more inclined to explain many cryptophytes as adaptations to various types of soil (p. 63). He had also other reasons to doubt that RAUNKIAER's biological spectra really gave »a correct expression of the 'plant-climate'» (p. 22). He thus pointed out that only for very few countries there was sufficient information available for such statistical treatment of the life-forms, and that his own work »Lagoa Santa» probably was the only thorough local flora existing from a tropical area only slightly modified by man. He also emphasized the very great changes made by man in the countries with a more well-known flora, and that many of the species used by RAUNKIAER for the characterization of plant-climate, *e.g.* in Denmark, probably had immigrated first after the destruction of the original forest-covering of the country by man. If also the little rest still left of the original forest of Denmark was destroyed by human action, »the statistics of life-forms in our flora had to be fundamentally changed, but 'the plant-climate' would still be the same» (p. 23).

Also quite independently of man »the flora of a country depends not only of the climate but also of the history of the country» (WARMING l.c. p. 23). The smaller number of phanerophytic species in the boreal coniferous zone compared with tropical South America, could not be explained by climate only, but was to a great extent caused by historical factors (the glacial period etc.). The very high number of species characteristic for regions with a very old flora was also exemplified by the flora of the Cape and of some parts of Australia. The conclusion of WARMING was that he »could not see that there was any necessity that the proportion of the life-forms should always be the same in countries with the same climate but widely differing age of the flora, and if this be the case, one should not build too certain conclusions upon this proportion

regarding the plant-climate» (p. 24). And he finished his criticism with the following considerations:

»South of the tundra-zone in Asia there follow the forests of the North-Siberian forest-country, enormous, but poor in species. One may say, it appears to me, that there is here an equally pronounced tree-climate as at the Amazon river, though the statistical proportion of the life-forms must be extremely different in Siberia and in Amazonas. The main point is that trees, and forest, can thrive here, just at the cold pole. Wealth in species and wealth in individuals depend of different conditions. It is the number of individuals of the species, which more than the number of species gives a measure of the character of the natural conditions. The species which in a certain locality is best adapted to the nature of the locality, will have the best prospect of producing the greatest number of individuals and thus of becoming the dominant one; this species gives the best expression of the plant-climate, and compared with it the rare species cannot be taken into consideration, even if they are very numerous.

Finally, there is still another factor which has influence upon the proportion of life-forms, namely the soil. This is seen very clearly in the Campos (Savannas) of Brazil, where the valleys with their river-courses are covered by forest, and the rest with campos (savannas), and the border-line between forest and savanna can be drawn absolutely sharp, as with a string. The proportion between phanerophytes and hemicyclopediae is quite different in forest and in campos; there are about twice as many of the former as of the latter in the forests, but on the contrary twice as many of the latter as of the former in campos, in spite of the fact that the climate is absolutely the same — the same rainfall, the same temperature, the same wind; only one factor is different: the soil. The more different habitats there are in a country, the greater will be the number of species; the more uniform the habitats, the smaller will be the number of species. A plain has not as great a chance of attaining wealth in species as a mountain country.

There are thus certainly various difficulties in getting a reliable scientific result concerning the 'plant-climate' with RAUNKIAER's method, and I believe that one should rather be content with studying the proportion between the life-forms within the various communities, conditioned by climate, soil, etc., of which there are several in every country, even within a completely uniform climate, or that one should in any case — begin with the studies of the communities and continue the work with them as a starting-point.» (WARMING 1908 a pp. 24—25.)

The life-form system proposed by WARMING in 1908, and presented in a somewhat more definite form in his »Oecology of Plants» (1909, pp. 5—12), had the following appearance:

- I. Heterotrophic plants (holosaprophytes and holoparasites).
- II. Aquatic plants.
- III. Muscoid plants (bryophytes, and perhaps *Hymenophyllaceae*).
- IV. Lichenoid plants (lichens, and perhaps some vascular plants like *Tillandsia usneoides*).
- V. Lianoid plants.
- VI. The rest of the autonomous terrestrial plants.
 - A. Hapaxanthic (or monocarpic) herbs.
 - 1. Aestival annual plants.
 - 2. Hibernal annual plants.
 - 3. Biennial-perennial (dicyclic, pleiocyclic) herbs.
 - B. Pollacanthic (polycarpic) plants.
 - 1. Renascent (redivivus) herbs (multicipital rhizomes, mat-geophytes, and rhizome-geophytes, each of them with several subordinate groups).
 - 2. Rosette-plants (besides the ordinary rosette-herbs and rosette-grasses also the *Musa*-form and the tuft-trees).
 - 3. Creeping plants.
 - 4. Land-plants with long erect long-lived shoots (cushion-plants, under-shrubs, soft-stemmed plants, succulent-stemmed plants, woody plants with long-lived, lignified stems, the last group divided into canopy-trees, shrubs, and dwarf-shrubs).

As a supplement to this system, WARMING gave a short sketch of the main biological types of leaves (1908 a pp. 79—86), but without giving it the form of a definite system.

In his English book (1909), WARMING introduced the term »growth-form» as an English equivalent to his Danish »lifsform» and German »Lebensform», without giving any reason for not using the term »life-form» in English.

RAUNKIAER's reply to WARMING's criticism was published in a paper on the life-forms of plants on new ground (1909 a). The »plant-climate» was here defined as »the climate as a condition for a certain vegetation, expressed by the statistical proportion between the life-forms of all the species, determined by the adaptation to survive the unfavourable season» (p. 3). To WARMING's remarks regarding the importance of the changes in the flora by the action of man, RAUNKIAER replied (pp. 50—55, 68—70) that such changes never affected the proportions of the life-forms in his biological spectrum, since 1) »the spectrum of the naturalized species always had the centre of gravity in the same part of the spectrum as the original flora» (p. 54), and 2) even the eradication of all individuals of trees and shrubs in Denmark would not change the dominance of hemicryptophytes in the biological spectrum of Denmark. To WARMING's statements as to the importance of the history of the flora, RAUNKIAER replied (pp. 55—58), that there was no reason to believe that the biological spectrum would ever be changed by immigration of new species either in Siberia or in any other country, and that 1200 new species of trees and shrubs would be necessary to change the biological spectrum of the Jenisei Valley from its present hemicryptophyte-climate type into the phanerophyte-climate type of the Amazonas. Finally, RAUNKIAER replied to WARMING's last remark regarding the importance of the soil, that his biological spectra were founded upon the total flora of a certain region, not upon the flora of special plant-communities, and that even if campos and forest at Lagoa Santa would give different spectra, the spectrum of the total flora would give just the right expression of the plant-climate of the region concerned (pp. 60—61). As to the new investigations of RAUNKIAER presented in this paper, their most important result was »that the geological age of a country had no noticeable influence upon the biological spectrum of the flora (p. 62).

In 1911, RAUNKIAER presented a more thorough analysis of »the Arctic and the Antarctic Chamaephyte-climate», illustrating his methods in a very clear way. In this paper he stated (p. 8), that »the plant-climate of a given region should be characterized by the life-form (or the life-forms) which in the biological spectrum of the region exceed the percentage of the same life-form in the normal spectrum». The »normal spectrum» was defined theoretically as »the spectrum given by the whole flora of the earth», though it was determined practically in the way mentioned above (p. 13).

RAUNKIAER fully realized the importance of the study of the life-form composition not only of whole regions but also of special plant-communities, and in a series of papers (1909 a, b, 1913, 1914) he presented a considerable material of such analyses from various countries. Among the early works of this type

also those of M. VAHL (1911 a, b, 1913 a, b, 1919) must be specially mentioned. VAHL divided the main life-forms of RAUNKIAER in his own way into subordinate types. Thus the chamaephytes and hemicryptophytes were divided into »epigeic» and »diageic» types (the former corresponding to OSTENFELD's »sedentary» and »epiterraneous», the latter to his »subterraneous» type). The further division was made into xeromorphic and mesomorphic, and into evergreen and deciduous types.

Important contributions to the criticism of RAUNKIAER's life-form system and life-form statistics were published by C. SKOTTSBERG (1912, 1913, and 1914). SKOTTSBERG was probably the first author who pointed out the very heterogenous character of RAUNKIAER's type »chamaephytes» (1912 p. 7). He also showed that in most of the hemicryptophytes of the Falkland Islands, »although they are built up like H and have shoots that only live one year, their innovations develop in the autumn and endure the winter without special protection, in the shape of large, leafy shoots» (1913 p. 93). From this fact he drew the conclusion that »the Falkland H really endure winter like Ch», and that »the difference between these classes are, *in this special case*, more morphological than biological». And he continued: »I must emphasize once more the fact that the peculiarity of the vegetation of the Falklands does not lie in the fact that the percentage of Ch or H is so and so great, but in the circumstance that both of them are evergreen. But I fail to see how we should express this by means of RAUNKIAER's biological spectrum. His brilliant idea was to show how the plants, in different climates, survive the unfavourable season. To show this, in our special case, it seems necessary to subdivide both Ch and H, taking the evergreen species into consideration; if not we shall get the same spectrum for Spitzbergen and the Falkland Islands although they have a different climate and different physiognomical character. I have come to just the same conclusion as when dealing with South Georgia: that there is no climate that we may call *the Chamaephyte* climate; in any case, it is rather the Austral one that makes the entire stock of H endure the winter like Ch, than the Boreal one that would deserve such a name.» (SKOTTSBERG 1913 p. 93.) — In his first paper on Juan Fernandez (1914 pp. 53—54), SKOTTSBERG demonstrated another remarkable fact, namely the fallacy of RAUNKIAER's statement (comp. above p. 16) that the original and the introduced flora of a certain region always show the same type of biological spectrum. While the original flora of Juan Fernandez showed a clear phanerophyte-climate spectrum, the introduced flora showed a spectrum of a rather different type (with more hemicryptophytes and therophytes). According to SKOTTSBERG, this spectrum is probably more in accordance with the climate than that of the original flora, which appears to be more historically conditioned.

Before leaving the period of RAUNKIAER's first life-form works, we must mention some other works on the same problem which appeared during this period but quite independently of the schools of RAUNKIAER and WARMING.

In 1906, N. SYLVÉN published a monograph of the early developmental stages of Swedish dicotyledons, in which an elaborate system of 75 types was presented, illustrated by carefully described and pictured examples. The primary

division was made into plants without and plants with postembryonal hibernation; in the subdivision of the latter group the morphology of the hibernating shoots was much more utilized than in most other life-form systems.

As another contribution to the life-form problem published in the same year (1906), L. DIELS' monograph of the vegetation of the southern part of Western Australia must be mentioned. DIELS only used a very simple life-form system, consisting of the main types generally accepted before RAUNKIAER, but he made some important statements regarding the correlation of these types with the climate. He thus pointed out the extreme scarcity of perennial herbs with tubers and bulbs (geophytes) in the southwestern corner of Western Australia, and the remarkable contrast in this respect between the region concerned and other winter-rain regions with a very rich representation of geophytes, especially the Cape. According to DIELS this difference can not be explained by the climate only, but must be due partly to historical factors (p. 162). An analogous case is formed by the annuals in the same region (p. 163). For the discussion of the correlation between life-forms percentage and climate these statements by DIELS are of the utmost importance, though they seem to have been completely overlooked both by RAUNKIAER and by all other authors dealing with this problem. Of great interest are also DIELS' studies of »Epharmose und Formbildung» in certain West-Australian genera, illustrating the correlation between leaf-types and climate (pp. 191—198). The very strong belief in the life-form-transforming power of the climate expressed by DIELS in this connection, certainly adds considerably to the weight of his statements regarding the lacking correlation between life-form percentage and climate in the cases mentioned above.

Here it will probably also be the best place to mention the system of »ecological groups» established by J. MASSART (1908 pp. 255—256) and worked out further by J. JESWIET (1914). It was based mainly upon the duration of the assimilation-period of the plant, combined with the duration of the epigeous and the hypogeous stem. 13 types were distinguished, named simply by the letters A—L and illustrated by means of very suggestive diagrams (MASSART 1908, diagr. 6), and the distribution of these types in the duneflora of Belgium and Holland was very carefully investigated. It is interesting to note that MASSART applied this system simultaneously with the system of RAUNKIAER and completely independently of it.

4. The Period of Beginning Reaction against the Onesided Epharmonic Point of View in Life-form Classification (1913—1920).

As we have seen above, the life-form systems of RAUNKIAER and WARMING have very little in common with the early »vegetation-form» systems of HUMBOLDT, GRISEBACH, HULT, etc. While the early »vegetation-form» systems were meant to supply plant-geography with the elementary units necessary for the description of the physiognomy of vegetation, the modern »biological life-form systems»

had no such aim at all, but only claimed to express the epharmonic component of the vegetation-physiognomy. WARMING, as well as RAUNKIAER, fully realized that many of »the physiognomically most characteristic forms» could not be referred to this epharmonic component, but were »rather indifferent in biological respect» (comp. above p. 14). But from this consideration they only drew the conclusion that physiognomy was of little scientific importance and that the old physiognomical period in the study of life-forms marked a very low and primitive stage compared with the modern »biological» period. It never occurred to them that also another conclusion could be drawn from the lack of parallelism between physiognomical and »biological» types, namely that the purely »biological» types were insufficient for one of the most important tasks of plant geography, namely the accurate and objective picturing of the morphology of vegetation.

This conclusion, however, was drawn by another one of the fathers of the »biological» life-form systems, namely by DRUDE in his »Ökologie der Pflanzen» (1913, comp. also DRUDE 1914). In this work, DRUDE was the first modern ecologist to give up the onesided »biological» or »epharonical» view upon the life-form problem. This was emphasized already in the title of the chapter dealing with this problem: »Die physiognomischen Lebensformen der Pflanzen». DRUDE's new views in this fundamental question are best illustrated by the following abstracts:

»Es galt als ein Axiom, dass die Vegetationstypen, nur auf Vegetationsorgane sich stützend, nicht mit Familiencharakteren vermischt werden dürfen. Sie mussten, wie sehr richtig betont wurde, physiologisch-anatomische Merkmale tragen, wie Hartlaub, Succulenz, Blattlosigkeit, Chlorophyllmangel.

Aber es mag wiederholt werden, dass die natürlichen Familien auch in der Verwendung dieser vegetativen Anpassungsmerkmale beschränkt sind und oft ihre ganz eigenen Wege gehen; das liefert den Untergrund dazu, hier eine festere Verbindung zu suchen.» (DRUDE 1913, p. 6—7.)

»Und so glaube ich jetzt einen bisher nicht so streng vertretenen Standpunkt einnehmen zu sollen, nämlich in der Stellung der physiognomischen Gruppenbildung des gesamten Pflanzenreichs zum phylogenetischen System.

Natürlich bleibt der alte, von mir auch früher oft betonte Standpunkt bestehen, dass die physiognomischen Gruppen nicht systematische Einheiten darstellen sollen, dass sie im Gegenteil frei in den der schnellen Umänderung und Anpassung unterworfenen Vegetationsorganen wählen; sie ziehen die Blütenbildung und Fruchtreife allein als Kampfmittel um Erwerbung neuer Standorte, nur im Hinsicht auf ihre Funktion und auf die äusseren dabei in Frage kommenden Gesichtspunkte der Periodizität und Dauer mit heran. Nicht können es also die systematischen Gruppen selbst sein, welche zu physiognomischen Gruppen sich verwenden lassen, sondern nur deren ökologisch gleichwertige Glieder. Die physiognomischen Gruppen durchschneiden häufig grosse, sehr natürliche Systemfamilien — man denke nur z. B. an Gräser von *Bambusa* bis zu *Vulpia Myurus*, an die jüngst erst von ENGLER und KRAUSE genauer beschriebene baumartige Cyperacee: *Schoenodendron Bücheri* aus Kamerun neben den anderen Arten dieser Familie, an die Liliaceen mit *Dracaena*, *Asparagus*, *Lapageria*, *Paris* neben den vielen, Zwiebeln besitzenden Gattungen mit *Bowiea volubilis!* — und anderseits verbinden sie gleichartige Besiedelungsgenossen aus recht verschiedenen Familien: aber in allen grossen als Hauptstämme des Pflanzenreichs zu bezeichnenden Abteilungen folgt die vegetative Formbildung besonderer Ausprägung, und die hierdurch in einseitigere Bahnen gelenkte Besiedlungskraft beschränkt sich auf gewisse Formtypen, um an anderen Stellen solche von anderen Hauptstämmen an ihre Stelle treten zu lassen. Sind in WARMINGS Hauptgruppen ausser den Heterophyten, welche die Pilze wenigstens nach ihrem Er-

nährungscharakter mit wenigen Phanerogamen verbinden, noch die Muscoiden und die Lichenoiden fast als reine systematische Gruppen abgetrennt, so möchte ich noch einen starken Schritt weiter gehen und unter den Wasserpflanzen, zumal den ozeanischen, die Algen von den wenigen dort vorkommenden Moosen und den Blütenpflanzen getrennt halten, und unter den Landpflanzen, soweit als es angeht, die Farne und Cycadeen, die Coniferen und gewisse physiognomische Gruppen der Dikotylen und Monokotylen gleichfalls in Parallelreihen trennen.

Es ist beispielsweise durchaus unnötig, die Farnbäume, die *Cycas*-Stämme und die Palmen, *Dracaena*, *Pandanus*, weil sie eine Rosette grosser Blätter auf oft kurzem, dictem Stamm tragen, in eine einzige physiognomische Gruppe zu vereinigen; mindestens müssten sie in verschiedenen »Typen« dieser Gruppe geschieden werden, wie das auch meistens beim Eingehen auf solche heterogene Gruppe stillschweigend zu geschehen pflegt. Die beiden auf S. 20 folgenden Fig. 1 von *Borassus* und Fig. 2 von *Cyathea* erläutern die ungefähre Ähnlichkeit beider in ihrer physiognomischen äusseren Erscheinung, aber sie verraten dem Pflanzenkenner auch sogleich die in ihrer inneren Organisation unverrückbar mitgegebenen ökologischen Verschiedenheiten. Denn die periodischen Erscheinungen in der Entwicklungsfolge der Blätter, der Bau dieser Blätter, ihr Widerstand gegen Sturm, Regen und Dürre, die Verbreitungsmittel durch Sporen oder Samen mit den Einrichtungen der Keimung, die Wurzelbildung und Verankerung der Stämme im Boden, kurz: ausserordentlich vieles, was ihre Besiedlungskraft auf der Erde und ihre Bedeutung für den Formationsanschluss reguliert, sind stark verschieden. Dasselbe kann man von den Coniferen gegenüber den di- und monokotyledonen Bäumen sagen; diese werden sogar fast immer von den Reisenden scharf geschieden und gut erkannt, was hier nur mit Bezug auf die Natürlichkeit ihrer »Physiognomie«, ihres Habitus, hervorgehoben werden soll.

Denn es handelt sich hier nicht um eine Klassifikation der Formen für Laien; es soll sich um biologische Charaktere handeln, die gleichwohl nur von bestimmten, phylogenetisch auf der Erde auf bestimmte Plätze verteilten Entwicklungsreihen getragen werden. Jede dieser Entwicklungsreihen zeigt je ein besonderes Mass von Anpassungsmodalitäten, die, zum grossen Teil aus den alten Charakteren der Organisation hervorgegangen, mit zu den wesentlichen Merkmalen jener Reihe gehören. Und in diesen Reihen zeichnen sich nun die einzelnen natürlichen Familien erst recht durch die Verschiedenheit ihrer Anpassungsmodalitäten aus. Es hat doch wohl seinen besonderen Grund, dass die Coniferen und Palmen in der Besiedelung der Erde sich nahezu ausschliessen und dass zu ihren Gliedern beispielsweise keine Staude mit alljährlicher Sprosserneuerung gehört. Welche Formenmannigfaltigkeit haben im Vergleich hiermit die Farne, die Liliaceen und die Leguminosen entwickelt!» (DRUDE 1913 pp. 18—20.)

In order to prevent misunderstandings, DRUDE added the following remark (p. 22): »Es mag ja erlaubt sein, den Namen von Palmen, Coniferen usw. für eine solche physiognomische Gruppe mit zu verwenden; gemeint ist jedenfalls nicht der systematische Charakter und Umfang, sondern die biologische Umgrenzung.»

According to DRUDE, the aim of the physiognomical life-form system is »die ökologisch gleichartigen Glieder der phylogenetischen Hauptreihen des Pflanzenreichs herauszufinden und nach morphologisch-physiognomischen Gesichtspunkten zusammenzustellen. Das Wort 'physiognomisch' soll dabei stets ein streng morphologisches Merkmal in ein ökologisches von gleicher physiologischer Funktion umwandeln» (p. 22).

As a base for his physiognomical life-form system, DRUDE took the following »Hauptgruppen von Grundformen«, »bestimmt durch die Anordnung und den Bau der Spross-systeme (Ausgestaltung der Achsenorgane) einschliesslich der Bewurzelung, durch die Grösse und Lebensdauer der Pflanzen, letztere wiederum gewährleistet durch die Form der Knospenbildung und Verjüngungsweise» (p. 25):

1. »Wipfelbäume und
2. von Grund aus verzweigte Gesträuche mit unbegrenzten Verjüngungsknospen.
3. Schopfbäume und baumartige Rosettenträger, mit meist nur einer einzigen endständigen, dauernd Blätter bildenden Wachstumsknospe.
4. Pflanzen mit windenden Stengeln von kurzer Sprossdauer oder mit verholzenden Schlingstämmen, Klimmblättern, Ranken.
5. Langlebige Pflanzen mit (adventiven) Kletterwurzeln.
6. Langlebige Pflanzen mit in der Regel unverzweigten, knospenschutzlosen Säulen- oder Kugelstämmen (Beispiel *Echinocereus*).
7. Kriechende Zwerg- und Halbsträucher, bzw. solche mit unterirdischer Ausläuferbildung.
8. Kriechstauden und Wanderstauden mit oberirdischen Läufern oder unterirdische Kraftknospen bildenden Rhizomen; Adventivwurzeln.
9. Bodenständige langlebige (wenigstens 2-jährige) Kräuter mit Rosette oder kopfartiger Rhizomverzweigung.
10. Kurzlebige Gefäßpflanzen ohne vegetative Verjüngung für die nächste Vegetationsperiode.»

Through the combination of these »Hauptgruppen von Grundformen» with several other points of view (comp. DRUDE l.c. pp. 29—30) DRUDE worked out an elaborate system of physiognomic life-forms, probably the most detailed and complete one that had ever been presented. It covered 54 pages (together with 15 pages »Anmerkungen und Literaturzusätze») in his book, and contained the following main groups, most of them divided into several subordinate groups, often of several stages:

- I. Aërophyten (Holzpflanzen, ausdauernde und einjährige Kräuter).
1. Monokotyle Schopfbäume.
2. Monokotyle Palmgebüsche und Palmlianen.
3. Kurzstämmige Zwerpalmien,
4. Baumfarne und Cycadeen.
5. Nadelhölzer, Bäume und Sträucher der Coniferae.
6. Dikotyle Laubbäume, immergrün belaubt und blattwechselnd.
7. Dikotyle Hochsträucher und Büsche.
8. Dikotyle Holzlianen.
9. Dikotyle amphibische Gehölze mit Wasserwurzeln (Mangroveform).
10. Dikotyle Federbuschgehölze.
11. Baumgräser.
12. Smilaceenbüsche und -lianen.
13. Blattlose (armlaubige) dikotyle Rutengehölze und Dornsträucher.
14. Armlaubige Tonnenstämme.
15. Stammbildende und immergrüne Blattrosetten tragende Blattsucculenten.
16. Dikotyle Stammsucculenten.
17. Immergrüne und blattwechselnde Zwerggesträucher und Kriechstämme der Dikotyledonen. (Niedergehölze und Reiser.)
18. Holzparasiten.
19. Scheidenstämmige Hochstauden und Grossblattrosetten der Monokotyledonen.
20. Monokotyle Wurzelkletterer.
21. Grossblatt-Rosetten der Farne und Cycadéen.
22. Knollenstamm-Epiphyten.
23. Perenne und redivive Gräser.
24. Binsen mit unterdrückter Blattbildung.
25. Aufrecht wachsende Halbsträucher und Holzkopfstauden.
26. Mit Kriechstamm oder Ausläufern wurzelnde Halbsträucher und Kriechstauden.
27. Dikotyle Polsterbildner.

28. Succulentenpolster der Mono- und Dikotyledonen.
 29. Zweijährige und perenne Rosettenstauden.
 30. Redivive und annuelle Weichstamm-Lianen und Klimmpflanzen.
 31. Redivive, unterirdische Stockknospen am saftigen Rhizom bildende, vielköpfige Hochstauden.
 32. Geophile Stauden mit wandernder Kraftknospe.
 33. Geophile Knollengewächse.
 34. Geophile Zwiebelgewächse.
 35. Monokotyle Therophyten.
 36. Dikotyle Therophyten.
 37. Dikotyle kurzlebige (prävernale) Kräuter.
 38. Saprophyten und Parasiten.
- II. Wassergewächse: Hydrophile und Hydrophyten. (Gruppen 39—44.)
- III. Die Lebensformen der Zellenpflanzen (Moose und Thallophyten). (Gruppen 45—55.)

In 1914, C. A. M. LINDMAN published a study in the life-forms of ligneous plants, emphasizing the confusion in botanical literature regarding the concepts of trees and shrubs, and proposing the following system:

- I. Aëroxyles, air-lignoses. The ligneous stem and its ramification above the ground.
 - A. Trees, high stem trees. A distinct main stem below the crown. The height varies from 150 m down to a few m (small trees), 1 m (dwarf trees), or a few dm (miniature trees and pygmy trees).
 - B. Shrub-trees or low stem trees. Only a short or indistinct main stem below the crown.
 1. Tall (e.g. young *Pinus silvestris* and *Picea abies*, *Ilex aquifolium*, *Juniperus communis*, etc.).
 2. Small, dwarf-shrubs or microaëroxyles, often humifuse (e.g. *Calluna*, *Empetrum*, *Dryas*, etc.).
 - C. Creeping lignoses. Ligneous stem simple or branched, supraterraneus but rooting, either climbing (e.g. *Hedera*) or prostrate (e.g. *Linnaea borealis* and sometimes *Oxycoccus*).
- II. Geoxyles, ground-lignoses. Ligneous stem partly hypogeous, of long duration (ligneous rhizome), partly epigeous, of several homologous aerial stems of only a few year's duration.
 - A. True shrubs.¹ The whole supraterraneus shoot-system lignified.
 1. Tall; subterraneous stem more or less contracted (e.g. *Rosa*, *Bambusa*).
 2. Small, dwarf-shrubs or microgeoxyles; subterraneous stem mostly with long runners (e.g. *Vaccinium myrtillus*, *V. vitis idaea*, *Salix herbacea*). *Oxycoccus* is in some cases a prostrate shrub.
 - B. Herbaceous shrubs or Half-shrubs. Supraterraneus system also with herbaceous, not hibernating shoots (usually the fructificating shoots). Examples: *Rubus idaeus*, *Lavandula spica*, *Helianthemum chamaecistus*, *Artemisia campestris* etc. (transition to perennial herbs).

In this paper, LINDMAN also pointed out the important fact (p. 282) that the geoxyles are at the same time phanerophytes and hemicryptophytes, and that while RAUNKIAER had counted the species of *Rubus* to the hemicryptophytes (because he considered the hemicryptophytic buds more important for the preservation of the life of the individual than the phanerophytic ones), he had not drawn the same consequence for the geoxyles with more than biennial supraterraneus

¹ The distinction made by LINDMAN between »true shrubs» and »shrub-trees» coincides with that made by S. BLOMQVIST (1911 pp. 52—53) between »typical shrubs» and »tree-like shrubs».

shoots like *Rosa* etc. Nor had RAUNKIAER drawn the same consequence in the cases of *Vaccinium myrtillus* and *Vaccinium vitis idaea*, which were classed by RAUNKIAER as chamaephytes, not as geophytes as would be done if their subterraneous runners were taken into consideration.

In the third edition of his »Lehrbuch der ökologischen Pflanzengeographie» (WARMING-GRAEBNER 1914—1918), WARMING made a new revision of his life-form system. He now took up the same distinction between »Lebensform» and »Grundform» as DRUDE 1913, pointing out that the »Grundformen» »wohl zum grössten Teile Vererbungsformen sind, die aber vielfach den Charakter von Anpassungsercheinungen zeigen, zum Teil aber auch nichterbliche Abänderungen darstellen» (p. 154). Most of WARMING's old groups were kept unchanged, but for the pollacanthic plants the following new system was presented (pp. 167—168):

»I. Aufrechte und mehr oder weniger gerade (orthotrope) Laubsprosse.

A. Kräuter.

a. Stauden (ohne Grasform).

1. Die Assimilationsorgane (Blätter) sitzen an Langtrieben. Die meisten Arten ausdauernd. Pollakanthe Langstauden.
2. Die Assimilationsorgane sind einzelne Blätter. Blattstauden.
3. Die Assimilationsorgane (Blätter) sind zu typischen Rosetten gedrängt. Rosettentauden.

b. Grasform.

4. Die Assimilationsorgane (Blätter) sind schmal, bandartig bis sehr schmal, nach dem Typus der Gräser gestaltet. Grastyphus.

B. Halbsträucher. Niedrige, meist sommergrüne, aber auch oft immergrüne Pflanzen, deren jüngste Sprosse mehr oder weniger krautartig und daher einjährig sind.
Hier anschliessend die meisten Polsterpflanzen.

C. Weichstämme. Dicke, grüne, weiche Stämme, meist immergrün; offene oder nur durch Scheiden des jüngsten Blattes geschützte Knospen. Gewöhnlich grosse Blätter.

D. Stamsukkulanten. Blattlose grüne sukkulente Stämme mit sehr kleinen, oft eingesenkten Knospen.

E. Echte Gehölze. Aufrechte, verholzte, mehr oder weniger langlebige Sprosse, die in einem Jahre oder länger (immergrüne) die Assimilationsorgane (Blätter) tragen.

a. Sträucher und Zwergsträucher.

b. Typus der Bambusgräser und Rohrpalmien.

c. Wipfel (Kronen-)bäume.

d. Schopfbäume mit unverzweigtem nur eine Blattrosette tragendem Gipfel.

II. Kriechpflanzen. Sprosse plagiotrop, wurzelschlagend oder dem Substrat eng angedrückt.

Wieder einzuteilen in:

A. Kräuter.

B. Halbsträucher.

C. Gehölze (Spaliersträucher).»

In the first issue of the third part of WARMING's »Dansk Plantævækst», dealing with the forests of Denmark, the following detailed system of the life-forms of ligneous plants was presented (WARMING 1916 pp. 9—34):

A. True lignoses.

I. Trees.

II. Erect shrubs.

1. Tall shrubs.

2. Dwarf-shrubs.

- a. Without runners.
- b. With underground runners or horizontal underground shoots.
- III. Creeping shrubs.
 - a. Espalier shrubs.
 - b. Rooting.
- IV. Climbing plants (lianes).
- B. Half-lignoses.
 - 1. Erect.
 - 2. Creeping.
 - 3. Climbing.

The proposal of LINDMAN to restrict the term »shrub» to geoxyles, was severely criticized by WARMING (l.c. pp. 30—32), who pointed out that the use of the term shrub also for aéroxyls with a stem divided near its base was generally established both among botanists and other people since very long ago.

At the meeting of Scandinavian naturalists in Kristiania (now Oslo) in 1916, WARMING presented a paper on »Life-form and habitat» (printed in 1918), in which his system of pollacanthic herbs was worked out in still greater detail. He now proposed the following system of the life-forms of herbaceous plants (WARMING 1918 a p. 532):

- A. Hapaxanths.
 - 1. Summer-annuals.
 - 2. Summer- and winter-annuals.
 - 3. Winter-annuals.
 - 4. Varying between 1, 3, and biennials.
 - 5. Biennials (and pluriennials).
- B. Pollacanths.
 - a. With orthotropic shoots.
 - 6. Tuft-plants (with mesocormus).
 - a. With long-shoots.
 - b. » rosette-shoots.
 - c. » semi-rosette shoots.
 - d. The grass-type.
 - 7. Orthotropic with tubers or bulbs.
 - 8. With rooting stem-basis.
 - b. With plagiotropic shoots (travelling shoots).
 - 9. Creeping herbs.
 - 10. With foliage leaf rhizomes or foliage leaf suboles (subterraneous runners).
 - 11. With supraterraneous runners.
 - a. With long-shoots.
 - b. » rosette-shoots.
 - c. » semi-rosette shoots.
 - d. The grass-type.
 - 12. With subterraneous runners.
 - a. With long-shoots.
 - b. » rosette shoots.
 - c. » semi-rosette shoots.
 - d. The grass-type.
 - 13. With travelling rhizomes.
 - a. With long-shoots.
 - b. » rosette shoots.
 - c. » semi-rosette shoots.
 - d. The grass-type.

This system was used by WARMING to a statistical survey of the distribution of life-forms in various habitats of Denmark. Contrary to RAUNKIAER his aim was not to characterize the plant-climate but to study »the adaptations of the life-form to the soil or the medium in which the plant grows» (p. 530), and for this purpose he found the system of RAUNKIAER quite useless. He also emphasized the heterogeneity of RAUNKIAER's chamaephytes, which contained »not only ligneous and subligneous plants, but also herbs, among the ligneous plants both dwarf shrubs like *Calluna*, prostrate shrubs like *Arctostaphylos* and *Empetrum* (espalier shrubs) or *Linnaea* (creeping lignose, 'reflignos' of LINDMAN); of subligneous plants for instance *Genista*; of herbs so widely differing types as *Cerastium arvense*, *Veronica officinalis*, *Antennaria dioica*, *Galium saxatile*, *Lamium Galeobdolon*, *Lycopodium*, *Sedum acre*, *S. album*, etc.» And he continued: »The only thing that binds all these together, is that the renewal-buds are not placed higher than 25 cm above the ground, but it is just such differences as those occurring within the Chamaephytes, that I want to get elucidated» (p. 531).

In this paper WARMING also explicitly reacted in the same way as DRUDE (1913) against the one-sided epharmonic point of view in the life-form systems of the previous period. He pointed out, that »there is one side of the life-form that has stepped too much into the back-ground compared with the adaptation of the photophilous shoots, namely what has recently been called their »Grundform» (pp. 527—528). And he also stated that this »Grundform» was just the same as the »main types» of his first life-form paper (1884), and that it could be defined as »general shoot-form or shoot-type» and combinations of shoot-types. As to the epharmony of these forms with the environment, he stated that they must »to some extent be in epharmony with the habitat». It is quite clear that WARMING had now altogether left the idea of a life-form system based only upon epharmonic characters.

In the same paper, WARMING also pointed out the great confusion in botanical literature as to the morphological system of subterraneous stems, and proposed a more definite terminology for these organs. This terminology was presented in greater detail in his monograph of subterraneous runners (1918 b). It appears to be of such a general importance for the methodology of the study of life-forms, that it will be well worth while to quote WARMING's English summary of it *in extenso* (WARMING 1918 b pp. 367—368):

»There are in vascular plants several different types of plagiotropic shoots which have not, however, been given definite names, so that we find, for instance, the same type referred to by some writers as a stolon, by others as a rhizome. Distinction should at any rate be made between the following.

1. In many herbaceous species, the orthotropic aerial shoots send out plagiotropic overground root forming shoots (runners) with elongated internodes, and naturally, with foliage-leaves. These runners should be called stolons (a certain type flagellum). Their biological function is to effect the migration of the plant.
2. Many species with orthotropic aerial shoots have pale, slender underground runners with scale leaves and elongated internodes; they take root, and ramify irregularly. These should be kept distinct from the stolons, and it is suggested that they be called suboles (planta subolifera). They are probably never produced by direct transformation of the primary shoot, but are shoots of a second and higher order. Their biological function is likewise to effect the migration of the

plant. It is this type more particularly which is dealt with in the present paper. An example is shown in fig. 1, *Asperula odorata*.

3. In some cases, they terminate in a nutritive organ, which may be a stem-tuber, fleshy root, or bulb; the hibernating buds are connected with this organ, the nourishment of which is used next spring, but the true migratory part of the shoot dies off sooner. Example, *Solanum tuberosum*, fig. 37; *Stachys Sieboldii*, fig. 34; *Cyperus esculentus*, fig. 39; etc.

4. Underground — and consequently pale — plagiotropic shoots, with short internodes, and rich in nutritive matter and therefore thick, — and which often live for several years, are called rhizomes; they form an important central organ of the plant, and that from which the aerial shoots proceed. These last are in most species developed from the terminal bud of the rhizome (sympodial rhizomes); in a smaller number of species, from the lateral buds (monopodial rhizomes). The rhizome is often formed directly from the primary shoot (example: *Anemone nemorosa*, *Polygonatum multiflorum*). A somewhat divergent form of rhizome is found in *Dentaria bulbifera*, where not only the stem, but also the scale leaves are nutritive (fleshy); see fig. 2.

5. Between the suboles and the rhizomes we have another type, resembling the former in being slender, with elongated internodes, but more like the rhizome in the fact that its lateral shoots are formed from certain main buds, situate in the axil of a certain leaf, the leaf in question being often numerically definable. These are often but short-lived. Examples: *Hippuris vulgaris*, *Heleocharis palustris* etc. See p. 302. We might perhaps call them rhizodes.

6. We may here further mention two other types of plagiotropic shoots, which are not lateral shoots on an orthotropic aerial shoot, and which in some forms run above ground, in others below, but in all cases directly bearing the green foliage-leaves, besides occasionally having scale leaves. The overground root-forming types are thus creeping (*repentes*) and should perhaps be called creeping plants (creepers), e.g. *Lysimachia nummularia*, *Hydrocotyle vulgaris*. The underground forms have a thinner or thicker stem, from which foliage-leaves proceed, and have thus either character of suboles or of rhizomes or rhizodes (example: *Polypodium vulgare*, *Pteridium aquilinum* and other ferns; *Aspidistra luvida*) and must for the present, failing any better name, be called leaf-bearing suboles and leaf-bearing rhizomes. They must of course as a rule be found close under the surface of the earth, rarely deep down (*Pteridium* and other ferns) as the leaves cannot force their way through the earth for any distance. The stem in some species may be found both creeping over and wandering in the earth (e.g. *Hydrocotyle vulgaris*).

7. The term rhizome is also generally used for those stems with short internodes, but erect, branched or unbranched, lying close above and below the surface of the earth, which bear the winter buds, and which are surviving basal parts of orthotropic aerial shoots (Ex.: *Primula elatior*, *Plantago maritima*). This type of shoot has been called »Rhizome (root-stock)» or »radix multiceps»; it was distinguished already by H.J. NILSSON from the true rhizomes under the name of »pseudorhizome»; it was also formerly called »mesocormus», a good and suitable name. It may be found combined with aerial or subterranean runners but may also lack these, and will then be non-migratory; the vegetative reproduction is then insignificant.»

The following detailed system of the life-forms characterized by underground runners (or suboles), was proposed by WARMING (1918 b p. 369):

- I. Underground runners not combined with nutritive reservoirs.
 - A. Herbaceous plants with orthotropic shoots (not climbing).
 - B. Herbaceous lianas with suboles.
 - C. Ligneous plants with underground runners.
 - D. Pollacanthous herbs with rosette.
 - E. » » » semi-rosette.
 - F. » » » graminoid shoots.
- II. Suboles with nutritive organs.
 - A. The potato type.
 - B. Suboles with fleshy roots.
 - C. » » bulbs.

In the last issue of his monograph of Danish forests (comp. above p. 23), WARMING presented a new, rather detailed variant of his life-form system for herbaceous plants (WARMING 1919 pp. 417—437):

- I. Heterotrophic herbs.
- II. Autotrophic herbs.
 - A. Autonomous.
 - 1. Hapaxanthos.
 - 2. Pollacanthos.
 - a. Mesocorms with erect aerial shoots.
 - 1. Spot-bound species.
 - α . Without nutritive reservoirs.
 - β . With nutritive reservoirs.
 - 2. Species with travelling shoots.
 - α . With epigeous runners (stolons).
 - β . With hypogeous travelling shoots.
 - 1) Hypogeous travelling shoots with elongated internodes (suboles or rhizodes).
 - a) Without nutritive reservoirs.
 - b) With nutritive reservoirs.
 - 2) Hypogeous travelling shoots with short internodes (rhizomes).
 - b. Mainly or only travelling shoots.
 - 1. Epigeous travelling shoots (creeping herbs).
 - 2. Hypogeous travelling shoots with foliage leaves (leafy suboles or other hypogeous travelling stems): »Bladstauder».
 - B. Climbing plants.

In this connection WARMING also summarized one of the main points in his opposition against RAUNKIAER's system in the following very suggestive way: »It is ecologically rather unimportant whether a species is a 'cryptophyte', a 'hemicryptophyte', or perhaps even a 'chamaephyte', as long as it is spot-bound, but far more important is whether it has got the power of vegetative travelling, because it then has got a possibility of forming societies in this way, more or less suppressing other species; it will then get many more points in statistical surveys than without such travelling shoots» (WARMING 1919 p. 433).

During the same years as these works were published by WARMING, RAUNKIAER presented some important additions and improvements to his life-form system. In 1916, he published a system of leaf-size classes (comp. also FULLER and BAKKE 1918), which was used by him in connection with his ordinary life-form system, and proved to give a valuable help in the characterization of vegetation physiognomy and its relation to climate. It contained the following classes (RAUNKIAER 1916 p. 229):

Leptophylls:	leaf area below	25 mm ² .
Nanophylls:	»	between 25 and 225 (9×25) mm ² .
Microphylls:	»	225 and 2025 ($9^2 \times 25$) mm ² .
Mesophylls:	»	2025 and 18225 ($9^3 \times 25$) mm ² .
Macrophylls:	»	18225 and 164025 ($9^4 \times 25$) mm ² .

In order to facilitate a rapid determination of the leaf-size classes, RAUNKIAER added a plate containing schematic pictures of 4 leaves with the sizes marking the limits between the 5 classes (reprinted by FULLER and BAKKE 1918).

In his earlier works on life-form statistics, RAUNKIAER had used a »normal spectrum» based upon only 400 species (comp. above p. 13), and explicitly stated by RAUNKIAER to be only provisional. In a paper published by RAUNKIAER in 1918, a more definite »normal spectrum» was presented, based upon 1000 species taken out in 10 groups from different parts of »Index Kewensis», and differing only slightly from the old one. In this paper, phanerophytes and chamaephytes were united into one superior unit, »epigeous plants», while hemicryptophytes and cryptophytes were united in the same way into one »hypogeous» group.

In 1918, a critical treatment of the life-form problem was published by H. GAMS in his well-known work »Prinzipienfragen der Vegetationsforschung». It contained, *inter alias*, a detailed account of the historical development of the problem, and culminated into a new life-form system presenting many new and original points of view. In this system the purely epharmonic life-form concept was driven to its utmost extreme. Plants and animals were mixed together into one system, based exclusively upon a few types of characters considered by GAMS to be more »epharmonic» than all others. In the first place he put the degree of spatial stability and the way in which the organism is fastened to its substrate. He thus divided all animals and plants into 1) the adnate type or Ephaptomenon, 2) the radicant type or Rhizumenon, 3) the errant type or Planomenon. As the adnate and errant types contained only animals, cryptogams and phanerogamic hydrophytes, we are here only concerned with the radicant type. The further division of this type was made by GAMS mainly according to the system of RAUNKIAER, but the main principle of RAUNKIAER was followed with extreme consistency much further than in RAUNKIAER's own system. Thus the therophytes of RAUNKIAER were united with the geophytes by GAMS, because the seed of a therophyte survives the unfavourable season in the same subterraneous way as the bud of the geophyte, and the difference between buds and seeds is held by GAMS to be »organographic», not epharmonic (GAMS 1918 p. 326). Epiphytes and succulent-stemmed phanerophytes were not admitted as separate life-forms, and RAUNKIAER's subdivision of the phanerophytes was not accepted. Another important novelty was that mosses and lichens, as far as they belonged to »the radicant type», were included into the chamaephytes. The further division of GAMS' »radicant type» or »Rhizumenon» was as follows:

- | | |
|--|-----------------------------------|
| A. Überdauerungsorgane hoch über dem Boden | 8. Kl. Phanerophyten |
| a) völlig selbstständig
(Baumförmige oder Dendrodea, Strauchförmige oder Thamnodea und die »Krautluftpflanzen« inkl. Stamsukkulanten umfassend) | Unterkl. Stammpflanzen (Hylemata) |
| b) stützbedürftig | Unterkl. Holzlianen |
| c) mehr oder wenig parasitisch | Unterkl. Holzparasiten |
| B. Überdauerungsorgane wenig über dem Boden | 9. Kl. Chamaephyten |
| a) Wasseraufnahme vorwiegend oberirdisch | Unterkl. Bryochamaephyten |
| b) Wasseraufnahme ober- und unterirdisch | Unterkl. Polsterpflanzen |
| c) Wasseraufnahme vorwiegend unterirdisch | Unterkl. Euchamaephyten |
| C. Überdauerungsorgane an der Bodenfläche | 10. Kl. Hemikryptophyten |
| a) Laubblätter schmalspreitig | Unterkl. Poiodca |
| b) Laubblätter breitspreitig | |
| c) nur Rosettenblätter | Unterkl. Basiphylla (Rosetten) |

$\beta)$ nur Stengelblätter	Unterkl. Thrysophylla
$\gamma)$ Rosetten und Stengelblätter	Unterkl. Basithrysophylla
D. Überdauerungsorgane im Boden (Kryptophyta)	
a) Vegetative Organe ständig im Wasser	11. Kl. Hydrokryptophyta
b) Vegetative Organe amphibisch	13. Kl. Amphikryptophyta
c) Vegetative Organe nur ausnahmsweise im Wasser (Geophyta)	
a') autotroph (inkl. Hemisaprophyten und Hemiparasiten)	
$\alpha)$ Bodenruhe aus andern Gründen als	
Wassermangel	13. Kl. Eugeophyta
$\beta)$ Bodenruhe aus Wassermangel	14. Kl. Xerogeophyta
b') heterotroph	13. Kl. Heterogeophyta
$\alpha)$ saprophytisch	Unterkl. Saprogeophyta
$\beta)$ parasitisch	Unterkl. Parageophyta

In 1920, a new critical revision of the life-form problem was presented in F. E. CLEMENTS' great work »Plant Indicators». After a short historical summary, CLEMENTS restored the old term »vegetation-form», since »the most useful and consistent view of life-form is obtained from a single point of view, that of vegetation. The development and structure of vegetation are chiefly a matter of dominants and subdominants, and it is the life-forms shown by these which are of paramount importance. Hence it becomes desirable to speak of them as vegetation-forms, as DRUDE did originally, following GRISEBACH and HUMBOLDT.» (CLEMENTS 1920 p. 62). The term »growth-form», on the other hand, was reserved by CLEMENTS for »the immediate quantitative response made by a plant to different habitats or conditions» (p. 68). The following system of vegetation-forms was proposed by CLEMENTS (p. 63):

- | | |
|-----------------------------|-----------------------|
| I. 1. Annuals. | 9. Carpet-herbs. |
| II. 2. Biennials. | 10. Succulents. |
| III. Herbaceous perennials. | IV. Woody perennials. |
| 3. Sod-grasses. | 11. Halfshrubs. |
| 4. Bunch-grasses. | 12. Bushes. |
| 5. Bush-herbs. | 13. Succulents. |
| 6. Cushion-herbs. | 14. Shrubs. |
| 7. Mat-herbs. | 15. Trees. |
| 8. Rosette-herbs. | |

5. The Modern Period of Re-established Purely Physiognomic Life-form Systems (1921–1930).

The reaction against the onesided epharmonic point of view in the study and classification of life-forms was brought to its climax in 1921, in the present author's work »Zur methodologischen Grundlage der modernen Pflanzensoziologie». In this work, the life-form systems in earlier literature were critically reviewed, and a new life-form system on a purely physiognomic basis proposed. While the authors initiating this reaction in the previous period (DRUDE, WARMING, etc.), had remained on their old »Neolamarckian» (or better »Nägelian») basis, and kept their belief in the fundamental difference between »indifferent» and »ephar-

monic» characters (»Organisationsmerkmale» and »Anpassungsmerkmale» of NÄGELI), this distinction was now stated to be »purely hypothetical» (DU RIETZ 1921 pp. 56, 82, 83, etc.) and consequently abandoned. The consequence of this abandonment was that any life-form concept founded upon that distinction had to be rejected, and that the claim was raised that the »Grundformen» should be founded upon a purely physiognomic point of view, without any attempt to a subjective valuation of the characters, *i.e.* that ecology should return to the old point of view held by HUMBOLDT, KERNER, GRISEBACH, and HULT. The author strongly emphasized the fundamental difference between these »Grundformen» and the epharmonic life-forms, to which the term »Lebensformen» was restricted: »Im Gegensatz zum Grundformbegriff ruht also der Lebensformbegriff auf einer Reihe von Hypothesen und steht und fällt wie alle aufgestellten Lebensformssysteme mit diesen» (l.c. p. 83). The main causes to the »epharmonic convergence» were sought for not in »adaptation» but in the »homologous mutations» of E. BAUR (1919 pp. 293—294, comp. DU RIETZ 1921 p. 13), *i.e.* in what is now generally known as »VAVILOV's law of homologous variation» (VAVILOV 1922, PHILIPSCHEK 1926 pp. 63—81, SEYBOLD 1927, TROLL 1928 pp. 90—91, HALL 1928 p. 8, DU RIETZ 1930 b pp. 346 and 412), but a certain rôle of natural selection in the process of »Grundformen»-differentiation was also admitted (DU RIETZ 1921 p. 14). Like KERNER (1863), the author found it necessary to avoid the old ambiguous vernacular names, as »trees», »shrubs», etc., in a scientific system of »Grundformen», and to replace them by »rein wissenschaftlicher, internationaler Fachausdrücke, die nicht durch eine frühere Anwendung in verschiedenen Bedeutungen kompromittiert sind» (l.c. p. 130). In the system worked out by the author (pp. 131—132), the names of the »Grundformen» were formed as much as possible in accordance with the »ecologic-physiognomic» system of formations (= isocoenoses according to the author's present terminology) published by BROCKMANN-JEROSCH and RÜBEL in 1912 — a work forming one of the first important steps towards the general rehabilitation of the physiognomic point of view in modern ecology. As it proved impracticable to make all these names as short and handy as desirable, they were substituted in the ordinary sociological practice with short formulae. The system proposed had no claim of being applicable outside Scandinavia, though the author expressed the hope that it would have a certain applicability also in other parts of Northern and Middle Europe. It had the following composition (DU RIETZ 1921 pp. 131—132):

»A. Gefäßpflanzen.

I. Ligniden (Holzpflanzen). Überirdische Stammteile hauptsächlich verholzt.

- a) Magnoligniden, m (Bäume). Grosse, nicht kletternde Holzpflanzen von einer Höhe von über 2 m, in den meisten Fällen mit einem deutlichen Hauptstamm.
 - 1. Deciduimagnoligniden, md (Fallaubbäume). Laub in der ungünstigen Jahreszeit abfallend.
 - 2. Aciculimagnoligniden, ma (Nadelbäume). Immergrüne, nadelförmige Blätter.
 - 3. Laurimagnoligniden, ml (Lorbeerlaubbäume). Immergrüne, nicht nadelförmige Blätter.
- b) Parvoligniden, p (Sträucher). Kleinere, nicht kletternde Holzpflanzen von einer niedrigeren Höhe als 2 m, aber höher als 0,8 m, in den meisten Fällen mit mehreren stark verzweigten Hauptstämmen.

4. Deciduiparvoligniden, pd (Fallaubsträucher). Laub in der ungünstigen Jahreszeit abfallend.

5. Aciculiparvoligniden, Na (Nadelsträucher). Immergrüne, nadelförmige Blätter.

6. Lauriparvoligniden, pl (Lorbeerlaubsträucher). Immergrüne, nicht nadelförmige Blätter.

c) (7). Nanoligniden, n (Zwergsträucher). Kleine, nicht kletternde, Holzpflanzen von einer Höhe unter 0,8 m).

d) (8). Lianen, li. Kletternde Holzpflanzen von verschiedener Höhe.

II. Herbiden (Kräuterpflanzen). Überirdische Stammteile hauptsächlich unverholzt.

a) Terriherbiden (Landkrautpflanzen). Assimilationssystem hauptsächlich in die Luft hinausragend.

9. Euherbiden, h (Kräuter). Spross nicht vom Grastypus.

10. Graminiden, g (Gräser). Spross vom Grastypus.

b) Aquiherbiden (Wasserkrautpflanzen). Assimilationssystem hauptsächlich unter Wasser lebend oder auf der Wasserfläche schwimmend.

11. Nymphaeiden, ny (Schwimmblattppflanzen). Im Boden wurzelnde Pflanzen mit Schwimmblättern.

12. Elodeiden, e. Im Boden wurzelnde, mit ihren vegetativen Teilen völlig untergetauchten Pflanzen ohne Schwimmblätter, mit langen, flutenden Sprossen.

13. Isoetiden, i. Im Boden wurzelnde, mit ihren vegetativen Teilen völlig untergetauchte Rosettenpflanzen ohne Schwimmblätter.

14. Lemniden, le. Freischwimmende Pflanzen mit kurzen Sprossen.

B. Moose (Bryiden).

15. Eubryiden, b. Laub- (exkl. *Sphagnum*) und Lebermoose.

16. Sphagniden, s. Torfmoose (*Sphagnum*).

C. (17). Flechten (Licheniden, l).

D. (18). Algen.

E. (19). Pilze.»

Like the old physiognomical systems of HUMBOLDT, KERNER, GRISEBACH, HULT, etc., this system had no claims at all of being »epharmonic» or of expressing the »plant climate» or any other relation of the plants to the environment. It was a purely physiognomic system claiming only to express the main physiognomic types clearly recognizable in the Scandinavian flora, and to provide the elementary units necessary for the study of the physiognomy of vegetation and for the establishment of physiognomic vegetation-units or »formations» (= »isocoenoses» according to the present terminology of the author).

During the last decade, this system has been in general use in Swedish plant sociology (comp. DU RIETZ 1923 a, b, 1924, 1925 a, b, c, 1930 a, DU RIETZ and NANNFELDT 1925, OSVALD 1923, 1925, 1929, SERNANDER 1925 a, b, LARSSON 1929, and BOOBERG 1930). It has also been used by single plant sociologists in several other European countries, namely in Finland (WARÉN 1926), Estland (VILBERG 1927, 1929), Russia (KATZ 1926, 1927, 1929), Germany (HUECK 1925, KAISER 1926, 1930), Czechoslovakia (RUDOLPH, FIRBAS and SIGMOND 1928), Austria (VIERHAPPER 1925, HUBER 1927, ZUMPF 1929), and Hungary (RAPAICS 1923, von Soó 1927 a, b). It seems at any rate to have been of some use for the practical grouping of the species in analyse-lists from plant sociations, and for giving some impression of the physiognomy of the various species in such analyse-lists as well as of the plant sociation as a whole.

An interesting new life-form system for herbaceous plants was proposed in

1922 by K. LINKOLA. It was the result of a thorough investigation of the hibernation of weeds in southern Finland, and was based upon »die Verschiedenheit, die für jede Pflanzenart zwischen ihrer winterlichen Tracht und Gestalt und der gewöhnlichen Sommerform eines voll entwickelten Individuums besteht» (LINKOLA 1922 p. 103). The various life-forms were defined and named as follows (l.c. pp. 103—104):

- »I. Pflanzenarten, die nur als Samen überwintern: Samenüberwinterer.
- II. Pflanzenarten, welche die winterliche Jahreszeit mittelst mehr oder minder geschlossenen Knospen, auf Stengel- oder Wurzelbildungen in der Erde oder ganz an der Erdoberfläche aufsitzend, überdauern: Knospenüberwinterer.
- Die Knospenüberwinterer werden hauptsächlich nach der Lage ihrer Erneuerungsknospen in zwei Hauptabteilungen eingeteilt:
 - A. Knospenüberwinterer, deren Erneuerungsknospen in der Regel mehr oder weniger tief in der Erde liegen: Knospenüberwinterer mit Erdknospen.
 - B. Knospenüberwinterer, bei denen die Erneuerungsknospen beinahe oder ganz an der Erdoberfläche überwintern: Knospenüberwinterer mit Erdshürfeknospen.
- III. Pflanzenarten, bei denen ein an der Erdoberfläche befindlicher, mehr oder minder offener und wintergrüner Rosettenspross als oberirdischer Pflanzenteil überwintert: Rosettenüberwinterer.
- IV. Pflanzenarten, an welchen wintergrüne, niederliegende und gestrecktgliedrige Sprosse, deren winterliche Form von der sommerlichen mehr oder weniger bedeutend abweicht, überwintern: Kriechsprossüberwinterer.
- V. Pflanzenarten, die im Winter ganz oder ziemlich dasselbe Aussehen haben wie im Sommer, die meisten sogar, oft oder ausnahmsweise, in vollem Floralstadium auftretend: in Sommertracht überwinternde Pflanzen.»

In 1923, the long series of life-form works published by WARMING was crowned with a comprehensive monograph of the life-forms of plants (»Ökologiens Grundformer»), in which his life-form system was thoroughly revised and worked out in greater detail than in any of his earlier contributions. The definitive life-form system of WARMING published in this work contained the following main units:

- A. Autotrophs.
- I. Water-plants; Hydatophytes (7 classes, which are left out here).
- II. Aërial plants; Aërophytes.
 - a. Autonomous.
 - 1. Epiphytoids. Aërial water absorbed by the assimilators the only or the main source of water (*Epiphytes*, *Epilithes*).
 - α. Water absorbed by the whole surface of the assimilators. Classe 8. *Atmophytes*.
 - β. Water, mainly rain-water, absorbed by roots or other special, limited parts of the plant-body, or partly stored in various ways. Classe 9. *Ombrophytes*.
 - 2. Chtonophytes. Terrestrial water absorbed by roots from the soil.
 - α. Plants from various reasons prevented to absorb much water.
 - 1) Plants growing on a physically dry, hard substrate (rock, tree-trunks), or on any other substrate difficult for the roots to penetrate, or on any other soil permanently poor in water. Classe 10. *Chlylophytes*.
 - 2) Plants growing on more or less porous and wet, but physiologically dry soil: salt-soil. Classe 11. *Halophytes*.
 - β. Plants growing on ordinary porous soil with fresh-water or air between the mineral particles, not physiologically dry and not, except at certain seasons, physically dry.

1) Herbs (*Herbae, pl. herbaceae*).

- a) More or less broad-leaved (not grass-like) herbs. Classe 12. *Agrophytes*.
- b) Graminoid herbs; leaves long, narrow, with parallel nerves.

Classe 13. *Pooids*.

2) Plants with ligneous stems (ligneous plants, lignoses and sublignoses).

Classe 14. *Xyloids*.

- b. Not autonomous. Herbs or lignoses needing support for ascending into the air, up into the light. Soil similar to that of the agrophytes. Classe 15. *Klinophytes*.

B. Allotrophs.

- I. Nourishment dead organic substances.
- II. Nourishment taken from living organisms.

Classe 16. *Saprophytes*.Classe 17. *Parasites*.

As is easily seen from this scheme, this new system differs from the older ones by the extensive use made of physiological points of view. It is really a sort of a compromise between WARMING's old growth-form system with the system of »oecological classes» used in his »Oecology of Plants» (WARMING 1909 p. 136), or the »habitat-forms» of CLEMENTS (1920 pp. 64—65). On the other hand, the adoption of the distinction between agrophytes and pooids means the inclusion also of the purely physiognomic point of view into the system.

Each of the 17 main classes is divided by WARMING into several subordinate groups, in many cases even into a great number of subordinate groups of several stages. Of special interest is the following system of the various main types of agrophytes (pp. 152—166).

I. Hapaxanthic herbs.

- A. Summer-annuals (monoecytic).
- B. Winter-annuals (dicyclic).
- C. Biennials (dicyclic).
- D. Polyennials (pleiocyclic).

II. Pollacanthic, non-crassipedic herbs without travelling shoots.

- A. Semipervirent (subtypes with long-shoots, rosette-shoots, or semirosette-shoots).
- B. Semivirent (» » » » » » » »).
- C. With sealed winter-buds (the same subtypes as in A and B).
- D. Cushion-plants.

III. Crassipedic types with xylopodia, i.e. thick, lignified mesocorms.

IV. Crassipedic types with sarcopodia, i.e. fleshy mesocorms.

A. With tubers.

1. With permanent tubers.
 - a. With aerial tubers.
 - b. With subterranean tubers.
2. With tubers forming short-lived nutritive reservoirs.
 - a. With root-tubers.
 - b. With stem-tubers.

B. Bulb plants.

1. With sympodial perennial bulbs.
2. With monopodial perennial bulbs.
3. With annual bulbs.

V. Pollacanthic herbs with supraterreneous travelling shoots, and mostly thin mesocorm.

- A. With prostrate shoots (not rooting).
- B. With curved (ascending) shoots rooting at the base.
- C. With aerial runners (stolons) from an erect assimilator. (Subtypes with long-shoots, rosette-shoots, or semirosette-shoots, sometimes of »flagella»-type.)

- D. Creeping herbs (*herbae repentes* with creeping shoots only).
 - 1. With unlimited creeping shoots.
 - 2. With limited creeping shoots.
 - 3. With sealed winter-buds.
- VI. Pollacanthic herbs with slender subterraneous travelling shoots having long internodes.
 - A. With foliage-leaved travelling shoots. (Bladstauder, Blattstauden).
 - 1. With travelling shoots carrying only foliage-leaves.
 - 2. Both foliage-leaves and scales.
 - B. With only scaly travelling shoots.
 - 1. Without special nutritive reservoirs on the travelling shoots.
 - a. With travelling shoots irregularly branched, i.e. not branched from special leaf axils (suboles).
 - b. With travelling shoots regularly branched from certain main buds, situated in the axil of a certain leaf (rhizodes).
 - 2. With special nutritive reservoirs on the travelling shoots.
- VII. Pollacanthic herbs with thick, fleshy subterraneous travelling shoots having short internodes and being plagiotropic (rhizomes).
 - A. With rhizomes carrying long-shoots.
 - B. With rhizomes carrying Musa-shoots.

In the system of the xyloïds (or *planta lignosae*, pp. 169—178) the most important feature is the new division into sublignoses (half-lignoses) and per-lignoses (whole-lignoses).

During this period, RAUNKIAER's life-form system and life-form-statistical method have become more and more widely spread not only in Denmark, where they have been in general use ever since the publication of RAUNKIAER's first life-form papers, but also in other countries, and at present RAUNKIAER's system certainly is the most widely accepted of all life-form systems. The continued study of the percentage of RAUNKIAER's main life-forms in whole regions and in special plant-communities have led to interesting results especially in tropical and subtropical countries, where matters have been found to be much more complicated than was expressed by the first scheme of RAUNKIAER (comp. above p. 13). While RAUNKIAER's »therophyte-climate spectrum» has been found to recur not only in the Transcaspian desert region (PAULSEN 1912) and the lowland belt of the Canary Islands (BÖRGESEN 1924), but also in the Australian desert (OOLDEA, ADAMSON and OSBORN 1922), very different spectra were found by ADAMSON and OSBORN (1924, comp. also OSBORN 1925) as well as by WOOD (1929, 1930) in the less arid parts of South Australia, indicating that the very high percentage of therophytes found in arid subtropical winter-rain regions is not characteristic for subtropical winter-rain regions with a higher rainfall and a more closed vegetation, such regions being far more characterized by a high percentage of nanophanerophytes and to some extent of chamaephytes also (comp. also ADAMSON 1927). And while moist tropical countries certainly are characterized by a high percentage of phanerophytes, as stated by RAUNKIAER, BÖRGESEN (1924) and HAGERUP (1930) showed that in very dry tropical areas there may be found a spectrum with a much higher percentage of chamaephytes than of any other life-form.

Also RAUNKIAER's leaf-size classes have been used by several authors for the characterization of vegetation physiognomy and for the study of its correlation with the climate, and have proved very useful for both purposes (comp. COOPER 1922, BÖRGESEN 1924, 1929, ADAMSON 1927). COOPER, however, did not find the delimitation of RAUNKIAER's leaf-size classes very suitable, and found it necessary to add one transition-class between the nanophylls and the microphylls as well as another one between the microphylls and the mesophylls (l.c. pp. 93—94).

An important contribution to the criticism of RAUNKIAER's »chamaephyte-climate» has been given by R. NORDHAGEN (1928, p. 594—599). Already in 1913 J. BRAUN(-BLANQUET) had pointed out »dass die Bewohnbarkeit der klimatischen Stufen der Alpen (alpine, hochalpine und nivale Stufe) für Pflanzen wohl weniger von deren Anpassung an die ungünstige (Winter) als an die giinstige Jahreszeit abhängt» (BRAUN 1913 p. 38), and applied the same point of view also to the »arctic chamaephyte-climate» of RAUNKIAER (l.c. p. 39). On the basis of his studies of the high alpine vegetation of Norway NORDHAGEN comes to similar results, and especially emphasizes the very good protection offered by the snow to high-alpine plants in winter, except in localities exposed to strong wind. He thoroughly discusses the problem of RAUNKIAER's arctic and high-alpine chamaephyte-climate, and comes to the result that this problem is still forming an open question, but that in any case chamaephytes plant-communities do not appear to increase in importance with increasing altitude.

A modification of RAUNKIAER's life-form system was published in 1926 by A. HAYEK, differing mainly in the subdivision of the phanerophytes, in which the old types »trees», »shrubs» and »dwarf-shrubs» were substituted for RAUNKIAER's mega-, meso-, mikro-, and nanophanerophytes. HAYEK also opposed the use of the occurrence or non-occurrence of bud-scales for the sub-division of phanerophytes in RAUNKIAER's system, stating that this was an »Organisationsmerkmal» which only secondarily had got an ecological importance (p. 102).

A more radical modification of RAUNKIAER's life-form system was presented in 1928 by J. BRAUN-BLANQUET, who had made extensive use of RAUNKIAER's main life-forms in several previous plant-sociological papers (comp. for instance BRAUN-BLANQUET 1915, 1918, 1926, BRAUN-BLANQUET and MAIRE 1924). Only slight alterations were made in the main units of RAUNKIAER, but their subdivision was radically changed, and new terms (in German and Latin) created for many of the subordinate units. The following units were distinguished, described, and illustrated by examples:

- I. Phyto-Plankton (mikroskopische Schwebepflanzen).
- II. Phyto-Edaphon (mikroskopische Bodenflora).
- III. Endophyten (Innenpflanzen).
- IV. Therophyten (Einjährige).
 - a. Thallotherophyten.
 - b. Bryotherophyten.
 - c. Pteridotherophyten.
 - d. Eutherophyten.
- V. Hydropthyten (Wasserpflanzen).
- VI. Geophyten (Erdpflanzen).

1. Pilzgeophyten (*Geophyta mycetosa*).
 2. Wurzelschmarotzer (*Geophyta parasitica*).
 3. Eugeophyten.
 - a. Knollengeophyten (*Geophyta bulbosa*).
 - b. Rhizomgeophyten (*Geophyta rhizomata*).
 - c. Wurzelknospengeophyten (*Geophyta radicigemma*).
- VII. Hemikryptophyten (Erdschürfepflanzen).
1. Thallushafter (*Hemikryptophyta thallosa*).
(Haftalgen, Krustenflechten und Thalloide Moose.)
 2. Wurzelnde Hemikryptophyten (*Hemicryptophyta radicantia*).
 - a. Horstpflanzen (*Hemicryptophyta caespitosa*).
 - b. Rosettenpflanzen (*Hemicryptophyta rosulata*).
 - c. Schaftpflanzen (*Hemicryptophyta scaposa*).
 - d. Klimmpflanzen (*Hemicryptophyta scandentia*).
- VIII. Chamaephyten (Oberflächenpflanzen).
- a. Deckenmoose (*Bryochamaephyta reptantia*).
 - b. Strauchflechten (*Chamaephyta lichenosa*).
 - c. Kriechstauden (*Chamaephyta reptantia*).
 - d. Blattsukkulanten (*Chamaephyta succulenta*).
 - e. Polsterpflanzen (*Chamaephyta pulvinata*).
 - f. Bültenmoose (*Chamaephyta sphagnoidea*).
 - g. Hartgräser (*Chamaephyta graminidea*).
 - h. Spaliersträucher (*Chamaephyta velantia*).
 - i. Halbsträucher (*Chamaephyta suffrutescentia*).
- IX. Phanerophyten (Luftpflanzen).
- a. Sträucher (*Nanophanerophyta*).
 - b. Bäume (*Makrophanerophyta*).
 - c. Stammsukkulanten (*Phanerophyta succulenta*).
 - d. Krautstämme (*Phanerophyta herbacea*).
 - e. Lianen (*Phanerophyta scandentia*).
- X. Epiphyta arboreola (Baumepiphyten).

The »Lebensform»-concept was defined by BRAUN-BLANQUET (p. 247) as »Lebewesen deren Gesamtbau mehr oder weniger deutlich ausgeprägte gleichartige Anpassungserscheinungen an den Lebenshaushalt aufweist». But BRAUN-BLANQUET also emphasized that »genotypisch verankerte Anpassungen können in der Vergangenheit, vielleicht unter von den heutigen völlig verschiedenen Bedingungen, selektiv entstanden sein». And he continued: »Aus ihrem Vorkommen unter bestimmten klimatischen oder edaphischen Verhältnissen dürfen wir wohl schliessen, dass sie sich mit denselben in Einklang befinden, nicht aber, dass sie ihnen auch ihre Entstehung verdanken. Unsere Lebensformen können demnach nicht als eine eindeutige Antwort der Lebewesen auf die herrschenden Außenbedingungen betrachtet werden, sondern sie stellen die durch den Standort bedingte Ausformung der mehr oder weniger fest geprägten phylogenetischen Grundlage der Pflanze dar.» (BRAUN-BLANQUET 1928 pp. 257—258).

In British ecology of the last decade the life-form problem has been discussed especially by TANSLEY (1923 pp. 197—199) and TANSLEY and CHIPP (1926 pp. 11, 19—24). The »vegetation-form» system of CLEMENTS (1920 comp. above p. 29) is characterized as »simple, and practical, though not sufficient for all purposes» (TANSLEY and CHIPP p. 20), while the life-form system of RAUNKIAER is mentioned

as »one of the most useful and important classifications of the life-forms of vascular plants» (l.c. p. 21). According to TANSLEY and CHIPP »the independent student of evolution will do well, however, to make his own classification of the life-forms of the communities he actually studies» (p. 20). The life-form concept is defined as »the characteristic vegetative form of a species» (l.c. p. 11). Like CLEMENTS, TANSLEY and CHIPP lay strong emphasis upon the sociological point of view in the study of life-forms: »It must be remembered, however, that since vegetation is primarily determined by dominant species, it is the life-forms of these which are by far the most important in characterising vegetation, and, therefore, in addition to the 'spectrum' of life-forms worked out for all species of a regional flora or of a plant community, the life forms of the dominants of the various grades of communities should be stated separately. It is also useful to note the life-forms of the species which show the higher degrees of frequency and the higher degrees of constancy» (l.c. pp. 23—24).

A thorough, manysided, and in many respects original treatment of life-forms is found in the long series of monographs of New Zealand vegetation published by L. COCKAYNE during the last three decades. Though only a part of them belong to the last period of life-form history, they form together such a continuous piece of work that it seems most practical to deal with them here as one entity. The life-forms or growth-forms of COCKAYNE — who uses these two terms as synonyms — are (at least practically) based upon a purely physiognomic point of view, and already in 1908 he expressed grave doubts as to the validity of the current theories of the fundamental rôle of »adaptations» for the composition of vegetation: »In fact, the composition of the forests depends far more upon the history of the vegetation — *i.e.*, upon the plants which by chance came to settle down on the new ground — than upon any special adaptations these may have possessed». (COCKAYNE 1908 a p. 16.) In most of his special vegetation monographs (comp. for instance COCKAYNE 1907 a, 1908 b, 1909 a, 1927 b, 1928 a, COCKAYNE and FOWERAKER 1916), he described the life-form of each species in a special column in the flora-list, without using any fixed system of life-forms. In his general monograph of New Zealand vegetation (1921, 1928 b), he gave statistical data of the life-form composition for the three main parts of New Zealand vegetation distinguished by himself (coastal, lowland, and high mountain vegetation), using a comparatively fixed system of life-forms (comp. COCKAYNE 1919 pp. 17—20, 1927 a pp. 23—27, ALLAN 1928 p. 7), named by himself in a very significant way. Four main classes of life-forms were used: 1. Trees. 2. Shrubs. 3. Herbs and semiwoody plants. 4. Lianes, epiphytes, and parasites. The method of treatment is most easily shown by some examples:

In the 87 species of trees belonging to the lowland vegetation, the distribution of life-forms was stated to be as follows: »Tuft-trees 10 (tree-ferns 7), canopy-trees 34, bushy-trees 26, fastigiate tree 1, araliad-form 5, leafless juncoid 5, rhododendron-form 6». (COCKAYNE 1928 b p. 128.) But it was also mentioned that of these 87 species »4 are very tall, 7 tall, 14 of medium height and 62 of low stature, but at least 39 are epharmonically shrubs and in some 10 cases it is a matter of opinion merely whether they should be classed as such or as trees; nearly all are evergreen, only 7 species being deciduous or semi-deciduous; perhaps 9 may be considered semi-xerophytes» (l.c.). And a special statistics was given for the leaves of the same 87 species of trees: »evergreen 70,

deciduous or semi-deciduous 7, compound 19, simple 63, broad 67, narrow 15, very large 10, large 12, medium-sized 29, small 17, very small 14, leafless except in juvenile 5, thin 34, coriaceous 48, glabrous 62, hairy 20 (tomentose beneath 8), waxy beneath 6, glossy 20» (l.c. p. 131).¹ — In the same way the shrubs were divided into bushy-shrubs, divaricating-shrubs, straggling shrubs, switch-shrubs, etc., and separate statistics were given for their life-forms and for their leaves etc. Also the other life-form classes were treated in an analogous way.

A method similar to that of COCKAYNE was used by SKOTTSBERG in a lecture on the plant-communities of Juan Fernandez, presented before the International Congress of Plant Sciences at Ithaca 1926 (printed in 1929). Like COCKAYNE, SKOTTSBERG wanted a purely physiognomic system of life-forms enabling him to make his descriptions of exotic plant-communities as enjoyable as possible also for readers quite unfamiliar with the flora concerned. He found that while the life-form system of DRUDE »pays too much attention to purely organographic details and cannot serve our purpose», that of RAUNKIAER does not either »express all that we would like to have expressed» (p. 565). And he proposed that »it might be more convenient to put off the making of such all-comprising classification and to start with separate systems for separate regions, to use, wherever possible, well-established and generally accepted terms which are understood far and wide, and to make special types for special needs, as few as possible and as many as necessary» (l.c.). For the vegetation of Juan Fernandez he proposed the following system (pp. 567—568):

- I. Trees.
 - A. Larger (Palm, Magnolia, Urticoid, Myrtoid, Vaccinoid, Xanthoxylon, and Coronilla forms).
 - B. Dwarfed (Urticoid form).
 - C. Rosette (Cordylinoid, Palmoid, Brassicoid, Draeacnoid, and Crassuloid forms).
- II. Shrubs.
 - A. Larger (Bamboo, Berberis, and Vaccinoid forms).
 - B. Dwarfed (Urticoid, Vaccinoid, and Ericoid forms).
 - C. Trailing (Convolvuloid and Vaccinoid forms).
 - D. Parasitic (Loranthus forms).
- III. Herbs.
 - A. Foliose erect (various forms).
 - B. Arboriform (Gunnera form).
 - C. Rosulate (Aloe form).
 - D. Aphyllous succulent (Salicornia form).
 - E. Trailing.
 - F. Cushion (Azorella form).
- IV. Grasses.
 - A. Soft tufted.
 - B. Hard tufted (Stipa form).
 - C. Rush form.
 - D. Iris form.

¹ The leaf-size classes used by COCKAYNE were defined as follows (1928 b p. 69): »very large = 20 cm long; large = 10—20 cm long; medium = 5—10 cm long; small = 2,5—5 cm long; very small = less than 2,5 cm. For all the sizes breadth proportional to length is understood, so that the length is decreased or increased according to increase or decrease of the 'normal breadth'. What is aimed at is to get a relative idea of the area of the transpiring surface. Evidently these estimates possess no real exactitude, but, as they are estimated in a uniform manner and by one person, they may serve for purposes of comparison, and no more is claimed than this.»

These life-forms were combined with the leaf-size classes of RAUNKIAER in a comparative table of the whole flora as well as in special analyses of plant-communities. A similar system was proposed also for the ferns.

A rather original, simple, and useful life-form system is found in the many papers on Russian steppe- and desert-vegetation published by B. KELLER (comp. especially KELLER 1923, 1925, 1927, and 1930). It contains the following main types (according to KELLER 1930), used by KELLER as a basis for the delimitation of his »Genossenschaften» or »Convictiones», *i.e.* synusiae in the sense of GAMS 1918 and DU RIETZ 1930 a:

1. Bäume.
2. Große Sträucher.
3. Zwerghalbsträucher und -Sträucher.
4. Mehrjährige Kräuter.
 - a. Dikotylen-Stauden.
 - b. Gräser und Riedgräser.
5. Einjährige Sommer- und Herbstpflanzen.
6. Frühlings- und Herbst-Frühlings-Ephemere (»Ein ausgeprägter Ruhestand im Sommer. Die Pflanzen verbleiben als Samen und teils als Zwiebeln.« KELLER 1925 p. 122).
7. Niedere Pflanzen auf dem Boden (Moose, Flechten, und Algen).

In his introduction to the volume »Pflanzengeographische Ökologie» in ABDERHALDEN's »Handbuch der biologischen Arbeitsmethoden» (1928), DRUDE presented the following new edition of his life-form system, containing several new terms (*e.g.* Xylochamaephytes, Podochamaephytes, etc.) and minor modifications, but based upon the same physiognomic principles as his system of 1913 (DRUDE 1928 pp. 43—47):

- I. Terrestrische, epilithische und epiphytische Aërophyten.
 - A. Autotroph und frei für sich bestehende Holzgewächse.
 - a. Holzgewächse der Monokotyledonen.
 1. Schopfbäume.
 2. Rohrstammgebüsche mit Ausläuferwurzelstock.
 3. Niederstämmige Grossblatthüsche.
 4. Baumgräser.
 - b. Holzgewächse der Gymnospermen und Archegoniaten.
 5. Baumfarne und Cycadeen.
 6. Nadelholzbäume und Sträucher.
 - c. Reich beblätterte Holzgewächse der Dikotyledonen.
 7. Wipfel- oder Kronenbäume.
 8. Stelzwurzler, Banyanen, Mangroven.
 9. Dauerlaub-Schopfbäume.
 10. Grossträucher und Büsche.
 11. Federbuschgehölze. (Strauchform zu Klasse 9).
 - d. Xeromorphe Sträucher und microphylle Zwerggesträuche.
 12. Blattarme Dornsträucher und Rutengehölze.
 13. Zwergsträucher, Kriech- und Spaliergehölze.
 - B. Winder, Klimmer und Ranker.
 14. Palmlianen.
 15. Holzlianen der Dikotylen.
 16. Smilaceen-Lianen.
 17. Redivive und annuelle Weichstammlianen, Klimmer und Ranker.

- C. Epiphyten, autotroph oder parasitisch lebend, auch Felswurzler.
 - 18. Kletterwurzel-Epiphyten.
 - 19. Knollenstamm-Epiphyten.
 - 20. Nest-Epiphyten.
 - 21. Grossblattrossetten der Monokotyledonen.
 - 22. Stamm-parasiten und Hemiparasiten.
- D. Chylophyten, xeromorphe Succulenten.
 - 23. Stamm-succulenten, Tonnen- und Fleichstämme.
 - 24. Blattsucculenten.
- E. Grasartige Gewächse der Monokotyledonen.
 - 25. Poioïden (Gräser, Riedgräser, Seggen mit beblätterten Halmen).
 - 26. Scirpoïden und Juncoiden (vieljährig sprossende, blattlose Schäfte mit Blattschopf und Spirren treibende Simsen und Binsen).
- F. Autotrophe, seltener saprophytisch-parasitisch lebende, 2 bis ∞ Jahre ausdauernde Kräuter der Monokotylen, Dikotylen und Archegoniaten.
 - a. Perenn, d. h. oberirdisch, ausdauernd, Dauerstauden.
 - 27. Xylochamaeophyten, Holzstauden und Halbsträucher.
 - 28. Podochamaeophyten, Horststauden auf holzigem Wurzelkopf, der alljährlich neu sprosst.
 - 29. Polsterstauden.
 - 30. Kriechstauden.
 - 31. Rosettenstauden.
 - b. Rediviv, d. h. unterirdisch ausdauernd und aus Kraftknospen Neutriebe entwickelnd.
 - 32. Geophyten.
- G. Therophyten.
 - 33. Halophile Chylophyten.
 - 34. Ephemere und annuelle Dikotylen.
- H. Bryophyten (3 Gruppen).
- J. Lichenen (3 Gruppen).
- K. Myceten.
- II. Limnische, fluviatile und ozeanische Hydrophyten (5 Gruppen).

The most recent life-form system is that published by RÜBEL in his »Pflanzengesellschaften der Erde» (1930). In his review of earlier systems, RÜBEL makes some linguistic corrections in BRAUN-BLANQUET's system (BRAUN-BLANQUET's »Geophyta rhizomata» should be »Geophyta rhizomatosa», his »Geophyta radicigemma» »Geophyta radicigemmata» etc.), and emphasizes the bad delimitation of RAUNKIAER's chamaephytes »nach oben und unten»: »Viele Arten, wie die erikoiden Reiser, sind dadurch zugleich Chamaephyten und Phanerophyten, da sie bei jener 20 cm Bodenhöhe durchaus keine massgebende Lebensformgrenze besitzen» (RÜBEL 1930 pp. 30—31). He considers his own system »ein weiteres Ausbau» of RAUNKIAER's system (p. 30), and attempts »im übrigen den Versuch von DU RIETZ, die skandinavischen Lebensformen in Übereinstimmung mit BROCKMANN-JEROSCH's und RÜBEL's Formationsgruppen, auszubauen» (p. 31). According to RÜBEL, it »ergibt sich dabei, dass sie sich im allgemeinen recht gut mit dem RAUNKIAERSchen System parallelisieren» (p. 31). The result is the following system:

»Magniligniden, Bäume.

Pluviomagniligniden, Immergrüne Bäume ohne Knospenschutz, Ombromakrophanerophyten.

Laurimagniligniden, Immergrüne Bäume mit Knospenschutz und Lorbeerblatt, Daphnomakrophanerophyten.

Durimagniligniden, Immergrüne Bäume mit Knospenschutz und Hartlaubblatt, Skleromakrophanerophyten.

Aestimagniligniden, Laubwechselnde Bäume mit Knospenschutz und Sommerblatt, Theromakrophanerophyten.

Hiemimagniligniden, Laubwechselnde Bäume mit Knospenschutz und regengrünem Blatt, Cheimomakrophanerophyten.

Aciculimagniligniden, Bäume mit Nadelblatt, Belonidomakrophanerophyten.

Parviviligniden, Sträucher.

Pluviiparviviligniden, Immergrüne Sträucher ohne Knospenschutz, Ombromikrophanerophyten.

Lauriparviviligniden, Immergrüne Sträucher mit Knospenschutz und Lorbeerblatt, Daphnomikrophanerophyten.

Duriparviviligniden, Immergrüne Sträucher mit Knospenschutz und Hartlaubblatt, Skleromikrophanerophyten.

Ericiparviviligniden, Immergrüne Sträucher mit Knospenschutz und erikoidem Blatt, Ericomikrophanerophyten (inkl. Spaliersträucher).

Aestiparviviligniden, Laubwechselnde Sträucher mit Knospenschutz und Sommerblatt, Theromikrophanerophyten.

Hiemiparviviligniden, Laubwechselnde Sträucher mit Knospenschutz und regengrünem Blatt Cheimomikrophanerophyten.

Aciculiparviviligniden, Sträucher mit Nadelblatt, Belonidomikrophanerophyten.

Semiligniden, Halbsträucher (Halbstrauch-Chamaephyten auct.), inkl. *Stipa tenacissima* usw.

Sukkulanten.

Epiphyten.

Jianen.

Herbiden.

Duriherbiden, Hartgräser und -kräuter mit Sommer- und Winterruhe, Sklerohemikryptophyten.

Sempervirentiherbiden, Immergrüne Gräser und Kräuter, Aeiblastohemikryptophyten und -chamaephyten.

Incruste Sempervirentiherbiden, Immergrüne Erdkrustenpflanzen, Aeiblastohemikryptophyten.

Supraeruste Sempervirentiherbiden, Immergrüne Oberflächenpflanzen, Aeiblastochamaephyten (inkl. Bryo- und Lichenochamaephyten).

Aestivirentiherbiden, Laubwechselnde Gräser und Kräuter, Tropohemikryptophyten.

Altherbiden, Hochstauden, Makrostelecho-Hemikryptophyten.

Sphagniherbiden, Torfmoose, Sphagnophyten.

Soliherbiden, Erdpflanzen, Geophyten.

Emersiherbiden, Sumpfpflanzen, Helophyten.

Sübmersiherbiden, Wasserpflanzen, Hydrophyten.

Aestiherbiden, Sommerpflanzen, Therophyten.

Saxiden, Stein- (und Holz)-Überzüge.

Extrasaxiden, Exolitho- (und xylo-)phyten.

Intrasaxiden, Endolitho- (und xylo-)phyten.

Errantiden, Schweber.

Aquerrantiden, Wasserschweber, Planktophyten.

Solerrantiden, Erdschweber, Edaphophyten.»

CHAPTER II.

A Revision of the Classification of Life-forms.

1. General Principles.

From the historical review presented above it is easily seen that there is still very little agreement between ecologists regarding the general theory of life-forms as well as their practical delimitation and classification. While some authors accept the principle that life-forms should be founded only upon »epharmonic characters», other authors claim that physiognomic characters should be used as they are without any attempt to such a subjective valuation. That no agreement in the practical life-form systems can be attained between these two opposite schools, is not astonishing — but even authors agreeing completely in this fundamental question very rarely agree in their practical delimitation and classification of life-forms. Characters taken as basis for the whole system by one author, are degraded by other authors to a quite subordinate rank, and vice versa. And at present the attaining of one stable and generally accepted system of life-forms certainly seems to be as far off as ever.

As to the fundamental problem whether the delimitation and classification of life-forms should be based only upon »epharmonic characters» or upon the physiognomy as a whole without any such valuation of characters, it must be said that the latter view has steadily won ground during the last two decades. In view of the strong movement towards a more inductive method that has characterized the development of sociological ecology during the last two decades (comp. DU RIETZ 1921), it seems only natural to claim that such important units as life-forms should be founded simply upon the characters observed by us, and not upon what we believe about the probable origin of these characters. For anybody used to the inductive methodic of modern sociological ecology it must also be quite clear that *only life-forms delimited independently of any adaptation theory can be of any use at all as units for the inductive study of the adaptation problem and of the actual correlation between life-form and environment*. This claim appears to be equally well founded whether we believe in any theory of »direct adaptation» or not. In the systems presented below, therefore no attempt is made to distinguish between »epharmonic» and »indifferent» characters. The

fundamental problem whether such a distinction can be upheld or not will not be taken up to discussion in this chapter. First when the correlation between the environment and the life-forms established on an inductive basis has been studied in some detail, the time will have come to consider that problem as well as the great problem of adaptation as a whole. An attempt to this will be made in the last chapter of this treatise.

If the degree of »epharmacy» is rejected as the fundamental principle in the delimitation and classification of life-forms, the question arises according to which principles the relative importance of the various characters should then be decided. It is often extremely difficult to decide which of two characters is most important for the physiognomy of vegetation, and there is little hope that agreement will ever be attained among ecologists in this respect. While some authors will use the size, duration, and mode of branching of the stem as the main basis for the life-form system, others will be more inclined to put the size, form and duration of the leaves in the foreground, and still others will insist that the primary division should be based upon none of these points of view, but upon the way in which the plant survives the unfavourable season. The only way out of these difficulties appears to be that of admitting not one single life-form system but several parallel ones, based upon different points of view, *i.e.* to accept the principle of the »dynamic system» developed by HAYATA (1921 a, b, 1928 a, b, c, comp. DU RIETZ 1930 b pp. 405—414) in idiobiological taxonomy. Attempts in this direction have already been made by several authors (especially by OSTENFELD 1908 and RAUNKIAER 1916, comp. above pp. 13 and 27). In this chapter an attempt is made to draw the full consequences of this principle for the delimitation and classification of life-forms in flowering plants.

The term »life-form» is used by me in this treatise in the widest sense possible, *i.e.* as a general designation for any class of plants based upon any other point of view than those of idiobiological taxonomy. I fully realize that the application of HAYATA's »dynamic system» in idiobiological taxonomy may gradually smooth out the difference between life-forms and taxonomical units, but at present the life-form definition given above seems to be sufficiently clear.

The application of this wide life-form concept implies the use of the term life-form for many categories in present-day biology which have not previously been designated by this term. There is thus no reason why we should not extend the life-form concept also to the various classes of plants established in pollination ecology (anemophiles, entomophiles, etc.), dispersal ecology (hydrochores, anemochores, zoothores, etc.), habitat ecology (the »oecological classes» of WARMING 1909 or »habitat-forms» of CLEMENTS 1920, *e.g.* oxylophytes, psychrophytes, halophytes, etc.), and physiology. In this treatise, however, we shall only deal with life-forms having an obvious importance for the characterization of vegetation physiognomy, *i.e.* life-forms in the traditional narrower sense of ecological literature. For the main purpose of the present work, namely the characterization of vegetation-physiognomy and the study of its correlation with the environment, it appears convenient to distinguish the following main types of such life-forms, and to deal with each of these types separately.

1. Main life-forms (»Grundformen«). The term »main life-form« is used here in the same sense as »Grundform« in my work of 1921 (comp. above p. 30), *i.e.* as a designation for types based upon the general physiognomy of the plants during the height of their annual vegetation-period, without regard to any details in their morphological structure or to their way of perduring the unfavourable seasons. The main life-form system thus corresponds not only to the »Grundformen«-system of DU RIETZ 1921, but also to the »Grundformen«-systems of KERNER, NORRLIN, and HULT (comp. above pp. 2—4), and to some extent also to that of DRUDE 1913 (comp. above p. 21) as well as to the life-form (or growth-form) systems of COCKAYNE (comp. above p. 37) and of SKOTTSBERG 1929 (comp. above p. 38). It is the main life-form of the plants that primarily determines the general physiognomy of vegetation.

2. Growth-forms. I herewith propose to restrict the term »growth-form« to life-forms based primarily upon shoot-architecture, *i.e.* to the sense in which it was first introduced by WARMING in 1909 (comp. above p. 16). The term »vegetation-form« introduced for the same concept by CLEMENTS in 1920 (comp. above p. 29) seems to be less suitable, since it may easily give the wrong impression of a sociological unit, instead of an idiobiological one.

3. Periodicity life-forms. With this term I propose to designate the life-forms based primarily upon the vegetative periodicity of the plants, *i.e.* the differences between their physiognomy in the different seasons, and the seasonal distribution of their vegetation- and resting periods. This point of view has been more or less utilized in most life-form systems of earlier literature, probably to the greatest extent in those of MASSART, JESWIET, and LINCOLA (comp. above pp. 18 and 32).

4. Bud-height life-forms. This term is used here for life-forms in the sense of RAUNKIAER, *i.e.* life-forms based upon the height above (or below) the ground-level of the uppermost buds perduring the most unfavourable seasons.

5. Bud-type life-forms. With this term I designate the life-forms based entirely upon the structure of the buds perduring the most unfavourable seasons.

6. Leaf life-forms. With this term I designate the life-forms entirely based upon the character (form, size, duration, structure, etc.) of the leaves. Leaf-type systems have been established by several authors (DRUDE 1905, WARMING 1908, RAUNKIAER 1916, SEYBOLD 1927, comp. above p. 11, 16, 27), but only RAUNKIAER seems to have used such systems as the basis of a real leaf life-form system, *i.e.* to have based the classification of the whole plants upon the characters of the leaves.

Of course it would be both possible and useful to establish a root life-form system in the same way as the systems based upon the stem and the leaves. Our present knowledge of the root-systems of plants, however, does not seem to be sufficient for the establishment of such a system, and therefore no attempt in this direction will be made here. As to the various types of root-systems,

on which such a system should be based, comp. especially SHANTZ 1911, KEARNEY, BRIGGS, SHANTZ etc. 1914, WEAVER 1919 and 1920, KORSMO 1930, KELLER 1930, etc.

2. The Main Life-form System.

As was mentioned above, the main life-form system is meant to express only the general physiognomy of the plants during the height of their annual vegetation-period. It seems most convenient to follow the old »Grundformen»-systems in choosing the well-established types »trees», »shrubs», »dwarf-shrubs», »herbaceous plants» etc. to the main units in this system, and to base the subdivision of these main units upon the height of the plants in the vegetation-period. In the following system this subdivision according to the height is based primarily upon the actual stratification of vegetation (comp. DU RIETZ 1921 pp. 133—134, 1930 a pp. 386—390). For the subdivision of the life-forms of the tree-stratum (or tree strata) the same height-limits have been used as in RAUNKIAER's life-form system. Since the main life-form system is meant to be generally used not only by professional botanists but also by general geographic travellers, foresters, etc., the names have been made as simple as possible. They have been chosen according to the same principles as those applied by SHANTZ (in SHANTZ and MARBUT 1923) and CHIPP (in TANSLEY and CHIPP 1926) in their general accounts of African vegetation.

- A. Woody plants or Holoxyles (»ligneous plants», »lignoses» of many earlier authors, »Ligniden» DU RIETZ 1921, »Xyloïds» WARMING 1923). All assimilating shoots with a more or less lignified, perennial stem (except the floral shoots in species with leafy floral short shoots of only one summer's duration).
- I. Trees. Holoxyles with a distinct main trunk remaining unbranched in its lower part. No hypogeous branching except in some tuft-trees with suboles (comp. below p. 55).
 - 1. High trees (or megaphanerophytic trees¹). Height more than 30 m.
 - 2. Tall trees (or mesophanerophytic trees). Height between 8 and 30 m.
 - 3. Low trees (or microphanerophytic trees). Height between 2 and 8 m.
 - 4. Dwarf trees (or nanophanerophytic trees²). Height between 0,8 and 2 m.
 - 5. Pygmy trees³ (or chamaephytic² trees). Height below 0,8 m.

¹ Comp. the life-form system of RAUNKIAER quoted above in p. 12.

² In RAUNKIAER's system the limit between nanophanerophytes and chamaephytes is drawn at 2,5 dm, RAUNKIAER's nanophanerophytes thus including not only true shrubs but also tall dwarf-shrubs. I find it more convenient to draw this line at the same height as the traditional limit between shrub-layer and field-layer, or between shrubs and dwarf-shrubs, i.e. at 8 dm.

³ LINDMAN 1914 (comp. above p. 22).

II. Shrubs. Holoxyles higher than 0,8 m not developing a distinct main trunk, with the stem branched from its basal part above or below the soil surface¹.

a. Chtonophytic, *i.e.* growing on the ground (WARMING 1923 p. 135, comp. above p. 32).

1. Very high shrubs (or mesophanerophytic shrubs). Height above 8 m.

2. High shrubs (or microphanerophytic shrubs). Height between 2 and 8 m.

3. Ordinary shrubs (or nanophanerophytic shrubs). Height between 0,8 and 2 m. In some cases it may be convenient to divide this type into »tall shrubs» (1,2—2 m) and »low shrubs» (0,8—1,2 m).

b. Epiphytoidic, *i.e.* growing on other trees or shrubs, but not parasitic, or on rocks etc. (WARMING 1923 p. 135, comp. above p. 32).

c. Parasitic on trunks and branches of other trees or shrubs.

III. Dwarf-shrubs. Holoxyles lower than 0,8 m with more or less shrubby ramification, not forming cushions. In my previous works I united the pygmy trees with the dwarf-shrubs under the name of »Nanoligniden» (DU RIETZ 1921 p. 121, comp. above p. 31), a course that has not proved quite convenient in the praxis.

a. Chtonophytic.

1. Tall dwarf-shrubs (or macrochamaephytic² dwarf-shrubs). Height between 0,25 and 0,8 m.

2. Low dwarf-shrubs (or mesochamaephytic² dwarf-shrubs). Height between 0,05 and 0,25 m.

3. Very low dwarf-shrubs (or microchamaephytic² dwarf-shrubs). Height less than 0,05 m.

b. Epiphytoidic.

c. Parasitic on trunks or branches of trees, shrubs, or other dwarf-shrubs.

IV. Woody cushion-plants. Holoxyles with all branches very tightly packed together into more or less compact »cushions».

V. Woody lianes. Holoxyles of various height and various type of ramification, climbing on the trunks and branches of trees, shrubs, rocks, etc.

B. Half-shrubs, or Hemixyles (semi-woody plants, »Semiligniden» RÜBEL 1930). Only the lower parts of the (epigeous) stem lignified and perennial, the upper parts annual and herbaceous.

I. Tall half-shrubs. Total height (including the annual branches) more than 0,8 m.

II. Dwarf half-shrubs. Total height (including the annual branches) less than 0,8 m.

¹ This shrub-concept corresponds to the wide shrub-concept of WARMING (comp. above p. 24) and most other botanists, not to the narrow one of LINDBMAN (comp. above).

² The extension of the chamaephyte-concept made above (p. 45) makes it necessary to subdivide the chamaephytes into three subordinate types: macro-, meso-, and microchamaephytes. Of these only the two last ones belong to the chamaephytes in the original sense of RAUNKIAER.

C. Herbaceous plants (»Herbiden« DU RIETZ 1921), *i.e.* herbs and grasses.
Overground stems wholly herbaceous.

I. Chtonophytic, non-lianoid.

- a. High herbaceous plants (high herbs and high grasses). Height more than 2 m.¹
- b. Tall herbaceous plants (tall herbs and tall grasses). Height between 0,8 and 2 m.²
- c. Medium herbaceous plants (medium herbs and medium grasses). Height between 0,25 and 0,8 m.
- d. Low herbaceous plants (low herbs and low grasses). Height less than 0,25 m.

II. Epiphytidic.

III. Parasitic on trunks or branches of trees, shrubs, or dwarf-shrubs.

IV. Herbaceous lianes.

3. The Growth-form System.

a. The Main Stem-types in Flowering-plants.

There are probably not many branches of modern botany in which such real chaos prevails in terminology as in the morphology of the stem, and especially the underground stem, of flowering plants. While many authors, especially taxonomists, are using the term »rhizome» for practically every underground stem except tubers and bulbs — sometimes also for some creeping overground stems —, or at least for every plagiotropic underground stem, other authors want to restrict this term to a certain class of underground stems, differently delimited by different authors. Similar conditions are found in the use of the term »stolon». Any attempt to establish a system of growth-forms appears to be of little use if it is not based upon a clear, logical, and scientifically well-founded terminology of stem-types, and before a comparative stability is reached in this terminology, there is little hope that stability will be reached in any growth-form system. I therefore find it necessary to start this discussion of the growth-form system with the following attempt to a system of stem-types. Since the system of underground stem types proposed by WARMING (1918 b, 1923, comp. above pp. 25—26)

¹ The limit between »high grass» and »tall grass» is put to 5 feet by SHANTZ (1923) and CHIPP (1926). It seems, however, more convenient to use the same limit as that between high and tall shrubs (comp. above), *i.e.* the limit between the tree- and shrub-layers according to HULT (1881), and between microphanerophytes and nanophanerophytes according to RAUNKIAER, or 2 m.

² The lower limit for »tall grass» is put to 3 feet by SHANTZ (1923) and CHIPP (1926), and to 2 feet by CLEMENTS (1920). COCKAYNE (1928 b p. 70) uses the following division: very tall (over 90 cm), tall (60—90 cm), medium (30—60 cm), low (15—30 cm), and very low (less than 15 cm). The lower limit of »tall» proposed here will probably be considered too high by many ecologists of temperate countries, but appears to be necessary if tropical vegetation is included. It is considerably lower than the limit used by SHANTZ and CHIPP in Africa, and implies a compromise between the demands of the tropical and the temperate workers.

appears to be the only system in modern literature that is worked out in any detail, and since very few, if any, botanists are likely to have had a field-experience of the problem concerned equal to that of WARMING, I have attempted to follow it as closely as possible, in spite of the fact that the very restricted use of the term »rhizome» proposed by WARMING probably will meet some opposition among contemporary botanists.

A. Geocorms. This new term (from γῆ, the earth, and κορμός, a stem), is herewith proposed as a short and handy designation for any hypogeous stem. The lack of such a term appears to have been at least one of the main reasons why so many botanists have felt inclined to use the term »rhizome» in the very wide sense mentioned above. WARMING (1923 p. 131) has used the term »geoblast» in the same sense. When only the stem is concerned, however, »corm» (*cormus*) appears to be a more adequate designation than »blast» (*blastus*), which refers to the whole shoot, including the leaves. As to the term »*cormus*» as a general designation of the stem of vascular plants comp. BISCHOFF 1833 p. 125.

I. *Plagiogeocorms*, or plagiotropic geocorms.

a. Primary plagiogeocorms. I propose this new term to designate those plagiogeocorms which are hypogeous from the first stage of their existence, i.e. which have not become hypogeous only by secondary burial of epigeous stems.

1. Rhizomes. »Underground plagiotropic stems with short internodes, usually thick and rich in nutritive matter, and often with only few and weak roots. Epigeous shoots proceed from them sometimes as lateral shoots (the rhizome is a monopodium), or usually by the terminal bud bending upwards, emerging into the air and developing foliage-leaves (the rhizome becomes a sympodium). The ramification is often rather scarce, and restricted to certain leaf-axils with a »power-bud» in the curve. This is often not much thicker than the rest of the rhizome. Many rhizomes are developed directly by the primary axis (e.g. in *Anemone nemorosa*, Fig. 13 in WARMING 1884: 67, *Polygonatum*, etc.), and this is certainly the most common type, but there are also rhizomes developed by the lateral shoots on the seedling (e.g. in *Scrophularia nodosa*, Fig. 12 in WARMING 1884: 65). The life of the rhizomes lasts — contrary to that of the suboles — often many years» (WARMING 1918 b p. 300 comp. also WARMING 1918 a pp. 549—550, 1918 b p. 367, 1919 p. 435, 1923 pp. 132, 165—166).

α. True, or scaly, rhizomes, carrying only scales. They may be divided into monopodial and sympodial rhizomes (comp. WARMING l.c.).

β. Leafy rhizomes, carrying either both scales and foliage-leaves, or only foliage-leaves (WARMING 1918 a pp. 545—547, 1918 b p. 299, 368, 1923 pp. 132, 163—164).

2. Rhizodes. Underground plagiotropic stems with elongated internodes, slender but with a regular architecture similar to that of the rhizomes: »sympodial structure (rarely monopodial, e.g. in *Paris*), with an often very fixed number of internodes in each division of the sympodium and one main bud in the axis of a numerically fixed leaf. There is also often developed a whole series of shoot-generations in the same vegetation-period, which, however, is also found in rhizomes, e.g. in *Asparagus officinalis*, species of *Scirpus* and *Juncus*, *Nardus stricta*, *Lygeum spartum*, etc. Also here it is often the primary shoot that develops directly into the hypogeous stem.» (WARMING 1918 b p. 302, comp. also WARMING 1918 a p. 549, 1918 b p. 367, 1919 p. 435, 1923 pp. 132, 163—165, 169).
- α. True, or scaly rhizodes. Like the rhizomes, these may be divided into one monopodial and one sympodial type, the former of which, however, is very rare (comp. above).
- β. Leafy rhizodes (WARMING 1918 b p. 368).
3. Subole-geocorms, or hypogeous stems formed by suboles (Danish »jordudlöbere») in the sense of WARMING, i.e. underground plagiotropic shoots with elongated internodes, slender, rooting, and with irregular ramification (WARMING 1918 a p. 548, 1918 b pp. 298, 367, 1919 p. 434, 1923 pp. 132, 163). »They are probably never produced by direct transformation of the primary shoot, but are shoots of a second and higher order.» (WARMING 1918 b p. 367). »In some cases, they terminate in a nutritive organ, which may be a stem-tuber, fleshy root or bulb; the hibernating buds are connected with this organ, the nourishment of which is used next spring, but the true migratory part of the shoot dies off sooner.» (WARMING 1918 b p. 367, comp. above p. 26).
- α. True, or scaly suboles. These may be divided into
- 1) Suboles without nutritive reservoirs (WARMING 1918 b pp. 305—337). These may be subdivided according to their longevity, some being so short-lived that the plant becomes »pseudo-annual» (WARMING 1918 a p. 542), and others being long-lived enough to become more or less completely lignified (WARMING 1918 b).
 - 2) Suboles with nutritive reservoirs (WARMING 1918 b pp. 337—349). These may be subdivided into one type with stem-tubers (the potato-type), one with fleshy roots, and one with bulbs (WARMING l.c.). All of them are usually very short-lived.
- β. Leafy suboles (WARMING 1918 a pp. 545—547, 1918 b pp. 299, 367—368).
- b. Secondary plagiogeocorms. This term is herewith proposed as a designation of primarily epigeous plagiotropic stems becoming hypogeous by secondary burial. Such secondary plagiogeocorms were mentioned

by H.J. NILSSON (1885 pp. 17—18, 92) as »accidental underground stems», but very little reference is found to them in more recent literature. According to my own experience they are regularly found in very many prostrate or stoloniferous herbs and dwarf-shrubs (comp. below pp. 61, 65, etc.).

- II. *Orthogeocorms*, i.e. orthotropic, or at least not distinctly plagiotropic, geocorms. It has recently been proposed by WARMING (1918 a p. 539, 1918 b pp. 302, 368, comp. above p. 26, 1919 pp. 430, 1920 p. 235, 1923 pp. 126—127, 152, etc.) to re-establish the old term *mesocormus* (Danish »Mellemtok») in this sense. It seems, however, more convenient to use the term »mesocorm» in a somewhat wider sense, namely, including also the epigeous stem-bases of longer duration than the ordinary assimilating and flowering shoots, i.e. the perduring basal part of a half-shrub, the long-lived basal trunk of a *Eucalyptus* of the »mallee-type (comp. below p. 58); etc. In this type a division into primary and secondary geocorms is not practicable, since most orthogeocorms are formed by the basal parts of more or less epigeous stems which are drawn into the soil by means of root contraction.
- a. *Leptoorthogeocorms*, or *leptopodia*, i.e. orthogeocorms not or only slightly incrassate. The leptopodia may be subdivided according to the degree of lignification into herbaceous and ligneous leptopodia, but owing to the very gradual transition between these two subtypes such a division seems to be of a rather doubtful practical value. More useful is probably a subdivision according to the ramification — analogous with the division of the plagiogeocorms applied above — into one irregularly ramified type (the »pseudorhizomes» or »stembasis-complexes» of H.J. NILSSON 1885 and ARESCHOUG 1896) and one not or only slightly ramified (the »rosette-stems» of NILSSON and ARESCHOUG l.c.). The latter type includes not only the monopodial orthogeocorms (growing with a terminal leaf-rosette), but also sympodial orthogeocorms with a regular architecture resembling that of the sympodial rhizomes, and developing only one bud in each year.
 - b. *Pachyorthogeocorms*, or *pachypodia*, i.e. orthogeocorms more or less incrassate.
 1. *Xylopodia* (LINDMAN 1900 pp. 109—11, 1914 DUSÉN and NEGER 1921, WARMING 1923 p. 157, comp. also WARMING 1892), or ligneous pachypodia.
 2. *Sarcopodia* (WARMING 1923 pp. 152, 157—160), or fleshy pachypodia.
 - α. Stem-tubers, consisting entirely or mainly of the incrassate orthogeocorm. They may be subdivided according to their longevity (comp. WARMING 1884, 1923 pp. 158—159), some being only short-lived nutritive reservoirs, and others permanent organs lasting for several years.
 - β. Bulbs, consisting of an only slightly incrassate orthogeocorm surrounded by fleshy scale-leaves. According to WARMING (1923

p. 160), they may be subdivided into sympodial perennial bulbs, monopodial perennial bulbs, and annual bulbs.

As to the morphology of stem-tubers and bulbs comp. besides the works of WARMING especially IRMISCH (1850, etc.). A transition between the typical sarcopodia and the plagiotropic geocorms is formed by the often plagiotropic stem-tubers and bulbs developed in the apices of suboles (comp. above p. 49, WARMING 1918 b pp. 337—349, RAUNKIAER 1907 figs. 65—69).

B. Aërocorms. This new term, formed in analogy with »geocorms», is herewith proposed as a designation of all epigeous stems.

I. *Herbaceous aërocorms.*

- a. Orthotropic herbaceous aërocorms, or herbaceous orthoaërocorms.
 - 1. Leafless (or at least without foliage-leaves): scapes (*scapi*).
 - 2. Leafy (*caules orthotropicae*).
- b. Plagiotropic herbaceous aërocorms (*caules plagiotropicae*), or herbaceous plagioaërocorms.
 - 1. Prostrate but not rooting.
 - 2. Creeping, i.e. prostrate and rooting: herbaceous stolons (*stolones*).

The term »stolons», often used in earlier botanical literature in a rather vague sense for all sorts of »runners», has recently been restricted by WARMING (1918 b pp. 299, 367, 1923 pp. 126, 161—162) to »plagiotropic overground rootforming shoots (runners) with elongated internodes, and, naturally, with foliage-leaves, sent out by orthotropic aerial shoots» (WARMING 1918 b p. 367, comp. above p. 25¹). Shoots of just the same type not sent out by orthotropic aerial shoots but forming the only assimilating shoots of the plant concerned (»creeping herbs, *herbae repentes*»), are not included into the stolon-concept of WARMING. The delimitation of this concept is thus based not upon the morphological character of the stolons themselves, but upon the occurrence or non-occurrence of orthotropic assimilating shoots in the plant concerned. This implies that a sympodial creeping stem should be called a stolon only if the orthotropic flowering shoots connected with it are leafy, but not if they are scapes without foliage-leaves. I am quite unable to find this a very natural or convenient delimitation of the stolon-concept, and I herewith propose to extend WARMING's stolon-concept to include all creeping epigeous stems, independently of the nature of the orthotropic shoots with which they may be connected.

The stolons may be subdivided into one sympodial and one monopodial type, and also according to the length of their internodes and the character of the leaves. These may be either ordinary foliage-leaves or more or less reduced, in extreme cases even into real-

¹ An earlier attempt to fix the term »stolon» in the same sense was made by HAUSSKNECHT (1884 p. 12).

scale-leaves. Such scaly stolons are probably always ended by a leaf-rosette. A peculiar type of stolons is the flagella, consisting of one single internodium ended by a leaf-rosette (*e.g.* in *Saxifraga flagellaris*, comp. WARMING 1884a pp. 52—53, fig. 6, 1923 p. 44) and *Androsace sarmentosa*, comp. GOEBEL 1923 p. 1473 fig. 1403.

II. *Ligneous aërocorms.*

- a. Orthotropic ligneous aërocorms, or ligneous orthoaërocorms.
A special subtypes of this type in the only partly lignified succulent stem (in the larger *Cactaceae* etc. comp. fig. 9).
- b. Plagiotropic ligneous aërocorms, or ligneous plagioaërocorms.
 - 1. Plagiotropic crown-branches.
 - 2. Prostrate but not rooting.
 - 3. Creeping (*i.e.* prostrate and rooting): ligneous stolons.

b. Growth-forms on the Basis of Stem-types and Stem-type Combinations.

In the following system of growth-forms I have followed WARMING as far as possible, but the subdivision of the various groups has been worked out in more detail, and in several cases even the larger groups have been delimited and arranged in a different way. The main groups are the same as in the main life-form system presented above.

A. *Holoxyles.*¹

I. Trees.¹

a. Long-shoot Trees.

This type corresponds to the »canopy trees» of WARMING (1909 p. 11) and to the »Wipfelbäume» of REITER (1885) and DRUDE (1890—1928). The crown is built up mainly by long-shoots, *i.e.* shoots with elongated internodes of more or less equal length right from the base (comp. WARMING 1918b p. 368). As to the crown-architecture of long-shoot trees comp. ARESCHOUG 1877, 1888.

1. Euchtonophytic long-shoot trees. Germinating on the ground and living their whole life as chthonophytes (WARMING 1923, comp. above p. 32).

α. *Sedentary* (spot-bound). The ordinary type of trees.
β. *Stoloniferous*. An example of a tree travelling overground is furnished by *Picea excelsa* near its alpine and maritime limits (comp. for instance SCHRÖTER and KIRCHNER 1908, figs. 42 and 43, H. RESVOLL-HOLMSEN 1918 pp. 178—181, figs. 25—28). The lower branches descend to the ground and become prostrate and rooting, but sooner or later they produce new erect trunks, and in this way more or less dense groups of trees originating from a single parent tree are

¹ Comp. above p. 45.

formed (fig. 1). These trees are kept together by prostrate stems which may become more or less hypogeous by secondary burial, but if the parent tree dies, they may eventually become isolated from each other. At the maritime limit of the spruce in the archipelagos of the Baltic coast of Sweden I have found this to be the usual life-form of *Picea excelsa* (fig. 1).

γ. *Root-travelling.* Root-shoots are common in many tree-species. One of the best known examples is *Populus tremula* (eomp. SCHRÖTER and TOEPFFER 1927), in which vegetative propagation by root-shoots plays a rather prominent rôle.

2. *Hemiepiphytic long-shoot trees.* Germinating on the trunks or branches of other trees and beginning their life as epiphytes, but later on developing



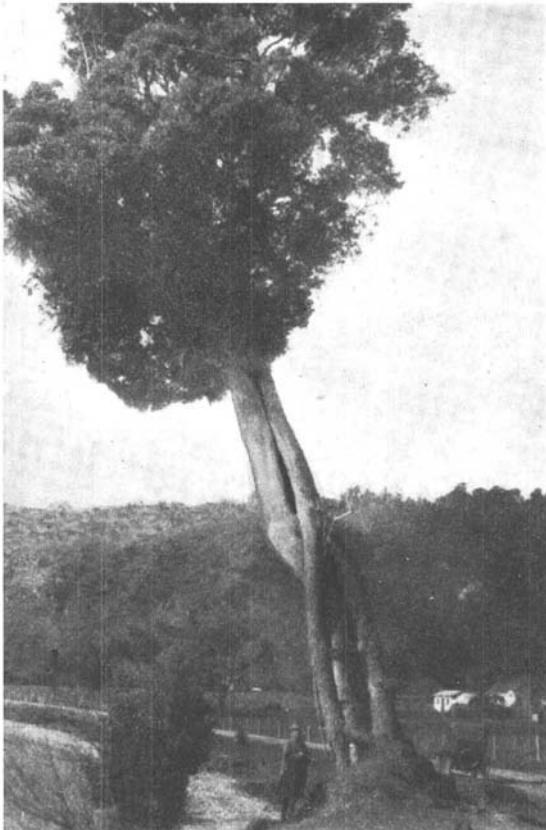
21. 6. 1918. Photo G. E. DU RIETZ.

Fig. 1. Small grove of low trees of *Picea excelsa* probably formed by a single individual. Eastern coast of Sweden, prov. Upland, Bodskär in the small archipelago of Björkskär, in the maritime birch-forest region (comp. DU RIETZ 1925 e).

descending roots which grow out into false trunks (»root-trunks» of COCKAYNE), often strangling the host-tree. The term »hemiepiphytes» was first introduced by SCHIMPER (1898 p. 340, comp. also 1888).

α. *Sedentary hemiepiphytic long-shoot trees.* Excellent examples of this type are furnished by the hemiepiphytic trees of the New Zealand rain-forest, all of which belong to the sedentary type (comp. KIRK 1872, 1889, CARSE 1902, COCKAYNE 1908 b, 1909 a, 1919, 1921, 1927 a, 1928 b, COCKAYNE and PHILLIPS TURNER 1928, POPE 1926, LAING and BLACKWELL 1927, OLIVER 1930, etc.). The most magnificent of these trees is *Metrosideros robusta*, usually germinating high up in the crowns of *Dacrydium cupressinum* or other tall rain-forest trees, and

ultimately, after strangling its host, growing out into one of the largest trees of the New Zealand forest (fig. 2, comp. also COCKAYNE 1908 b fig. 13, PHILLIPS TURNER 1909 p. 11, LAING and BLACKWELL 1927 fig. 101, OLIVER 1930 fig. 2). Only rarely it is to some extent horizontally travelling by means of aerial roots (comp. COCKAYNE 1907 b fig. 1, 1928 b fig. 28). Other New Zealand trees more or less regularly occurring as hemiepiphytes are *Weinmannia racemosa* (comp. COCKAYNE 1909 a fig. 10, 1921 fig. 26, 1928 b fig. 29), *W. sylvicola*, *Griselinia*



19. 5. 1927. Photo, GRETA DU RIETZ.

Fig. 2. Sedentary hemiepiphytic long-shoot tree in its hemiepiphytic stage: *Metrosideros robusta* strangling its host, *Laurelia novae-zelandiae*. New Zealand, North Island, Volcanic Plateau District, Southern shore of Lake Rotoiti.

littoralis (comp. COCKAYNE 1909 a fig. 12, 1919 fig. 30, 1921 fig. 22, 1927 a fig. 30, 1928 b fig. 26), *Nothopanax arboreum* and *N. Edgerleyi* (figs. in PHILLIPS TURNER 1909), etc. — Another well-known example of a sedentary hemiepiphytic tree is the West-Indian *Clusia rosea*, described in detail by SCHIMPER (1888 p. 56—60).

β. *Aerial root travelling hemiepiphytes*. This type corresponds to the »Banyanenform« of GRISEBACH 1872, or the »Stelzwurzler« of DRUDE 1913 and 1928. The best examples of this type are some tropical species of *Ficus* [*F. bengalensis* L., *F. retusa* L. (= *F. Benjaminia* Willd.), etc.], frequently pictured in



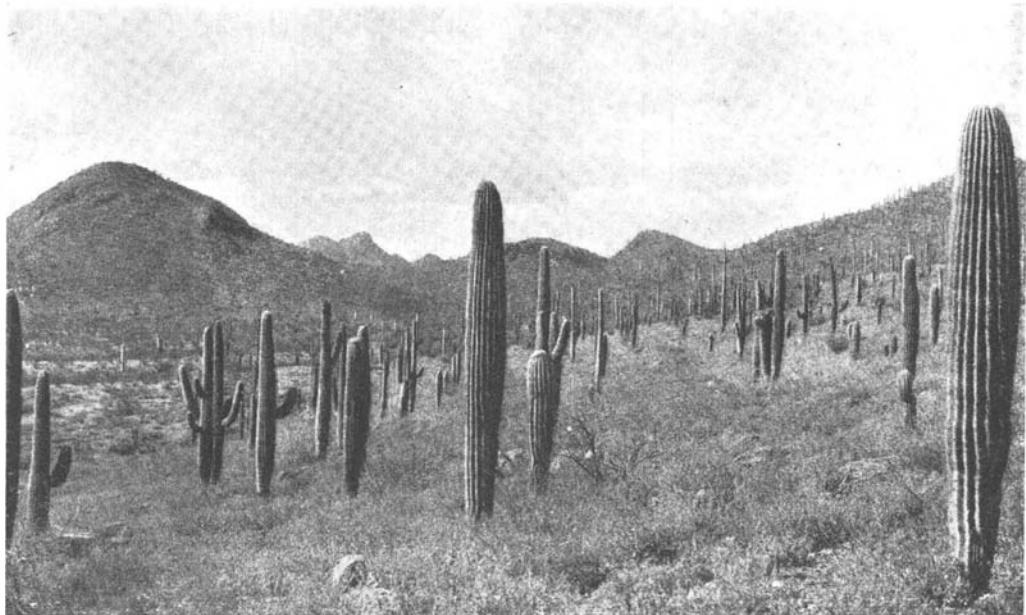
16. 9. 1927. Photo, GRETA DU RIETZ.

Fig. 3. Simple rosette tree: *Kingia australis*. In the background ordinary long-shoot trees of *Eucalyptus calophylla* (marri). Western Australia, Wongong near Perth.

a well developed crown resembling that of a long-shoot tree. Well-known examples are found in the *Liliaceae* (*Dracaena*, *Yucca*, *Cordyline*, *Aloë*, etc.), the *Velloziaceae* (comp. WARMING-GRAEBNER 1914–18 fig. 82), the *Pandanaceae* (*Pandanus*), the *Epacridaceae* [e.g. *Dracophyllum Traversii* (fig. 5, comp. also COCKAYNE and PHILLIPS TURNER 1928 fig. 114, OLIVER 1928 b fig. 22), *D. longifolium* (fig. 6), *D. recurvatum* (comp. OLIVER 1928 b fig. 23, which illustrates the mode of branching very clearly), etc.], the *Lobeliaceae* (e.g. some of the »Giant Lobelias» of Tropical Africa, comp. R. E. and TH. C. E. FRIES 1922 b fig. 4), the *Compositae* [most species of *Dendroseris*, *Robinsonia*, etc. (comp. SKOTTSBERG 1914 p. 60, 1921, 1929), several species of »Giant Senecio» in Tropical Africa (comp. R. E. and TH. C. E. FRIES 1922 a figs. 1—5), etc.]. Transitions between this type and the ordinary long-shoot trees are often found (comp. SKOTTSBERG 1914 p. 61, WARMING 1923 p. 174).

c. Leafless Succulent-stemmed Trees.

To this type belong many species of *Cactaceae* (fig. 9) and *Euphorbia*. Examples are easily found in botanical literature. As in the rosette-trees several types may be distinguished, from the completely unbranched type to types with a well developed crown.



From a post-card.

Fig. 9. Leafless succulent-stemmed trees: *Carnegiea gigantea* (Engelm.) Britt. & Rose.
U.S.A., Arizona, Tucson, on the road to San Xavier Mission.

II. Shrubs.¹

a. Chthonophytic² shrubs.

1. Long-shoot shrubs. This type is analogous to that of the long-shoot trees. To it belongs the vast majority of all shrubs.

α. Erect long-shoot shrubs. All trunks erect, not prostrate even in their basal parts.

1) Aëroxylic erect long-shoot shrubs. Without hypogeous ramification (root-shoots excepted), but divided above the soil-surface into several erect trunks. To this type belong many of the »shrub-trees» of LINDMAN (1914). Many species normally developed into trees may assume this life-form when growing near their climatic limits, or when the main trunk has been killed for some reason, e.g. *Betula alba* in the subalpine and maritime regions of Scandinavia (fig. 7, comp. also SYLVEÅN 1904, HAGLUND 1905, RESVOLL-HOLMSEN 1918, NORDHAGEN 1923 and 1927, etc.), *Sorbus aucuparia*, *Alnus glutinosa*, *Salix caprea*, *Prunus padus*, etc. (comp. LINDMAN 1914 pp. 241—242). There are also species normally developed into aëroxylic erect shrubs with a distinct differentiation of the aërocorm into one long-lived basal part — *i.e.* an epigeous mesocorm — and several more short-lived trunks arising from it. This epigeous mesocorm may be more or less incrassate; an extremely incrassate type is that of the giant *Myrmecodia* of the New Guinea mountains (comp. LAM 1924 Tab. 37 and 38, 1929 fig. 47). — The aëroxylic erect long-shoot shrubs may be subdivided into one sedentary type — to which all the species mentioned above belong — and one root-travelling type. To the latter belong, among others, *Prunus spinosa* (LINDMAN 1914 pp. 251—252, WARMING 1916 p. 107) and *Hippophaë rhamnoides* (WARMING 1907 pp. 150—155, figs. 101 and 102, 1916 p. 32, fig. 23, 1923 p. 178, PALMGREN 1912, LINDMAN 1914 pp. 252—253, etc.). Both these species form very dense thickets by means of root-shoots. Both may belong to the semi-prostrate type in some cases.

2) Geoxylic erect long-shoot shrubs. With a well developed hypogeous mesocorm — *i.e.* an orthogeocorm, often a xylopodium — from which the aerial trunks arise. To this type belong most of LINDMAN's (1914) »true shrubs» or »geoxyles» (the »microgeoxyles» excepted). Well-known examples from the North-European flora are the species of *Rosa* (figs. 8 and 10), *Berberis vulgaris*, and *Corylus avellana* (all of them pictured by LINDMAN 1914, comp. also BLOMQUIST 1911 and as to *Corylus* PALMGREN 1915 pp. 102—104). Also the bamboos must be mentioned in this connection. Probably also most desert-shrubs must be referred to this type, *e.g.* the »creosote bush» [*Schroeterella glutinosa* (Engelm.) Briquet (comp. BRIQUET 1925, = *Covillea glutinosa* Rydb.)] of the south-western United States (comp. SHANTZ and PIEMEISEL 1925 Tab. 4), and the »Mallee»-Eucalypts of arid Australia. While the hypogeous mesocorm of the creosote bush appears to be rather thin, that of the mallees is an enor-

¹ Comp. above p. 46.

² Comp. above p. 32.



3. 3. 1927. Photo, W. R. B. OLIVER.

Fig. 12. Semi-prostrate long-shoot shrubs and rosette-shrub: *Olearia Colensoi*, *O. Crosby-Smithiana* (with white flowers), *Senecio elevagnifolius*, *Coprosma* spp., *Nothopanax Colensoi*, etc. (long-shoot shrubs), and *Dracophyllum fiordense* W. R. B. Oliv. (rosette-shrub, near the right margin). New Zealand, South Island, Fiord District, southwestern slope of Mt. Barber, subalpine belt.

β. *Semi-prostrate long-shoot shrubs.* Trunks prostrate in their basal parts, but ascending and terminating by erect branches. The term »semi-prostrate» is taken up here from COCKAYNE (1909 b p. 192). In some cases the primary trunk becomes prostrate (*e.g.* in *Metrosideros umbellata*, fig. 11), in others the prostrate trunks are formed by secondary branches. The prostrate trunks may be more or less rooting, and in some cases the primary root may be entirely replaced by such adventitious roots. In other cases, however, the primary root remains during the whole life of the plant, and secondary roots are of little importance. Since, however, these conditions are yet very little investigated, they cannot be used at present for the classification. Equally impracticable at the present state of our knowledge is a subdivision into aëroxylic and geoxylic semiprostrate shrubs. Certainly most semi-prostrate shrubs belong to the aëroxylic type; examples of the geoxylic type are *Viburnum opulus* (BLOMQUIST 1911 pp. 60—62, LINDMAN 1914 pp. 270—272, WARMING 1916 p. 117) and *Lonicera xylosteum* (BLOMQUIST 1911 pp. 63—64, LINDMAN 1914 pp. 272—274, WARMING 1916 p. 115). Suboliferous (*e.g.* *Lonicera xylosteum*, comp. WARMING 1923 p. 178) and root-travelling (*e.g.* *Viburnum opulus*, comp. SYLVÉN 1906 p. 63, LINDMAN 1914 p. 271, WARMING 1916 p. 117) types are found also among the semi-prostrate shrubs. — Contrary to the erect long-shoot shrubs, the semi-prostrate are of little moment in arid regions, but in subalpine and subarctic regions they are the dominant type of shrubs. The »Krummholz» of the Alps (*Pinus mughus* and *Alnus viridis*, comp. for instance SCHRÖTER 1908 fig. 105, RÜBEL 1912 figs. 19—21) is formed by typical semi-prostrate shrubs, as well as the *Salix*-scrub of Scandinavian mountains (comp. for instance DU RIETZ 1925 f tab. 22 a, NORDHAGEN 1927—28 figs. 93, 96, 97, 98, 103, 107, etc.), the *Juniperus*-scrub of various European mountains, Swedish coast-districts, etc., the *Pinus aristata*-scrub of the Rocky Mountains of Colorado (excellent pictures in POOL 1920), most of the subalpine scrub of New Zealand (fig. 12, comp. also COCKAYNE 1909 a fig. 27, 1927 a fig. 76, 1928 b figs. 54, 57, 73, etc.), and the scrub of most other subalpine regions of various latitudes. In very windy maritime districts many ordinary forest-trees are reduced to semi-prostrate shrubs, *e.g.* the *Quercus*- and *Tilia*-scrub of some South-Swedish coast-districts (comp. for instance FRÖDIN 1912 figs. 1, 2, and 6, DU RIETZ 1925 e fig. 7, 1925 f Tab. 15 b and 16, etc.) and the *Metrosideros umbellata*-»forest» of the Auckland Islands (fig. 11, comp. also COCKAYNE 1904 p. 244—247 and Tab. XIII, 1909 b p. 192—194, fig. 4, 1921 figs. 87, 89, 1928 b figs. 97 and 100). In the case last mentioned the shrubs are so high and the main trunk so distinct that the term »semi-prostrate tree» would possibly be more appropriate (COCKAYNE l.c.).

The semi-prostrate as well as the erect long-shoot shrubs may also be subdivided according to the mode of branching of the crown, into bushy shrubs, divaricating shrubs, etc. (COCKAYNE, comp. above p. 38).

2. *Rosette-shrubs.* This type is analogous to that of the rosette-trees. Typical rosette-shrubs are comparatively rare and so little known that a further subdivision of this type seems impracticable at present. Good examples (of the semiprostrate type) are *Dracophyllum fiordense* W. R. B. Oliver (fig. 12, comp.

also OLIVER 1928 b fig. 15), a species recently discovered in the Fiord District of New Zealand¹, and *Senecio Stewartiae*, a species endemic on the Snares and some small islands at the coast of Stewart Island (comp. COCKAYNE 1909 b, 1928 b). Forms transitional between rosette-shrubs and long-shoot shrubs are found in several New Zealand shrub species, e.g. *Olearia operina* in the coastal scrub of the Fiord District, and *O. Lyallii* in the Snares and Auckland Islands (comp. COCKAYNE 1904 pp. 252—253, 1909 b p. 208, fig. 8, 1928 b p. 345, fig. 101). Suboliferous rosette-shrubs are DRUDE's »monokotyle Palmgebiische», e.g. *Baccharis major* (DRUDE 1913 p. 37, fig. 11).

3. Leafless succulent-stemmed shrubs. To this type belong many species of *Cactaceae* (e.g. most species of *Opuntia*), *Euphorbia*, etc. Examples and pictures are easily found in the literature concerned. The erect type is predominating.

b. Epiphytidic shrubs.

As mentioned above (p. 53) hemiepiphytic trees begin their life as more or less shrub-like epiphytes. There are also species living their whole life as epiphytic shrubs. In the New Zealand rain-forest there occur four such species: *Pittosporum Kirkii*, *P. cornifolium*, *Senecio Kirkii*, and *Griselinia lucida*, the species last mentioned some-times developing into a hemiepiphytic tree. All these species are also found as epilithes, some of them also as chthonophytes (comp. COCKAYNE 1928, OLIVER 1928, etc.). In the tropics, epiphytic shrubs are probably more common. Probably several types can be distinguished; a very peculiar one is that formed by the large species of *Myrmecodia* (comp. above p. 57, LAM 1924 Tab. 39—41, 1929 fig. 48).

c. Parasitic shrubs.

To this type belong a large number of species of *Loranthaceae*.

III. Dwarf-shrubs.

a. Chthonophytic.

1. Sedentary. Without any rooting stems.

α . Erect. All trunks erect even in their basal part.

1) Aëroxylic erect sedentary dwarf-shrubs. This type is analogous to the aëroxylic erect shrubs (comp. above p. 57). The young plant is often a

¹ Comp. also the photograph of *Dracophyllum Menziesii* in Stewart Island published by COCKAYNE (1909 a fig. 7, 1928 b fig. 54). It resembles *D. fiordense* so much that I think it would be well worth while to investigate in the field whether not a part of the Stewart Island *D. Menziesii* belongs to that species (which was not recognized at the time of COCKAYNE's field-work in Stewart Island). What I saw of *D. Menziesii* in the Fiord District was all dwarf-shrubs hardly higher than about half a meter, and never rising above *Olearia Colensoi* as in COCKAYNE's photograph.

more or less unbranched pygmy tree (comp. above p. 45), but after having reached a certain height the top of the primary shoot dies, and secondary shoots are developed from the persisting part of it. In some cases the lower part of the main shoot remains unbranched, and it is then difficult to tell when the term »pygmy tree» should be retained, but usually the branching starts quite near the ground. Some North-European dwarf-shrubs, e.g. *Calluna vulgaris* (comp. LINDMAN 1914 pp. 240, 255—257) may occasionally belong to this type, but I do not know a single example of a North-European dwarf-shrub species regularly belonging to it. On the other hand, this is one of the most common types of dwarf-shrubs in the heath-vegetation of the southern parts of Australia, and probably also in other regions with similar climate (e.g. the Cape). Excellent examples are easily found among the epacridaceous heath dwarf-shrubs common around Sydney: *Epacris microphylla*, *E. obtusifolia*, *Leucopogon microphyllus* (fig. 13), *L. esquamatus*, *Sprengelia incarnata*, *S. ponceletia*, *Styphelia tubiflora* (fig. 14), *Woollsia pungens*, etc. Another interesting example is *Euphrasia formosissima* Skottsb. in Juan Fernandez (Masafuera, comp. SKOTTSBERG 1921 p. 170), the only aëroxylic dwarf-shrub species known in the genus *Euphrasia*.

2) Geoxylic erect sedentary dwarf-shrubs. This type is analogous to the geoxylic sedentary shrubs (comp. above p. 57). New trunks are produced from a hypogeous mesocorm (*i.e.* an orthogeocorm), often more or less incrassate (*i.e.* a xylopodium). I have never met with this type in Northern Europe, but in the Australian heath-vegetation it seems to be about as common as the aëroxylic type mentioned above. A very good example is supplied by *Calectasia cyanea* (Liliaceae, fig. 15); species of the same type common round Sydney are *Xerotes flexifolia* (Liliaceae), *Baeckea linifolia* (Myrtaceae), *Hibbertia stricta* and other species of the same genus (Dilleniaceae), etc.

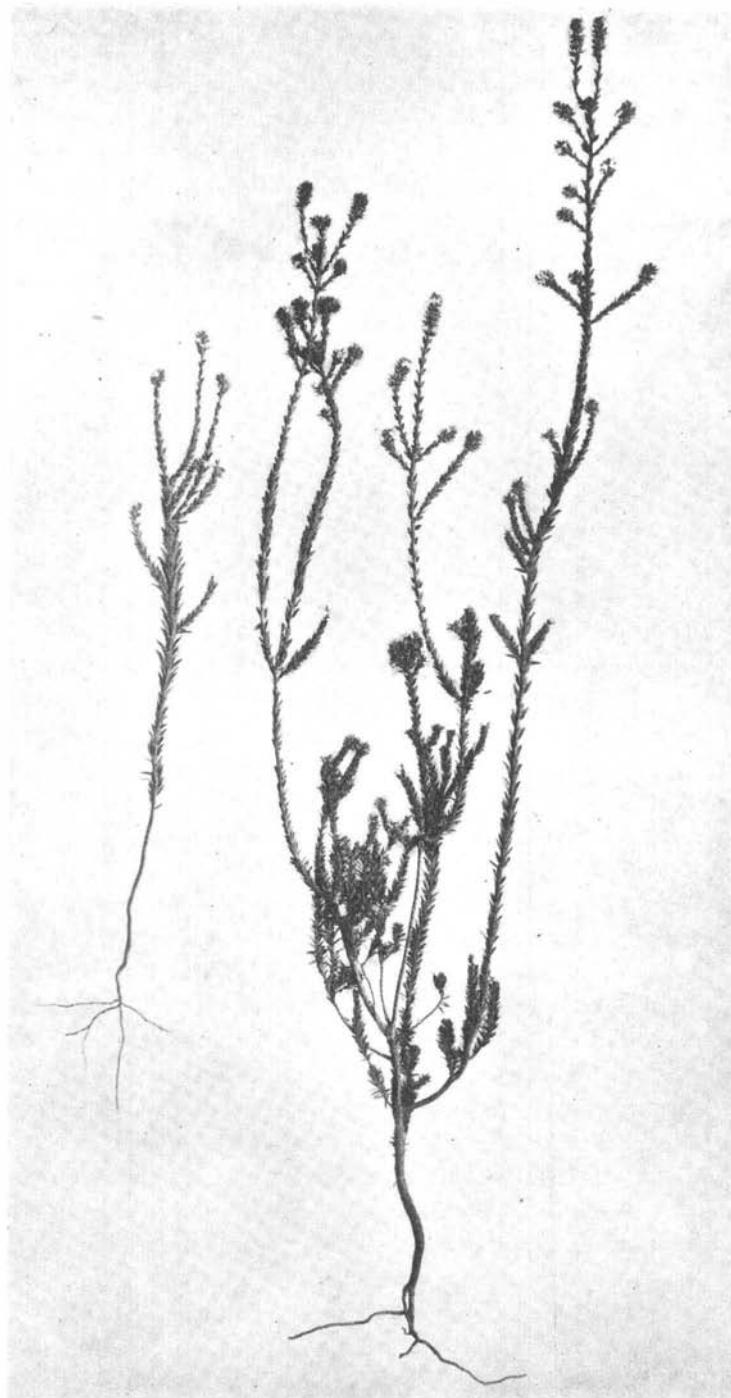
β. *Semi-prostrate sedentary dwarf-shrubs*. At least some trunks prostrate in their basal part, but not rooting.

1) Aëroxylic semi-prostrate sedentary dwarf-shrubs. This type is often found in young individuals of *Calluna vulgaris*. In *Rhododendron lapponicum* even old individuals often belong to it (on dryer soil, comp. WARMING 1885 p. 189, 1908 b p. 10, HAGLUND 1905 p. 18, while on wetter soil usually adventitious roots are developed from the prostrate trunks). According to my own collection of the New Zealand dwarf-shrub *Epacris alpina* (from the subalpine heath on Ruapehu, North Island) this species often behaves in the same way. The same may be the case in *Dracophyllum recurvum*, growing in the same plant-community (comp. COCKAYNE 1908 a p. 24). *Coprosma Petriei* is another good New Zealand example of this type (comp. FOWERAKER 1917 pp. 35—37).

2) Geoxylic semi-prostrate sedentary dwarf-shrubs. To this type possibly belongs *Hibbertia fasciculata*, a species rather common around Sydney.

2. Travelling dwarf-shrubs. With creeping trunks or underground travelling shoots (suboles).

α. *Creeping dwarf-shrubs*. Travelling overground by means of prostrate epigeous stems with adventitious roots and often developing into secondary geocorms.



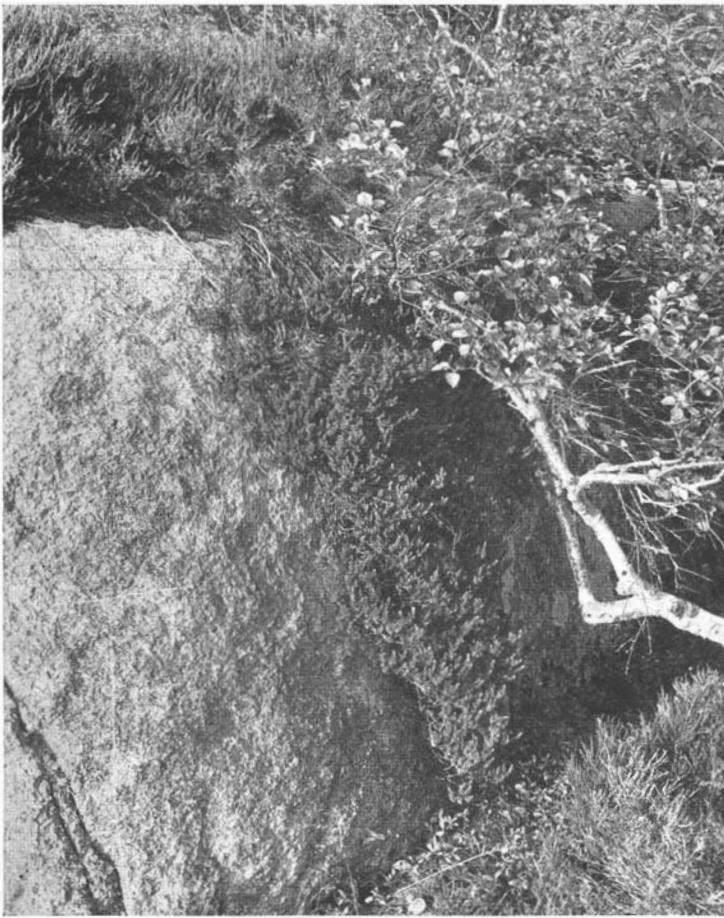
Photo, C. G. ALM.

Fig. 13. Aëroxylic erect sedentary dwarf-schrub: *Leucopogon microphyllus*. Australia, New South Wales, Port Jackson District, French's Forest, open heath on sandstone. 37. 1927. G. EINAR and GRETA DU RIETZ. no. 4008: 2. Ca. 1 : 2.



Photo, C. G. ALM.

Fig. 14. Aëroxylic erect sedentary dwarf-shrub: *Styphelia tubiflora*. Australia, New South Wales, Port Jackson District, French's Forest, open heath on sandstone. 3.7. 1927. G. EINAR and GRETA DU RIETZ no. 4008: 1. 1 : 2.



July 1929. Photo, CARL DU RIETZ.

Fig. 18. Creeping dwarf-shrubs: *Empetrum nigrum* (true creeper, hanging down over a rockface) and *Calluna vulgaris* (semi-sedentary). In the foreground some *Vaccinium vitis idaea* (suboliferous dwarf-shrub). To the right aeroxylic shrubs of *Betula alba* and *Sorbus aucuparia*. South-eastern coast of Sweden, Island Jungfrun, steep rocky slope on the northern side.



February 1927. Photo, J. SCOTT THOMSON.

Fig. 19. Creeping dwarf-shrubs of rosette-type (*Dracophyllum Menziesii*) and long-shoot type (*Celmisia Walkeri*). New Zealand, South Island, Fiord District, Upper Routeburn Valley, in the subalpine belt.

1) Semi-sedentary (creeping) dwarf-shrubs. The term »semi-sedentary» is herewith proposed as a designation for creeping plants with the primary root remaining during the whole life of the individual. In the semi-sedentary plants the individual is sedentary, but each prostrate stem travelling (creeping). The semi-sedentary dwarf-shrubs were not included into the »creeping shrubs» of WARMING (1898, 1916). To me, however, it seems more natural to unite the semi-sedentary dwarf-shrubs with the true creeping dwarf-shrubs than with the sedentary type. It is often very difficult to decide whether a certain dwarf-shrub belongs to the semi-sedentary or the true creeping type, transitional types are very common, and for physiognomy as well as competition the difference between a true creeping dwarf-shrub and a semi-sedentary one spreading over a large area is much smaller than the difference between the latter and the sedentary type.

A very good and well-known example of a semi-sedentary dwarf-shrub is that of *Calluna vulgaris* (fig. 16, comp. WARMING 1884 a pp. 46—47, 1916 pp. 121—122, MALME 1908, HOLMBOE 1909, LINDMAN 1914 pp. 255—257, GREVILLIUS and KIRCHNER 1923 pp. 135—137, KUJALA 1926 pp. 36—41, etc.). The trunks of *Calluna* normally become semi-prostrate at an early stage. An old trunk of *Calluna* usually consists of an ascending terminal crown and a rather long horizontal, simple or more or less branched part, running as a secondary plagiogeocorm in the upper layers of the soil and in the moss- or lichen-layer, and developing abundant adventitious roots. Such horizontal trunks may be one meter long or more, and in a luxuriant *Calluna*-heath — e.g. in the maritime heath of the South-Swedish coast districts — the secondary plagiogeocorms of *Calluna* are a very characteristic feature of the litter and duff layers (»Streuschicht» and »Vermoderungsschicht», comp. HESSELMAN 1926, DU RIETZ 1930 a p. 419). Usually several such trunks radiate from a strong and much branched primary root, which descends into the raw humus layer and fills it with its branches over a rather large area. Only in exceptional cases this primary root disappears and a true creeping dwarf-shrub is developed, e.g. sometimes in *Sphagnum*-bogs. — To the same type belong several other North-European dwarf-shrub species, e.g. *Cassiope tetragona*, *Phyllodoce coerulea*, and *Loiseleuria procumbens* (HAGLUND 1905, WARMING 1908 b), and probably also *Betula nana*, *Erica tetralix* (WARMING 1916 p. 123), *Erica cinerea*, etc. A somewhat different type is represented by *Ledum palustre* and *Vaccinium uliginosum*: in both species more or less typical suboles may be found, but they are of so little importance that these species are probably more naturally placed into the same class as *Calluna* than into that of the true underground travellers (comp. WARMING 1918 b pp. 324—325; both species may, however, sometimes belong to the true creeping dwarf-shrubs). — Of New Zealand dwarf-shrubs probably several species belong to the semi-sedentary type, though the duration of the primary root has not yet been studied sufficiently to allow any definitive classification. As mentioned above, *Epacris alpina* and *Dracophyllum recurvum* often belong to this type; also *Dracophyllum pronum* W. R. B. Oliv. gives the same impression.

2. True creeping dwarf-shrubs. In this type the primary root sooner or later disappears, and true creeping individuals — not only creeping branches — are formed. Very good examples of this type are *Empetrum nigrum*¹ (fig. 18, comp. WARMING 1884 a p. 47, 1916 pp. 129—130, HAGLUND 1905 p. 31, MENTZ 1909 b, HAGERUP 1922, GREVILLIUS and KIRCHNER 1925, KUJALA 1926 pp. 33—36) and *Arctostaphylos uva ursi* (fig. 20, comp. WARMING 1884 a p. 46, 1908 b p. 39, 1916 p. 129, MENTZ 1909 a pp. 264—268, LINDMAN 1914 p. 257, GREVILLIUS and KIRCHNER 1923 pp. 72—73, KUJALA 1926 pp. 41—43). Both species may remain on the semi-sedentary stage for many years, but sooner or later the primary root dies (at least in most cases), and true creeping dwarf-shrubs are formed. In both species the shoots may grow out over rather large areas even without any adventitious roots, which enables these species to colonize bare rock-surfaces as espaliers rooted only outside the rock-surface until sufficient

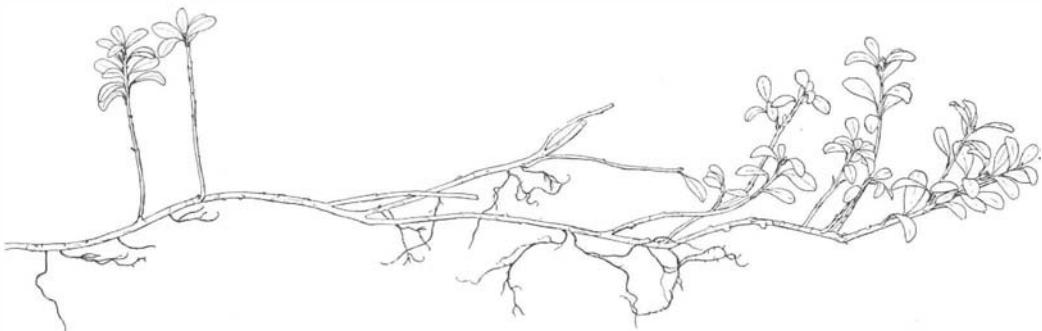


Fig. 20. True creeping dwarf-shrub: *Arctostaphylos uva ursi*, end of a branch (the other branches seen on the figure are cut off). Sweden, Upsala, Norbyskogen, rock in *Pinus sylvestris*-forest. 2.11. 1930. Drawn after living material. Ca. 1 : 3.

humus for the development of adventitious roots has been collected under the espalier. *Empetrum nigrum* may even exhibit a sublianoid habit, hanging down over steep rock-faces (fig. 18) or climbing old logs, stubs, etc.; I have even seen it climbing the lower branches of shrubby spruces (on the island Jungfrun). For the competition with *Calluna vulgaris* this sublianoid habit is of great importance, since it allows *Empetrum* to colonize bare rocks, logs, stubs, etc. much easier and faster than *Calluna*; on Jungfrun (except in bogs and near the sea-shore), I usually found that the patches of *Empetrum* often occurring in the large areas dominated by *Calluna*, were developed just on outcrops of rock, old logs, stubs, etc. — Other North-European examples of true creeping dwarf-shrubs of a similar type are *Arctostaphylos alpina* (HAGLUND 1905 p. 34, WARMING 1908 b p. 34, GREVILLIUS and KIRCHNER 1923 p. 82), *Cassiope hypnoides* (HAGLUND 1905 p. 26, WARMING 1908 b p. 22), and *Dryas octopetala* (HAGLUND 1905 pp. 32—33).

¹ *Empetrum nigrum* is here taken in the traditional wide sense, including *E. hermaphroditum* (Lge) Hagerup (comp. HAGERUP 1927). According to HAGERUP (p. 12) only *E. nigrum* belongs to the creeping type, *E. hermaphroditum* being sedentary and prostrate only (in the Färöes). Further investigations, however, are needed for the definitive decision of the taxonomic value of *E. hermaphroditum* as well as of the variability of its vegetative morphology.

JESSEN 1913 pp. 61—62, LINDMAN 1914 p. 258). All these examples belong to WARMING's subtype »espalier shrubs» (WARMING 1899, 1916, etc.). Creeping dwarf-shrubs of a more extreme type (WARMING's »rankende krypbuske», l.c.) with earlier disappearing primary root are *Oxycoccus quadripetalus* (WARMING 1884 a p. 49, 1908 b pp. 53—54, 1916 p. 130, LINDMAN 1914 pp. 275—276, GREVILLIUS and KIRCHNER 1923 pp. 121—122) and *Linnaea borealis* (WITROCK 1878—79, SERNANDER 1891, WARMING 1884 a p. 58, 1916 pp. 130—131, GIGER 1913, LINDMAN 1914 p. 257, HAGERUP 1915, KUJALA 1926 pp. 43—47). — Good examples of true creeping dwarf-shrubs from eastern North America are *Epigaea repens* and *Chiogenes hispidula*, and from New Zealand *Celmisia ramulosa*, *C. Walkeri* (fig. 19), *C. novae-zelandiae*, *C. brevifolia*, *Coprosma repens*, *Dacrydium laxifolium* (fig. 17), *Dracophyllum politum*, *D. prostratum*, *Drapetes Dieffenbachii*, *Forstera sedifolia*, etc. (comp. COCKAYNE 1908 a, 1928 b, etc.).

The creeping dwarf-shrubs may be subdivided not only according to the duration of the primary root, but also according to the shoot-architecture. While the examples mentioned above were all long-shoot types, there are also some creeping rosette dwarf-shrubs, e.g. *Dracophyllum Menziesii* (fig. 19; usually the rosette-type is more pronounced than shown by this photograph). Transitional types with »pseudorosette-shoots» (i. e. long-shoots terminated by a rosette) are also found, e.g. *Dracophyllum recurvum*, *Celmisia Hectori*, *C. viscosa*, some forms of *C. incana* and of the *C. discolor*-group, etc. Probably also some stem-succulents must be referred to the dwarf-shrub growth-form. Most of the creeping dwarf-shrubs mentioned above belong to the sympodial type; examples of the monopodial type are *Cassiope tetragona* (HAGLUND l.c., WARMING l.c.), *Empetrum nigrum* (comp. the literature cited above), *Epacris alpina*, the species of *Celmisia*, and *Linnaea borealis*. The species last mentioned is of a very peculiar type, with unlimited prostrate long-shoots and erect, more short-lived short-shoots of two types, one sterile and one fertile (comp. the literature cited above).

β. *Suboliferous dwarf-shrubs*. Travelling mainly underground by means of suboles, but sometimes also to some extent overground by means of semi-prostrate and rooting trunks. As mentioned above, a transition between the creeping dwarf-shrubs and this type is formed by *Vaccinium uliginosum* and *Ledum palustre*, species travelling mainly overground but also developing some more or less typical suboles and therefore referred by WARMING to the suboliferous type (comp. besides WARMING 1918 b also WARMING 1908 b pp. 45—46, fig. 29). Very good examples for the typical suboliferous dwarf-shrubs are afforded by *Vaccinium vitis idaea* (fig. 21 and 18, comp. WARMING 1884 a p. 77, 1908 b pp. 49—50, fig. 32, 1916 pp. 126—127, 1918 b pp. 325—326, fig. 24, MENTZ 1909 a pp. 279—283, figs. 10—12, DRUDE 1913 fig. 45, LINDMAN 1914 pp. 276—277, GREVILLIUS and KIRCHNER 1923 pp. 91—92, KUJALA 1926 pp. 14—24) and *V. myrtillus* (comp. WARMING 1884 a p. 76 fig. 18, 1908 b pp. 42—43, fig. 27, 1916 p. 126, 1918 b p. 325, LINDMAN 1914 pp. 276—277, fig. 24, GREVILLIUS and KIRCHNER 1923 pp. 103—104, KUJALA 1926 pp. 24—33, fig. 9). Both these species travel very effectively by means of horizontal suboles. I have digged out suboleocorms of *V. vitis idaea* more than 2 m long — the subole in fig. 21 was the end



Fig. 21. (Monopodial) suboliferous dwarf-shrub: *Vaccinium vitis idaea*, end of a more than 2 m long horizontal stem, running in the duff layer of a *Vaccinium vitis idaea* - *Hylocomium parvulum* - community on a rock in *Pinus sylvestris*-forest, Sweden, Norbyskogen, 2.II.1930. Drawn after living material. Ca. 1 : 4.

of one of them (comp. also KUJALA 1926 p. 14) — and certainly still longer ones may be found. In *V. vitis idaea* the main suboles are normally monopodial, and the aërial shoots are formed by secondary suboles branched off from the main ones (fig. 21), though some-times also these secondary suboles may continue their horisontal growth. *V. myrtillus*, on the other hand, has a sympodial subole-geocorm. The subole-geocorms of these species form an important part of the duff layer in most raw humus profiles within their distribution area, playing just the same rôle as the secondary plagiogeocorms of the creeping dwarf-shrubs, and usually sending down only roots into the raw humus layer. At least this is the case in the profiles studied by myself on rocky ground in South-Swedish coast-districts; B. LINDQUIST, however, tells me that the subole-geocorms may in some cases descend into the raw humus layer. There is a most remarkable similarity between an old subole-geocorm of *V. vitis idaea* and an old secondary plagiogeocorm of *Arctostaphylos uva ursi*: the assimilating shoots seem to arise just in the same way from the geocorm, and without seing its younger parts nobody would be able to tell that these geocorms have been formed in quite different ways in the two species (comp. figs. 20 and 21). — Other European examples of suboliferous dwarf-shrubs are *Andromeda polifolia* (WARMING 1908 b p. 29 fig. 19, 1916 p. 127, 1918 b p. 326, fig. 25, GREVILLIUS and KIRCHNER 1923 p. 53), *Chimaphila umbellata* (very similar to *Vaccinium vitis idaea*, comp. WARMING 1916 p. 127, 1918 b p. 327, fig. 26), *Myrica Gale* (WARMING 1916 p. 23, fig. 16, and p. 128), *Polygala chamaebuxus*, *Salix herbacea* (WARMING 1918 b p. 326, LINDMAN 1914 pp. 279—280, fig. 26), and *Salix polaris* (WARMING 1918 b p. 326). A good North American example, not represented in Europe, is *Gaultheria procumbens*. On the mountaintops of Eastern Java I found this type represented by *Leucopogon javanicus* (Zoll. et Mor.) de Vriese¹, in Australia by *Leucopogon virgatus*, among others, and in New Zealand by *Cyathodes pumila*, *Gaultheria depressa*, *G. perplexa*, *Hebe Petriei*, *Leucopogon Fraseri*, *Pentachondra pumila*, etc.

¹ Better known in recent literature as *Styphelia pungens* (Jungh.) Koorders (non F. v. Muell., nec non *Leucopogon pungens* Sond.).

b. Epiphytidic dwarf-shrubs.

I do not know any species normally belonging to this type, but some of the New Zealand epiphytidic shrubs mentioned above (p. 60) may occasionally be small enough to be referred to it.

c. Parasitic dwarf-shrubs.

Good examples of this type are *Viscum album* (comp. for instance WARMING 1916 pp. 124—125) and certain species of *Loranthus*.

IV. Woody Cushion-plants.

The woody cushion-plants are very nearly related to the dwarf-shrub type. Transitional forms are often found, and it may even be convenient to distinguish a transitional type as »woody semi-cushion plants», including such dwarf-shrubs which condense their shoot-systems into a sort of loose open cushions, resembling the true cushions in their external form, but differing from them by not being compact (»Kugelsträucher oder Luftkugelkissen» of HAURI and SCHRÖTER 1914). A very good example of a sedentary or semi-sedentary woody semi-cushion plants is *Pimeliaea sericeo-villosa*, a species common in the induced desert of Central Otago in the South Island of New Zealand (comp. COCKAYNE 1928 b p. 364); other examples are mentioned by HAURI 1912 p. 398. Comp. also the »Dornpolster» described and photographed by HANDEL-MAZZETTI (1912, 1913 a, b, 1914) in Kurdistan. Examples of creeping woody semi-cushion plants, forming a transition to the true creeping dwarf-shrubs, are *Raoulia australis*, *R. subulata*, *Celmisia sessiliflora*, etc.—There are also many species which may assume the growth-form of an ordinary dwarf-shrub or that of a woody cushion-plant according to the conditions under which they are growing. Several examples of this are described by COCKAYNE (1928 b p. 252, Figs. 53, 64, 65, 70): *Helichrysum coralloides*, *Dactylium laxifolium*, and *Dracophyllum politum*¹. I have seen just the same thing myself both in New Zealand (e.g. in *Dracophyllum prostratum*, comp. DU RIETZ 1930 b p. 375) and in other countries, e.g. in *Diapensia lapponica* in Lapland.

¹ Mentioned by COCKAYNE under the name of *D. rosmarinifolium* (Forst.) R. Br. [= *D. politum* (Cheesem.) Ckn of COCKAYNE's previous works]. The occurrence of *D. politum* in the Fiord District was discovered in 1927 by W. R. B. OLIVER and myself, and since this was quite near the type-locality for *D. rosmarinifolium* (Forst.) R. Br., and the species previously identified with this species (*D. rosmarinifolium* Hook. f. = *D. primum* W. R. B. Oliv.) did not seem to occur at all in this part of the Fiord District, it was supposed for some time by COCKAYNE, OLIVER, and myself that *D. politum* was the true *D. rosmarinifolium* (Forst.) R. Br. In his *Dracophyllum*-revision of 1928, however, OLIVER showed that FORSTER's *Epacris rosmarinifolia* was identical neither with *Dracophyllum politum* nor with *D. primum*, but with a third species, namely *D. uniflorum* Hook. f., and hence applied the name *D. rosmarinifolium* (Forst.) R. Br. to this species. I have reexamined the type of *Epacris rosmarinifolia* myself in the British Museum (in 1930), and can only confirm OLIVER's statement. *D. politum* thus has got to keep its old name (OLIVER 1928 b p. 687).

Analogous observations have been made also in herbaceous cushion-plants. According to COCKAYNE (1909 b p. 201, 1928 b p. 252) even such extreme cushion-plants as *Phyllachne clavigera* and the »vegetable sheep» species of *Raoulia* lose their cushion-form if cultivated in a moist green-house. Of course all these observations only show that the cushion-form, like most other growth-forms, is not the only phenotypical expression of a certain genotypical constitution, but merely the phenotypical response of a certain genotypical constitution to a certain environment.

In spite of all these transitions between the ordinary dwarf-shrub form and the growth-form of the woody cushion-plants it seems most convenient not to include the woody cushion-plants into the dwarf-shrub class of growth-forms, but to keep them as a separate class. As a whole they certainly form one of the most conspicuous and definite units of the whole growth-form system. The greatest difficulty in their delimitation is probably formed by their very gradual transition into the type of the herbaceous cushion-plants; but even this difficulty is hardly greater than that offered by the equally gradual transition between creeping dwarf-shrubs and creeping herbs.

An elaborate system of the various types of cushion-plants has been worked out by H. HAURI and C. SCHRÖTER (SCHRÖTER 1908 p. 569 etc., HAURI 1912 pp. 391—406, HAURI and SCHRÖTER 1914, SCHRÖTER 1925 pp. 767—790, comp. especially HAURI 1912 p. 401). After the exclusion of all »unechte Polster» or »Kissen» (»Luftkugelkissen», »Gesellschaftskissen», »Luftkrautkissen», »Hohlkugelkissen» etc.), the true »Polsterpflanzen» (including both woody and herbaceous types) are divided by HAURI into two main types: a. »Einfach wurzelnde Polsterpflanzen, morphologisch und physiologisch eine Einheit bildend und nie zerfallend in mehrere Individuen». b. »Vielfach reichlich an den Ästen wurzelnde Polsterpflanzen, die leicht zerfallen in unabhängige Teile», or »Horstpolster». Both types are subdivided into »Kugelpolster» und »Flachpolster». In the main type of »einfach wurzelnden Polsterpflanzen», both »Kugelpolster» and »Flachpolster» are subdivided into »Radialpolster» (with regularly radial ramification) and »Schopfpolster» (with more irregular ramification). In each of the six types obtained in this way the ultimate division is made according to the existence or non-existence of »Füllmaterial», resulting into the following 12 types of true »Polsterpflanzen»: 1. Radialvollkugelpolster. 2. Radialkugelpolster. 3. Vollschofpolster. 4. Schopfpolster. 5. Radialvollflachpolster. 6. Radialflachpolster. 7. Vollflachschofpolster. 8. Flachschofpolster. 9. Vollhorstkugelpolster. 10. Horstkugelpolster. 11. Vollhorstflachpolster. 12. Flachhorstpolster. The six types with »Füllmaterial» are illustrated by fig. 22; the six types without »Füllmaterial» are quite analogous. — A somewhat wider »Polsterpflanzen»-concept was used by SKOTTSBERG (1916 p. 126), who — on convincing arguments — included also HAURI's and SCHRÖTER's »Rosettenkissen» or »Hohlkugelkissen» into the »Polsterpflanzen», but accepted the rest of HAURI's and SCHRÖTER's system.

According to my own experience of woody cushion-plants the main division of this growth-form is certainly best made into the two main types of HAURI,

i.e. into one type with persisting tap-root and one with perishing tap-root and vegetative propagation. If we apply the same terminology as in the dwarf-shrubs, the former type ought to be called semi-sedentary — since adventitious

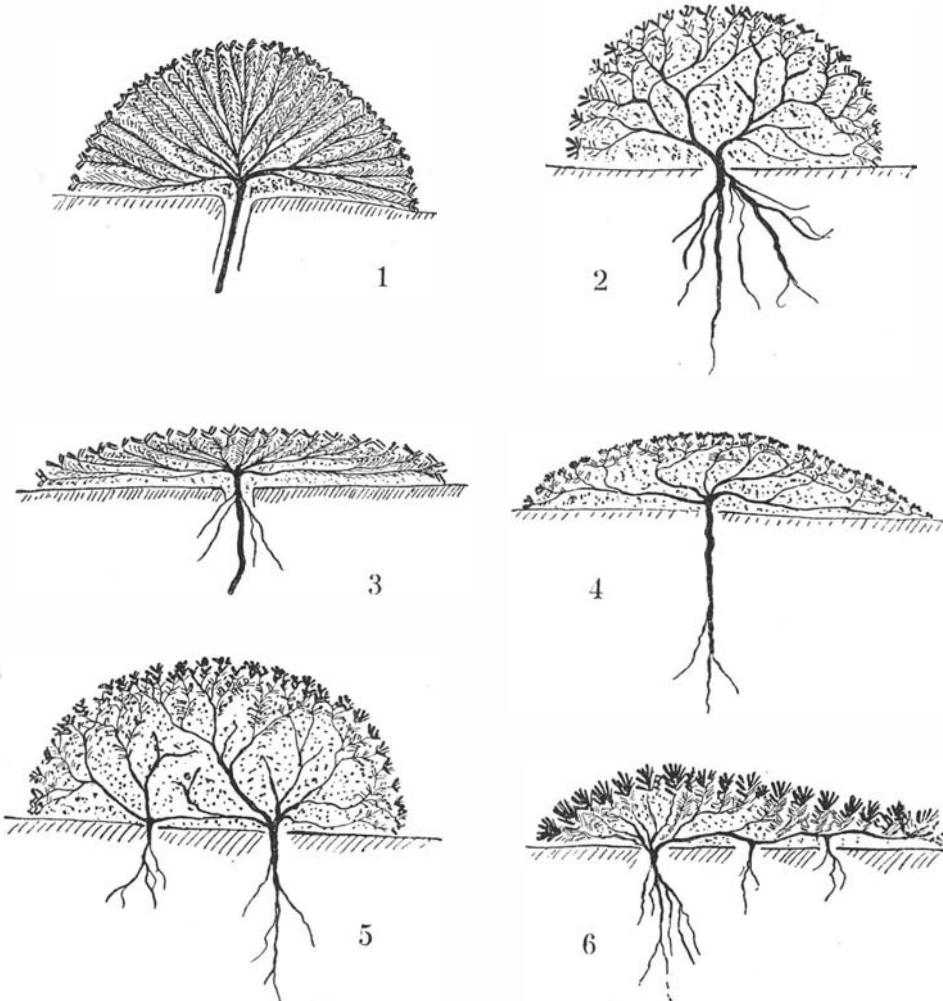
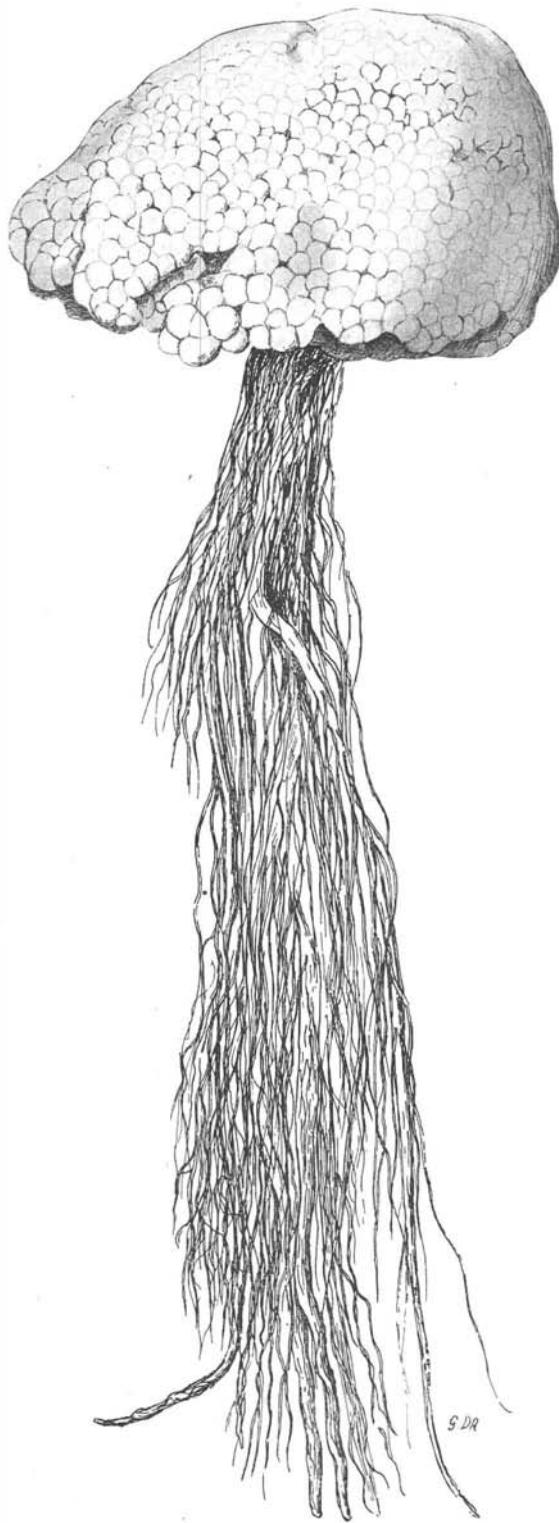


Fig. 22. Schematic sections through the 6 main types of filled cushion-plants (reprinted from HAURI 1912 p. 400). 1. »Radialvollkugelpolster» (e.g. *Androsace helvetica*, *Saxifraga caesia*). 2. »Vollschopfpolster» (e.g. *Eritrichium nanum*, *Minuartia sedoides*, various species of *Saxifraga*). 3. »Radialvollflachpolster» (e.g. *Silene acaulis*, especially young individuals). 4. »Vollflachschopfpolster» (e.g. old individuals of *Silene acaulis*, flat individuals of *Eritrichium*, *Saxifraga* spp.). 5. »Vollhorstkugelpolster» (e.g. *Androsace alpina*). 6. »Vollhorstflachpolster» (e.g. young individuals of *Carex firma*). Living leaves are drawn with thick, dead with thin lines. The variations of the root-system in 1—4 are not characteristic for the types, but only for the species used as examples. — Figs. 1—4 belong to the »tap-rooted cushion-plants», and figs. 5—6 to the »moss-like cushion-plants» of the present author.

roots are usually developed both in the prostrate branches and in the interior of the cushion — and the latter type creeping. The latter term, however, is not very suitable in this case, since — especially in peat-forming species — the rooting branches are often too orthotropic to correspond to the ordinary idea of



a »creeping» plant. I therefore prefer to designate the two main types of woody cushion-plants simply as »tap-rooted» and »moss-like».

a. Tap-rooted woody cushion-plants.

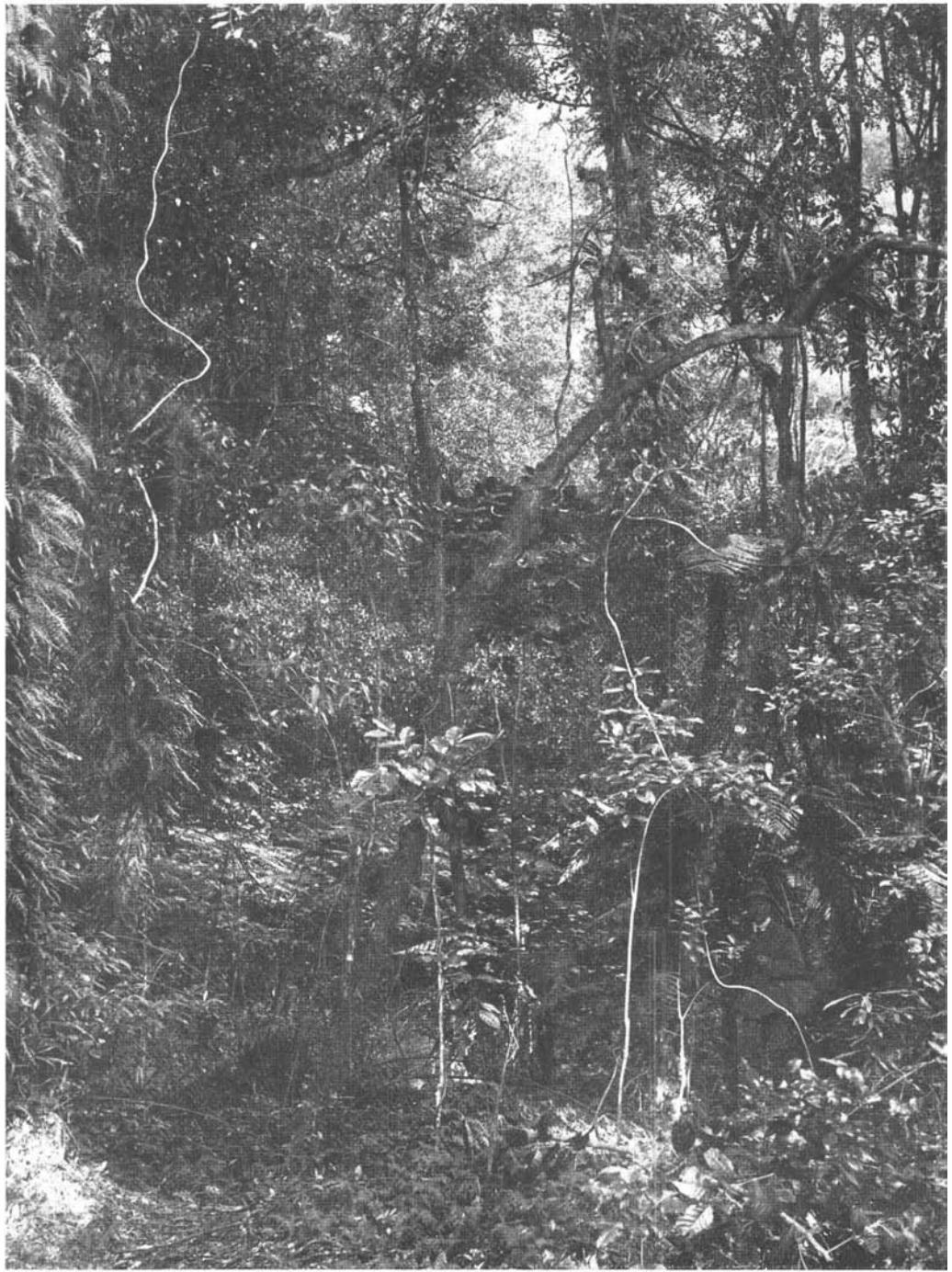
Splendid examples of this type are afforded by the famous »vegetable sheep» of New Zealand mountains, *i.e.* *Haastia pulvinaris* and several species of *Raoulia* (especially *R. eximia*, but also the smaller species *R. bryoides*, *R. Buchanani*, *R. Goyenii*, *R. mamillaris*, and *R. rubra*). They belong to the »Radial-polster» of HAURI and SCHRÖTER. Some of them are more or less hemisphaerical (»Radialkugelpolster» of HAURI and SCHRÖTER), *e.g.* *Haastia pulvinaris* (comp. COCKAYNE 1921 fig. 71, 1928 b fig. 58, SCHRÖTER 1925 fig. 275) and *Raoulia eximia* (figs. 23, 24, and 25, comp. also DRUDE 1913 fig. 66, COCKAYNE 1927 a figs. 64 and 65, LAING and BLACKWELL 1927 fig. 163, etc.). Others are more flat (»Radialflachpolster» of HAURI and SCHRÖTER), *e.g.* *R. Buchanani* (fig. 26). The only Scandinavian representative of this type, *Diapensia lapponica*, is less typical, and is referred to the »Luftkugelkissen» by HAURI and SCHRÖTER (1914 p. 641, comp. also H. E. PETERSEN 1908).

Fig. 23. Tap-rooted woody cushion-plant: *Raoulia eximia*, young individual. New Zealand, South Island, Eastern District, Mt. Wakefield (in the Mt. Cook massif), rock-fissure in the lower alpine belt. 15.3. 1927. G. EINAR and GRETA DU RIETZ no. 2151: 2. Museum of the Plant-Biological Institution, Upsala. Drawn after dried material. 2 : 3.



15. 3. 1927. Photo, GRETA DU RIETZ.

Fig. 24. Tap-rooted woody cushion-plant: *Raoulia eximia*. New Zealand, South Island, Eastern District, Mount Wakefield in the Mount Cook massif, rocky ridge in the alpine belt.



19. 5. 1927. Photo, GRETA DU RIETZ.

Fig. 30. Winding (*Rhipogonum scandens*) and root-climbing (*Polypodium pustulatum*) lianes in primeval *Dacrydium cupressinum* - *Laurelia novae-zelandiae* - *Beilschmiedia tawa* - forest. New Zealand, North Island, Volcanic Plateau District, Hongi's track (between Lake Rotoiti and Lake Rotoehu).

reach a tree or a rock, and then changing into a typical root-climbing liane. Good examples of this are *Hedera helix* in Europe (often covering the ground over large areas as a creeping dwarf-shrub in deciduous forests), and several species of *Metrosideros* [e.g. *M. perforata* and *M. diffusa* (Forst.) W. R. B. Oliver¹ (= *M. hypericifolia* A. Cunn.), comp. COCKAYNE 1909 a p. 14, 1927 a p. 73, BIRD 1916 p. 326] as well as *Freycinetia Banksii* (comp. COCKAYNE 1908 b p. 25) in New Zealand. The species last mentioned, however, is really too tall even when creeping on the ground to fit well into the concept of a creeping dwarf-shrub. In *Hedera* as well as in *Metrosideros perforata* also erect shrubby shoots — with a different type of leaves — may be formed in open habitats (comp. COCKAYNE 1907 b p. 9, Plate VI, 2, 1912 p. 22, 1921 fig. 25, 1927 a p. 76, fig. 34 C, 1928 b fig. 33). These species may thus belong to three different growth-forms: woody lianes, creeping dwarf-shrubs, and erect shrubs. In spite of such complications, however, it seems most convenient to keep the woody lianes as a separate unit in the growth-form system. In most cases a woody liane certainly is very different both from a shrub and a creeping dwarf-shrub. The greatest difficulty in the delimitation of this growth-form is caused by its gradual transition into that of the herbaceous lianes (comp. WARMING 1923 p. 181).

The first general division of lianes into twining plants, leaf-climbers, tendrill-bearers, hook-climbers, and root-climbers, was published in the classical work of CHARLES DARWIN (1875). With small changes it has been adopted by practically all subsequent authors. Most recent authors distinguish four main classes: scramblers, root-climbers, winders and tendril-climbers (comp. SCHENCK 1892, WARMING 1892, 1923, COCKAYNE 1927 a, 1928 b, etc.). As I have little to add to this system, I shall confine myself here to characterize those four types as briefly as possible. Further information is easily found in the general accounts published by SCHENCK and WARMING.

a. Scrambling woody lianes.

To this type — the »semi-lianes» of WARMING and the »Spreizklimmer» of SCHENCK — belong all such woody lianes that possess neither climbing-roots nor tendrils nor a winding habit, but climb only by means of divaricating branches with or without spines. The type is rather heterogenous, including both lianes without any special climbing-organs at all and such with the peculiar and extremely effective climbing-organs formed by the spiny »flagellum» of the climbing palms (rotangs), the spiny stalks of the leafs and leaflets in the climbing New Zealand species of *Rubus* (comp. BIRD 1916 figs. 1—4, Pls. XXIII and XXVI, COCKAYNE 1927 a fig. 34 A and B), etc. Anybody who has been in personal contact with such »lawyers» — the vernacular term for *Rubus australis* etc. in New Zealand as well as the species of *Calamus* in Queensland and northern New South Wales — will probably admit that they may be well worth of forming

¹ As to the intricate synonymy of the New Zealand species of *Metrosideros* comp. OLIVER 1928 a.

their own main group of woody lianes coordinated with root-climbers, winders, and tendril-climbers.¹ Since, however, the delimitation of this group towards that formed by the more innocent scramblers (e.g. *Fuchsia perscandens* in New Zealand, comp. COCKAYNE 1927 a p. 72) still appears to be rather unclear, it may be best to take the scramblers in the traditional wide sense until a more detailed analysis is available.

b. Root-climbing woody lianes.

The lianes belonging to this group are simply creeping dwarf-shrubs which possess the power of creeping not only on the ground but also on rocks and tree-trunks, *i.e.* of developing adventitious roots also on their aerial shoots and of fastening themselves by means of these roots to their substrate. Good examples are formed by the species of *Hedera*, *Metrosideros*, and *Freycinetia* mentioned above. In fig. 6 *Metrosideros perforata* is seen on one of the tree-trunks.

c. Winding woody lianes.

This type is more related to the shrubs than to the dwarf-shrubs, and transitions to the ordinary shrub-type are sometimes found. The winding habit of the stem is the only means of climbing. A good European example of this type is formed by *Lonicera periclymenum*. A New Zealand example — *Rhipogonum scandens* — is seen in fig. 30.

d. Tendril-climbing woody lianes.

Also this type is more related to the shrubs than to the dwarf-shrubs, and transitional types of shrubs with very primitive tendrils may be occasionally found. The tendrils may be formed either by the stem or by the leaves, and several well defined subtypes of tendril-climbers have been described by various authors. SCHENCK (*l.c.*) divides the tendril-climbers (»Rankenpflanzen») into »Blattkletterer», »Blattranker», »Zweigklimmer», »Hakenkletterer», »Uhrfederranker», and »Fadenranker». As to the characteristics and examples of these types the reader is referred to the original literature. In most parts of the world the genera *Clematis*, *Vitis*, *Cissus*, etc., provide us with good and well-known examples of tendril-climbers.

B. *Hemixyles*.²

I. True Half-shrubs (suffrutices).

Hemixyles with truly perennial ligneous aërocorms living more than two years and producing herbaceous long-shoots of only one years duration.

¹ The difference between the true »hook-climbers» and »merely scrambling» lianes was pointed out already by DARWIN (1875).

² Comp. above p. 46.

It is very difficult to draw a natural line between the true half-shrubs and the holoxyles (shrubs and dwarf-shrubs). Many shrubs (and even trees) develop floral shoots of only one years duration carrying foliage-leaves, and thus form a sort of a transition to the true half-shrubs. If these shoots are very short compared with the height of the whole shrub — e.g. in many species of *Salix*, several New Zealand species of *Olearia* and *Senecio*, *Anaphalis viscida* on the high volcanoes of Eastern Java, etc. — they are generally considered unimportant for the growth-form classification, and the species concerned are generally treated as true shrubs, not as half-shrubs. It is only when the annual shoots are of a length comparable with that of the perennial aërocorm, that they are generally regarded as a sufficient reason to classify the species concerned as true half-shrubs. Most of the species generally recognized as half-shrubs therefore belong to the dwarf half-shrub type (comp. above p. 46).

Another difficulty in the delimitation of the true half-shrubs is caused by species with annual floral long-shoots carrying only more or less reduced foliage-leaves, but attaining a considerable length compared with the perennial aërocorm. When the leaves of the floral shoots are reduced to typical bracts, the species concerned of course must be treated as dwarf-shrubs, but when those leaves have the character of real foliage-leaves somewhat reduced in size only, it is often very difficult to decide where to draw the line between the dwarf-shrub and the dwarf half-shrub type. Good examples of this difficulty are found in several New Zealand species of *Celmisia*, especially in the *C. discolor*-group, *C. densiflora*, etc.

As far as I know, there are only chthonophytic half-shrubs known at present. They are conveniently subdivided in just the same way as the chthonophytic dwarf-shrubs.

a. Sedentary true half-shrubs.

1. Erect.

a. Aëroxylic. Excellent examples of this type are provided by the North American *Artemisia*-species of the »sage-brush»-type, e.g. *Artemisia tridentata* Nuttall (fig. 31, comp. also KEARNEY, BRIGGS, SHANTZ, etc. 1914 figs. 4, 5, 13, and Pl. XLIV, CLEMENTS 1916 Pl. 32 B, 1920 Pl. 32, HALL and CLEMENTS 1923 Pls. 18—20, ALDOUS and SHANTZ 1924 Pl. 6 B) and *A. Bigelowii* A. Gray (fig. 32, comp. also HALL and CLEMENTS 1923 Pl. 9, HANSON 1924 Pl. I A). While *A. tridentata* sometimes belongs to the tall, sometimes to the dwarf half-shrub type — according to ALDOUS and SHANTZ 1924 p. 108 it varies in height between 1 and 7 feet — *A. Bigelowii* is a typical dwarf half-shrub. — Certainly also many of the Mediterranean half-shrubs belong to the aëroxylic erect type, but I do not know them well enough to make any definite statements about them. In Australia this type is very common. Good examples are *Euphrasia paludosa* (fig. 33) and other perennial lowland species of the same genus, *Stylium laricifolium* (*Styliaceae*), *Actinotus Helianthus* (*Umbelliferae*), *Poranthera ericifolia* and *P. corymbosa* (*Euphorbiaceae*), *Jonidium filiforme* (*Violaceae*, sometimes *geoxylic*),

and *Goodenia ovata* (*Goodeniaceae*, possibly sometimes geoxylic). In New Zealand this type is rarer, just as the aëroxylic erect dwarf-shrub type; probably *Linum monogynum* belongs to it. On the high volcanoes of Eastern Java I found a very good example in *Sweertia coerulescens*. Just as in the aëroxylic erect dwarf-shrubs, there are both types branched from quite near the ground and types with a comparatively long unbranched basal part of the main trunk, i.e. resembling the pygmy tree type. Of the species mentioned above, *Stylium laricifolium* and *Sweertia coerulescens* are good examples for the latter type.



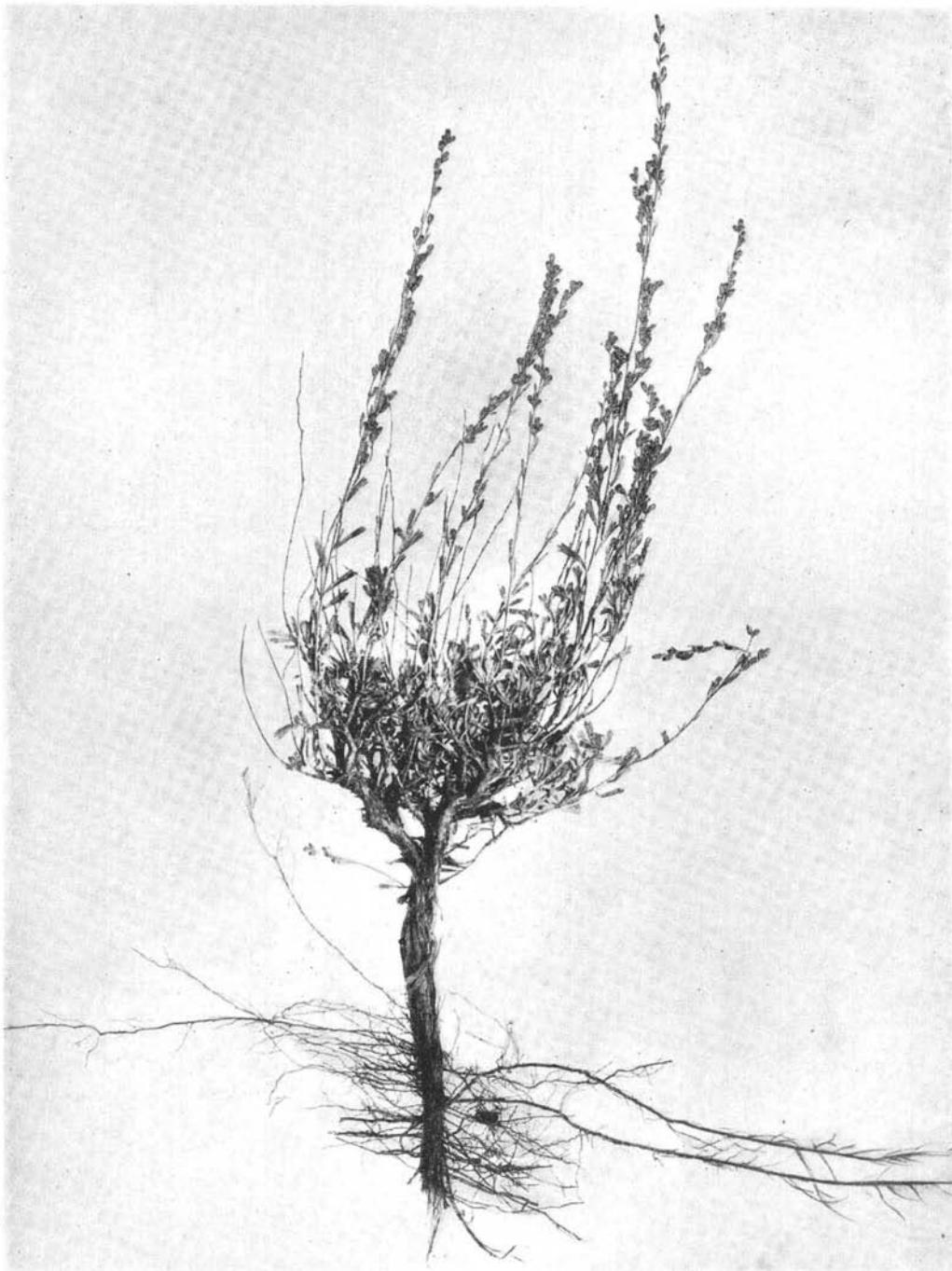
31.8. 1926. Photo, GRETA DU RIETZ.

Fig. 31. Aëroxylic erect sedentary true half-shrub: *Artemisia tridentata* Nuttall. U. S. A., Arizona, Grand Canyon, Coconino Plateau southwest of Grand Canyon Station, large patch of (secondary?) sagebrush desert in the *Pinus ponderosa*- and *Pinus edulis*-*Juniperus monosperma*-forests.

β. *Geoxylic*. A Middle-European example of this type is *Dorycnium germanicum* (sometimes approaching the semi-prostrate type). Probably also *Genista tinctoria* belongs here (comp. MENTZ 1906, WARMING 1916 p. 142). Australian examples common around Sydney are *Halorrhagis serra* (fig. 34), *H. tetracygna*, and *H. salsoloidea*. Probably also the species of *Tetradymia* (*Tremandraceae*) should be referred to this type. The type is probably common both in Australia and in the Mediterranean.

2. Semi-prostrate.

Just as in the dwarf-shrubs, this type is commoner than the erect type in Northern and Middle Europe. The best examples are provided by species of



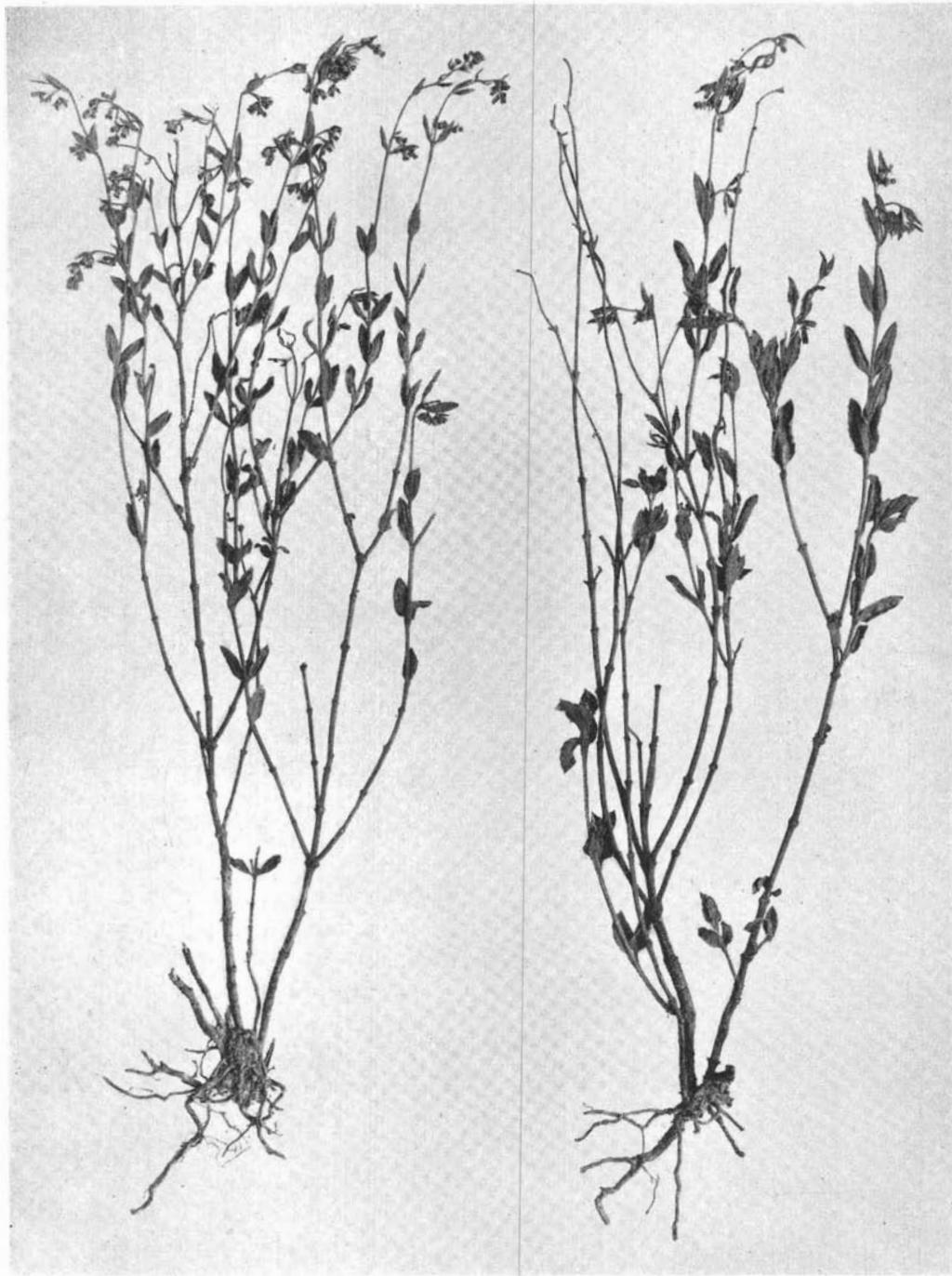
Photo, C. G. ALM.

Fig. 32. Aëroxylic erect sedentary true (dwarf) half-shrub: *Artemesia Bigelowii* A. Gray. U. S. A., Arizona, Grand Canyon, open *Pinus edulis* - *Juniperus monosperma* - forest on the southern rim near Maricopa Point. 31.8. 1926. G. EINAR and GRETA DU RIETZ. Ca. 1 : 1.



Photo, C. G. ALM.

Fig. 33. Aëroxylie erect sedentary true (dwarf) half-shrub: *Euphrasia paludosa*. Australia, New South Wales, Blue Mountains, Bell, open heath. 15.11. 1926. G. EINAR and GRETA DU RIETZ no. 895. Ca. 1 : 2.



Photo, C. G. ALM.

Fig. 34. Geoxylic erect sedentary true (dwarf) half-shrub: *Halorrhagis serra*. Australia, New South Wales, Blue Mountains, Bell, open *Eucalyptus*-forest. 15.11. 1926. G. EINAR and GRETA DU RIETZ no. 881. Ca. 1 : 1.

6—30830. G. Einar Du Rietz.



Fig. 35. Creeping true (dwarf) half-shrub: *Thymus serpyllum*, end of creeping branch, with the floral shoots of the year dead already. Sweden, Uppsala, Husbyborg, patch of *Thymus*-heath on morain. 4.II. 1930. Drawn after living material. 1 : 1.

Helianthemum (*H. canum*, *H. oelandicum*, *H. nummularium*, *H. ovatum*, etc.) as well as by *Fumana vulgaris*.¹ As far as I know, all these species are geoxyllic. An Australian example is *Pomax umbellata* (*Rubiaceae*, sometimes semi-sedentary) a New Zealand one *Epilobium glabellum*.

b. Creeping true half-shrubs.

Analogously with the creeping dwarf-shrubs, this type is commoner in cold countries than the sedentary type. Just as in the creeping dwarf-shrubs, one semi-sedentary and one true creeping type may be distinguished, but sufficient information is still lacking for the practical distribution of the creeping true half-shrubs upon these types. Well-known North- and Middle-European examples are *Thymus serpyllum* (fig. 35, comp. WARMING 1884 a p. 47) and many other species of *Thymus* (semi-sedentary or true creepers), *Veronica fruticans* (sometimes sedentary semi-prostrate, comp. MATHIESEN 1921 pp. 368—370, fig. 1), *Comarum palustre* (true creeper, comp. IRMISCH 1861, WARMING 1884 a p. 50, JESSEN 1913 p. 6, fig. 1, etc.), and *Helianthemum alpestre* (usually semi-sedentary, but sometimes sedentary semi-prostrate and sometimes true creeper). In some cases also *Helianthemum nummularium* and *H. ovatum* may belong to the semi-sedentary type. While the species of *Thymus* are monopodial, the other species mentioned above belong to the sympodial type. —

In Australia this type is much rarer

than the sedentary type, except in the Australian Alps and in Tasmania, but in New Zealand it is well represented and much commoner than the sedentary

¹ As to the nomenclature of these species comp. JANCHEN 1907, 1909, etc., and DU RIETZ 1923 c.

type. Good examples are several species of *Acaena*, *Euphrasia cuneata* (some of the mountain forms; the lowland forms are probably often of the sedentary type), *Raoulia subsericea* and *R. glabra* (comp. FOWERAKER 1917 pp. 24—29), *Gnaphalium trinerve*, *Helichrysum filicaule* and *H. prostratum*, *Leucogenes grandiceps* and *L. leontopodium*, etc. While the other species mentioned belong to the ordinary long-shoot types, *Leucogenes leontopodium* gives an example of a creeping true half-shrub of the semi-rosette type.

There is a considerable difficulty in drawing the line between creeping half-shrubs and creeping herbs, and transitional forms are very common. The difference lies often merely in the duration of the creeping stem as an aërocorm: in a creeping herb the creeping stem is often buried in the second or third year already — thus passing into a secondary plagiogeocorm — while in a creeping true half-shrub (as well as in a creeping dwarf-shrub) it remains over-ground long enough to become well lignified. A good series illustrating this difference is found in the alpine and subalpine species of *Euphrasia* in New Zealand, *i.e.* in the very compound species *E. cuneata* and *E. revoluta* (comp. DU RIETZ 1931 fig. 4). Of course there are also creeping herbs in which the creeping stem simply dies away before it gets the time to develop into a ligneous aërocorm, and also many types in which the tendency to lignification is more or less completely lacking.

c. Suboliferous true half-shrubs.

From my own experience I do not know any certain examples of this type, but according to JESSEN (1913 pp. 15—17, fig. 5) the North American species *Potentilla tridentata* may belong to it at least in some cases.

II. Cane Half-shrubs (*virgultae*).

Without truly perennial overground stems, the overground trunks living only two years, the first year as a sterile long-shoot, which the second year develops lateral floral shoots and then dies away. New biennial aërocorms are then developed from a persisting geocorm.

This type was first distinguished by KRAUSE (1891) under the name of »Virgulta« or »Büsche« (comp. above p. 9). By DRUDE (1896) it has been called »Schösslingssträucher» and by WARMING (1909) »cane undershrubs».

To this type belong most European species of *Rubus*. Good examples of the erect sedentary type are *Rubus idaeus* (comp. LINDMAN 1914 pp. 263—265, fig. 14), *R. suberectus*, *R. plicatus*, etc. (comp. RAUNKIAER 1907 p. 58). Most species of the section *Eubatus*, however, belong to the creeping type. In these species the biennial long-shoots are either prostrate or forming a curve ultimately redescending to the ground; their terminal part is fastened to the ground by strong adventitious roots, and from their terminal buds new biennial long-shoots are developed in the second year (comp. WIESNER 1902 p. 72, RAUNKIAER 1907 p. 58).

(To be continued.)

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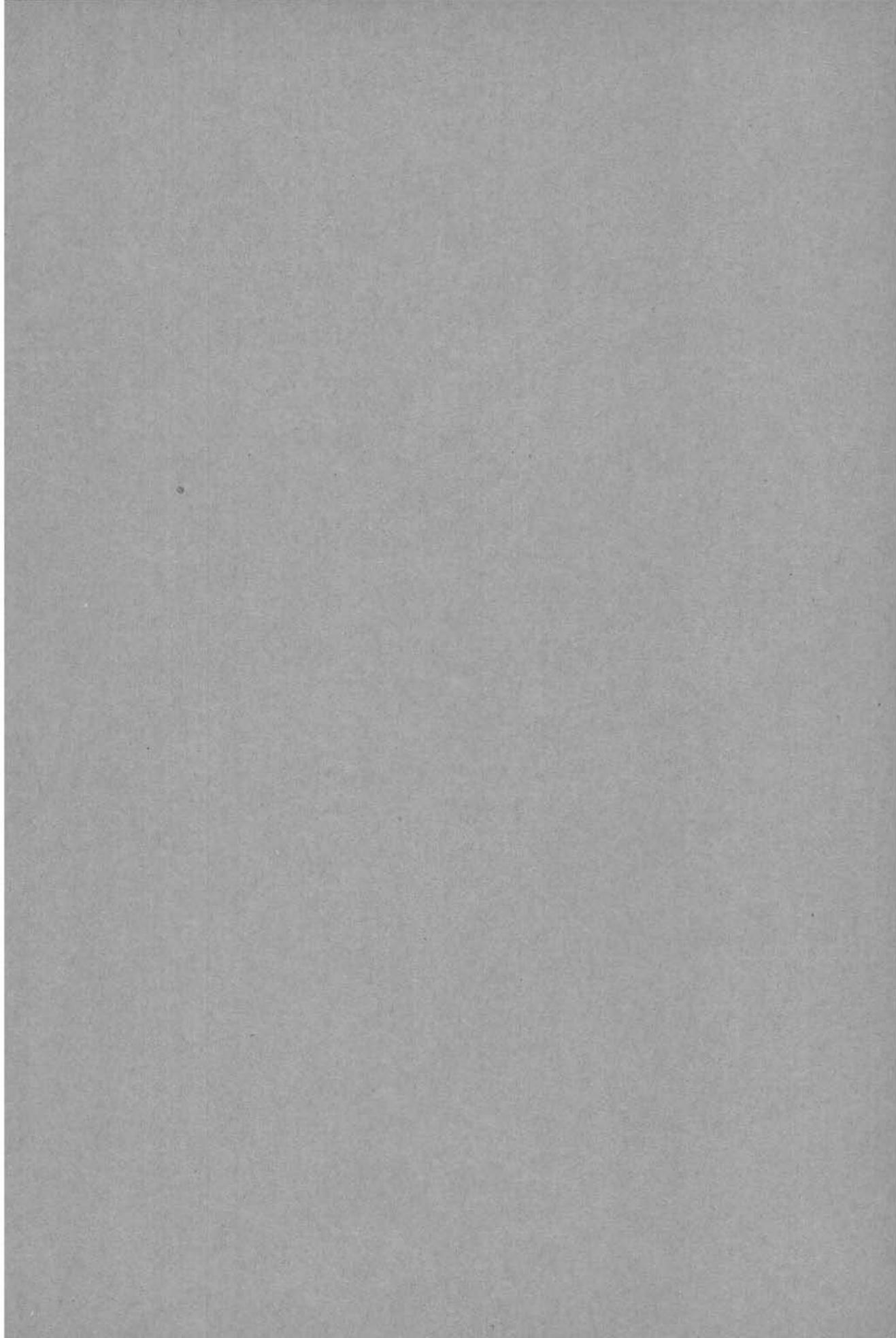
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