

# 4. Rhaeto-Liassic floras and their bearing on the stratigraphy of Triassic-Jurassic rocks

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This paper is a condensation of the following publications by the present author which together constitute an inaugural dissertation. In this summary, special reference is paid to the stratigraphical problems involved.

- I. 1949. A selaginelloid strobilus from East Greenland (Triassic). — Meddel. Dansk. Geol. Foren. Bd. 11, H. 3, 1948, pp. 351—363, 1 pl., 1 text-fig. København.
- II. 1949. De geologiska resultaten från borrhningarna vid Höllviken Del 3: Microbotanical studies of cores from Höllviken, Scania. — Sveriges Geol. Undersökn. Ser. C, No. 506; Årsbok 43 (1949), No. 4. 17 pp., 2 pls., 2 text-figs. Stockholm.
- III. 1949. De geologiska resultaten från borrhningarna vid Höllviken Del 4: On the presence of *Lepidopteris* in cores from "Höllviken II". — Sveriges Geol. Undersökn. Ser. C, No. 507; Årsbok 43 (1949), No. 5. 12 pp., 1 pl., 2 text-figs. Stockholm.
- IV. 1950. Studies in the Rhaeto-Liassic floras of Sweden. I. Pteridophyta, Pteridospermae, and Cycadophyta from the mining district of NW Scania. — K. Svenska Vet. Akad. Handl. Ser. 4, Bd. 1, No. 8. 82 pp., 13 pls., 30 text-figs. 4:0. Uppsala and Stockholm.
- V. 1950. On a fossil *Selaginella* from the Rhaetic of Hyllinge, Scania. — Svensk Bot. Tidskr., Bd. 44, H. 3, pp. 477—487, 2 pls., 2 text-figs. Uppsala.

- VI. 1954. Contributions to the geological history of the Hepaticae. Fossil Marchantiales from the Rhaetic-Liassic coal-mines of Skromberga (Prov. of Scania), Sweden. — Svensk Bot. Tidskr., Bd. 48, H. 2, pp. 381—417, 4 pls., 5 text-figs. Uppsala.
- VII. 1955. Contributions to the geological history of the Hepaticae. II. On a fossil member of the Marchantiineae from the Mesozoic plant-bearing deposits near Lago San Martin, Patagonia (Lower Cretaceous). — Botaniska Notiser, Vol. 108, Fasc. 1, pp. 22—39, 3 pls., 3 text-figs. Lund.
- VIII. 1956. On the stratigraphical value of the megaspores of *Lycostrobus scottii*. Preliminary report of some new finds and their interpretation. — Sveriges Geol. Undersökn. Ser. C, No. 547; Årsbok 50 (1956), No. 3. 12 pp., 1 pl., 1 text-fig. Stockholm.
- IX. 1958. On the presence of the genus *Pseudotorellia* (*Ginkgophyta*) in the Rhaetic of N. W. Scania. — Geol. Fören. Stockholm Förhandl., Bd. 79, H. 4, 1957, pp. 759—765, 1 pl., 1 text-fig. Stockholm.
- X. 1959. Studies in the Rhaeto-Liassic floras of Sweden. II:1. Ginkgophyta from the mining district of NW Scania. — K. Svenska Vet. Akad. Handl. Ser. 4, Bd. 6, No. 2. 40 pp., 6 pls., 9 text-figs. 4:0. Uppsala.
- XI. 1959. On *Ricciisporites tuberculatus* and its occurrence in certain strata of the "Höllviken II" boring in S. W. Scania. — Grana Palynologica, 2:1. 10 pp., 1 pl., 2 text-figs. Uppsala.

The papers will subsequently be referred to in the text by these Roman numerals.

## INTRODUCTION

Amongst the extensive descriptive work devoted to the plant-bearing rocks of the Triassic and Jurassic, that dealing with the floras of the passage beds between the two systems plays an outstanding part. The importance of the Rhaeto-Liassic floras of Europe lies in the fact that they contain representatives of a vegetation which reflects the transition to the more humid conditions prevailing in the Jurassic period as opposed to the arid conditions of the continental Trias. In the district with which I have been particularly concerned, N. W. Scania (Skåne) in South Sweden, this is accompanied by a transgression of the sea and the rapid establishment of marine conditions.

It is natural that the floral assemblages of Triassic-Jurassic rocks have been studied from various points of view, since research workers in this field have been separated not only by time or geographical distance but also by having different training in the fields of botany and geology. Nevertheless the most important limiting factor in the study of fossil plants is the state of preservation of the remains. The present review will principally deal with carbonized material in the state of compressions (the *фитолеймы* of Russian authors; see KRISTOFVIĆ 1957, pp. 34—36, and not with impressions or petrifications, of which the latter play a quantitatively subordinate part in Rhaeto-Liassic floras. The present account

is further limited to vascular plants and bryophytes; accordingly, terrestrial deposits only will be concerned here.

The information available may provisionally be grouped into the following categories:

- A) Palaeobotanical descriptions limited to the megascopical features of the fossil plant-remains.
- B) More elaborate descriptions of the external morphology of the megascopical remains, where special attention is paid to the microscopical investigation of leaf-cuticles and spore- and pollen-bearing organs.
- C) Palynological descriptions, i.e. descriptions limited to the study of detached spores and pollen grains (sporomorphs).
- D) Cuticle descriptions, referring to microbotanical studies of detached leaf-cuticles etc.

A) Material preserved both as compressions and impressions belongs to this category. It is natural that this line of research predominates 19th century work on the floras of the Rhaeto-Lias. Typical for this period are NATHORST's descriptions of the Pålshö (1876, 1878), and the Bjuv floras (1878—1886)<sup>1</sup>; as an exemplary study of this kind may be quoted ZEILLER's "Flöre fossile des gîtes de charbon du Tonkin" (1903). To limit the descriptive work to the megascopic features of the plants may still in many cases be a suitable approach in the study of fossil floras from little known districts. In the case of impressions, more detailed morphological studies are made impossible by the state of preservation of the plants. For instance, the flora of the Höör sandstone *sensu stricto* (cf. ANTEVS 1919) belongs here.

B) More valuable results from a botanical point of view have been obtained by the microscopical study of material preserved as compressions. This necessitates the employment of more refined methods of investigation such as oxidative treatment with Schulze's mixture or similar agents (see FLORIN 1931, pp. 35—36), or some modification of the transfer method (WALTON 1923). The most complete study of this kind is HARRIS's investigation of the Rhaeto-Liassic floras of Scoresby Sound, East Greenland (1926a, 1931b, 1932a, 1932b, 1935, 1937). This was later followed by a similar investigation of the floras of Yorkshire, England of mainly Middle Jurassic age. Studies including the description of leaf-cuticles of gymnosperms have also been carried out in France by CARPENTIER ("Les flores infraliasiques des Deux-Sèvres et de la Vendée", 1947—49) and others. Whereas

<sup>1</sup> For the position of the localities in N. W. Scania mentioned in the text, see the geological map in IV (p. 8, text-fig. 1). Pålshö is situated immediately northwest of Hälsingborg. Localities and boreholes outside the mining district are shown in TROEDSSON 1951 (p. 15, text-fig. 2).

the cuticle descriptions of the Liassic flora of Nuremberg studied by GOTHAN in 1914 are already rather out-of-date, modern standards are represented by KRÄUSEL's papers on the somewhat older (Keuper) floras of Lunz in Austria and Neuwelt near Basel, Switzerland (see in particular KRÄUSEL 1943, 1949). These investigations are limited to certain groups of gymnosperms, however. Before the first world war, NATHORST and ANTEVS made several investigations of plants from the Rhaeto-Liassic floras of Sweden using the "maceration" method mentioned above, to which NATHORST's name became specially attached. In spite of the great importance of these studies from a botanical point of view, the cuticle descriptions appear now rather primitive, like those in the memoir on the floras of the localities Skromberga and Stabbarp published by JOHANSSON in 1922. The highest accomplishments in this line of research have been reached by FLORIN's investigations of the epidermal structure of the gymnosperms, which to some extent include material from the Rhaeto-Lias of Sweden — his most well-known study of this kind deals with a cycad (*Palaeocycas integra-Bjuvia simplex*) from the Rhaetic of Bjuv (1933). In the case of the Swedish Rhaeto-Liassic floras there is a strongly felt need for a revision of the floras as a whole, however, carried out along the lines suggested by HARRIS's investigations of the Scoresby Sound floras. — In extra-European countries work on Triassic-Jurassic plants of the kind referred to here has been more sporadic.

C) Palynological studies of Triassic-Jurassic deposits began comparatively late, and have been pursued on a larger scale only after the second world war. Some of the pioneer study in this field has been carried out by the Russians (see POKROVSKAJA 1950, pp. 8—11, 23—24), but there are also early contributions from Germany (REISSINGER, THIERGART), Sweden (ERDTMAN), and Australia (DE JERSEY).

In the U.S.S.R., the Rhaeto-Liassic deposits of the Urals and adjacent regions have attracted particular interest (MAL'AVKINA 1949, 1953, 1956; cf. also POKROVSKAJA 1950). Similar studies have also been carried out in the Polish Lias by ROGALSKA (1954, 1956), and in the Hungarian Lias by GÓCZÁN (1956). A study of the spore and pollen floras of the Rhaeto-Lias of Scania has recently been published by NILSSON (1958). Somewhat older deposits were studied by LESCHIK (1955), who investigated the Neuwelt locality mentioned above. Younger floras have been studied i. a. by COUPER in 1958 (the British Mesozoic), and by BOLCHOVITINA in 1956 (Jurassic and Lower Cretaceous deposits of the Jakutsk district in Siberia).

D) Work of this category has hitherto attracted relatively little attention, probably because it requires a wide knowledge of the morphology of plants from the Older Mesozoic. Its importance has been emphasized by HARRIS's studies of the Rhaeto-Liassic floras of East Greenland and

particularly by his subsequent investigation of the floras of the Yorkshire Jurassic (see in particular HARRIS 1953). Similar work has also been made on a minor scale by Indian workers (cf. SITHOLEY 1954 and SAH 1955). Its great importance for the study of the Rhaeto-Liassic deposits of Sweden and for stratigraphical work in general has been pointed out by the present author in 1949 (II, pp. 3—4, III, p. 3; cf. also IV, p. 6).

The papers by the author treated in the present review fall into the following categories:

B) I, IV, V, VI, VII, IX, X

(VII is a description of material from the Lower Cretaceous but includes references to fossil remains from Triassic-Jurassic rocks and a general discussion.)

C) VIII, XI

D) II, III

It is natural that any attempt at a classification of this kind tends to be somewhat schematic. Attention is drawn to the fact that, for instance, palynological studies form a part also of the papers listed as I—VI.

## THE CORRELATION AND VERTICAL DISTRIBUTION OF THE RHAETO-LIASSIC FLORAS OF N. W. EUROPE AND E. GREENLAND

As early as in 1914 GOTHAN recognized two distinct floras in the "Grenzschichten" of Germany, viz. an older, Rhaetic one (occurring i.a. at Coburg and Seinstedt), and a younger, Liassic one, of which the chief representative is the Nuremberg flora. The absence of *Lepidopteris ottonis* in the younger flora was particularly mentioned by GOTHAN (1914, p. 165). Attention should be drawn to the fact that the older flora with *Lepidopteris* occurs at Coburg below the zone with *Psiloceras planorbis*, and that *Avicula contorta*, a bivalve characterizing the marine Rhaetic, was associated with the Seinstedt plants. A species of *Psiloceras* characteristic of the Planorbis zone has recently been found in a marine intercalation in the plant-beds at Sassendorf in Franconia, which represent the younger flora (KUHN 1955, cf. KRÄUSEL 1958, p. 68). These are overlain by an Oolithenbank and clayey beds with *Schlotheimia angulata* representing the Lias  $\alpha_2$ . The stratigraphical position of the German Rhaeto-Liassic floras is thus well defined.

In connection with his studies of the Rhaeto-Liassic floras of Scoresby Sound, East Greenland, HARRIS (1931a, p. 159) established the presence of two zones in the plant-bearing Rhaetic and Lower Lias of Europe and Greenland: "the *Thaumatopteris* Zone, corresponding approximately to the Hettangian, and the *Lepidopteris* Zone, corresponding approximately to the Rhaetic". According to HARRIS (loc. cit.) no flora outside this area could be satisfactorily correlated with the Rhaetic.



HARRIS published in 1937 a more comprehensive survey of the stratigraphy of the Rhaeto-Liassic beds of Scoresby Sound, comparing them with contemporary occurrences in Sweden, Germany, and other European countries as well as with plant-bearing deposits of similar age outside Europe. He pointed out the strong resemblance between the Swedish flora and the East Greenland one, illustrating it with tables of the vertical distribution of certain plant species in the areas mentioned and in Germany. The plant-bearing series of Scoresby Sound did not contain any remains of fossil animals of great stratigraphic value. It forms part of the Cape Stewart formation, which was discussed by HARRIS (1937) and more recently by DONOVAN (1957, pp. 23—27, 127).

HARRIS's conception of the *Lepidopteris* and *Thaumatopteris* floras was applied to the stratigraphy of the Rhaeto-Liassic of Scania in various papers by TROEDSSON, of which the most important ones were published in 1938 and 1951. As early as in 1934, however, TROEDSSON had put forward a revision of the old stratigraphical table outlined in principle by LUNDGREN (1881) and NATHORST (1880, 1894); see TROEDSSON 1951, p. 14 (for a review of part of TROEDSSON's work cf. LUNDBLAD 1946).

After the death of TROEDSSON, the question of the zonal stratigraphy of the Rhaeto-Lias of Scania was further discussed by REYMENT (1959) in connection with a study of ammonites of Sinemurian to Toarcian age from Southern Sweden. REYMENT draws attention to the important fact that for example ARKELL (1956, p. 465) placed the Swedish Rhaetic in the Trias in contradistinction to TROEDSSON (1951, p. 16), who regarded it as the basal part of the Jurassic. With TROEDSSON (1951, p. 121) REYMENT refers the Hälsingborg formation with the *Mytilus*-, *Cardinia*-, *Cyclas nathorstii*- and *Pullastra* levels (and the "Ostrea bank") to the Lias  $a_1$ — $a_2$ , i.e. the Hettangian.

Since my own studies of certain floras from N.W. Scania are unfinished, I have not thought it suitable to carry out a more extensive comparison between the floras of the Rhaeto-Liassic deposits of Scania and contemporary ones from several other districts. This will be postponed until a later occasion. Nevertheless it is already now possible to see in a general way to what extent the fundamental conception of the existence of two plant-bearing zones — the *Lepidopteris* and *Thaumatopteris* zones of HARRIS — is supported by the material studied in our papers IV—VI and IX—X. It should be noted that these in many cases contain revisions comprising all the Scanian material of a species. The comparison will for the present be confined to the Scoresby Sound flora.

The following species are restricted to the *Lepidopteris* zone in East Greenland, and have a similar distribution in Sweden (the Rhaetic, named by TROEDSSON "the Mine formation"): *Triletes pinguis* HARRIS (megaspore), *Neocalamites boerensis* (SCHIMPER) HALLE, *Todites scoresbyensis* HARRIS (in Sweden sterile foliage only), *Dictyophyllum exile* (BRAUNS) NATHORST, *Antevsia zeillerii* (NATHORST) HARRIS (the microsporophyll of *Lepidopteris*

*ottonis*, cf. below), *Ptilozamites nilssonii* NATHORST, *Doratophyllum astartensis* HARRIS, *Anomozamites minor* NATHORST, *Wielandiella angustifolia* NATHORST, *Pterophyllum compressum* LUNDBLAD (*Pt. schenki* in HARRIS 1937), *Pterophyllum kochii* HARRIS, *Pterophyllum ptilum* HARRIS (the Swedish material was designated *Pt.* cf. *ptilum* in IV), *Bennettistemon bursigerum* HARRIS, *Bennetticarpus exiguus* HARRIS, *Ginkgoites obovatus* (NATHORST) SEWARD, *Sphenobaiera paucipartita* (NATHORST) FLORIN (the author includes the East Greenland *Sph. amalloidea* in this species in X).

Since the main part of the material from the floras of Billesholm, Hylinge, and Vrams Gunnarstorp was obtained from Rhaetic strata (IV, pp. 6—7), my work has given comparatively little new information on the vertical distribution of the Liassic species. Only two species confined to the *Thaumatopteris* zone in Greenland have been studied by me, viz. *Cladophlebis svedbergii* JOHANSSON and *Ginkgoites marginatus* (NATHORST) FLORIN, which both occur only in the basal Lias of Sweden.

The following new species described by me (IV, V, VI, IX, X) are restricted to Sweden: *Ricciopsis florinii* (Liassic), *R. scanica* (Liassic), *Marchantiolites porosus* (Liassic), *Selaginella hallei* (Rhaetic), *Marattiopsis crenulata* (Rhaetic), *Doratophyllum scanicum* (Rhaetic), *Pseudoctenis florinii* (Rhaetic), *Desmiophyllum cyclostomum* (Rhaetic), *Ginkgoites troedssonii* (Rhaetic), *Pseudotorellia minuta* (Rhaetic), *Hydropterangium byllingense* (Rhaetic). It should be noted, however, that megaspores of the type found in *Selaginella hallei* (*Triletes pinguis* HARRIS) occur in the *Lepidopteris* zone of Scoresby Sound.

The following species studied by me, which occur both in the Rhaetic and Liassic of Greenland, were found to have the same vertical occurrence in Sweden: *Todites goeppertianus* (MÜNSTER) KRASSER, *Clathropteris meniscioides* BRONGNIART.

The differences in the vertical distribution of the species common to Sweden and Greenland studied by me do not concern a great proportion of the species but among them are some forms regarded as particularly important from a stratigraphical point of view.

It should be noted that the investigation of material of *Lepidopteris ottonis* (GOEPPERT) SCHIMPER from Scania published in IV (pp. 30—32) shows that the species may rarely extend into the basal Lias in Sweden. As mentioned above, it is regarded as a guide-fossil of the *Lepidopteris* zone, and is absent from the *Thaumatopteris* zone in Germany and East Greenland (cf. above). The author is of the opinion that sporadic finds of *Lepidopteris ottonis* outside the Rhaetic do not invalidate its use as a guide-fossil for the *Lepidopteris* zone (cf. III). In the sense of HEDBERG (1958, pp. 1887—1888) the latter is an assemblage-zone and not a range-zone. It has thus received its name from a form particularly representative of the "*Lepidopteris ottonis* Assemblage-zone".

Also *Thaumatopteris schenkii*, the guide-fossil of the *Thaumatopteris* zone of HARRIS (which following HEDBERG 1958 should be termed the "*Thaumatopteris schenkii* Assemblage-zone") extends its range in Sweden beyond the

limits indicated in Germany and East Greenland. The previously known localities in Scania (Hälsingborg, Höganäs, Höör, Stabbarp) all belong to the Liassic, but the species has now been recorded by the author from the Rhaetic of Billesholm (IV, p. 28; cf. also p. 7 for the stratigraphy).

Two other species regarded by HARRIS (1931a, p. 157, and 1937, p. 22) as characteristic of the *Thaumatopteris* zone, viz. *Thaumatopteris brauniana* POPP and *Phlebopteris angustiloba* (PRESL) HIRMER et HÖRHAMMER occur in the upper coal bed of Billesholm, which belongs to the Rhaetic.

The sporadic occurrence of *Thaumatopteris schenkii*, *Th. brauniana*, and *Phlebopteris angustiloba* in the Rhaetic does not invalidate their use as guide-fossils for the *Thaumatopteris schenkii* Assemblage-zone (cf. HEDBERG 1958, loc. cit.).

#### CORRELATION BY PLANT MICROFOSSILS IN TRIASSIC-JURASSIC STRATA WITH SPECIAL REFERENCE TO THE LOWER MESOZOIC OF SCANIA, SWEDEN

The material available for microbotanical studies in Triassic-Jurassic strata (cf. p. 6) has generally been obtained by methods involving the dissolution or disintegration of the rock, such as treatment with hydrofluoric acid, and with strong nitric acid (HARRIS 1926 b, cf. I—VI, VIII, XI). These may be extended by methods for the separation of plant material and mineral-matter by the aid of heavy fluids, preferably combined with centrifugation. The latter methods seem to have been little used except in the U.S.S.R., however. According to POKROVSKAJA (1950, pp. 44—45) oxidative treatment followed by centrifugation with THOULET's solution has been a standard method for the study of spores and pollen grains from Mesozoic and Cenozoic rocks at the All-Union Geological Institute (VSEGEI) at Leningrad. The present author has not used THOULET's solution, which is highly poisonous, but other methods. She has repeatedly carried out separation with bromoform-acetone mixture according to KNOX 1942 (I, VI, XI), and also tried a modification of a method for the separation of carbonaceous matter from the rock by carbon tetrachloride suggested by ZETZSCHE in 1932 (XI). Finally, successful results were obtained by the use of potassium-cadmium iodide instead of THOULET's solution [see DOROGANEVSKAJA, ŠENFINKEL, and GRIČUK 1952 (XI)].

In the present discussion the stratigraphical value of two categories of microfossils only will be considered, viz. the "sporomorphs" (ERDTMAN 1947), and the cuticles. The megaspores of the *Lycopsidea* (the systematic terminology used in the present paper follows ENGLER 1954), other kinds of spores of *Pteridophyta* as well as those of certain *Bryophyta*, and pollen grains of gymnosperms and angiosperms belong to the first-mentioned category. Leaf-cuticles from Triassic-Jurassic rocks may in practice be regarded as representing gymnosperms only, since those of the ferns



do not resist the strong oxidative treatment used for the preparation, and remains of angiosperms are exceedingly rare in Jurassic rocks. Stem cuticles of *Articulatae* may be expected to occur in rather large quantities in certain strata and may in some cases be specifically determinable. Besides sporomorphs and cuticles, seeds, sporangia, gymnospermous tracheids etc. may be found in samples treated according to the methods mentioned above, and be of use in certain connections.

The megaspores of the *Lycopsidea* are specially notable among the categories of microfossils that seem to be particularly suitable for stratigraphical correlation of Lower Mesozoic rocks (cf., for instance, DIJKSTRA 1951). We know that larger members of the *Lycopsidea* existed in the Older Mesozoic side by side with the herbaceous forms (cf. I, VIII). The former type is stratigraphically significant and may in cases have a wide horizontal distribution; this is indicated by the well-known *Pleuromeia*, a characteristic plant of the Lower Trias, which has been recorded from W. Europe to the Far East (see, for instance, KRIŠTOFOVIČ 1957, p. 191, and VACHRA-MEJEV 1957, p. 90). That megaspores occasionally may be used for long-distance correlations is suggested by the finds of similar megaspores in the *Glossopteris* flora of Brazil, and Katanga (PIÉRART, 1958) and by recent studies of megaspores from the Lower Cretaceous by COOKSON and DETTMANN (1958), who found spores similar to those of the Wealden deposits of Europe as far away as in Australia. The present author has hitherto only studied megaspores from the Rhaeto-Liassic, viz. those of *Lycostrobus scottii* (VIII), and *Triletes pinguis*, a species which includes the megaspores of *Selaginella hallei* (IV, V).

HARRIS (1935, p. 154) had come to the conclusion that *Lycostrobus scottii* "appears to be a useful zone fossil of the *Thaumatopteris* Zone", and this is supported by the evidence brought together by the present author in 1956 (VIII). The megaspores of *Lycostrobus scottii* are regarded as characteristic of the Lower Liassic strata of Sweden, East Greenland, and Germany<sup>1</sup>. As regards their vertical distribution it should be noted that the megaspores of *Lycostrobus scottii* occur in the *Thaumatopteris* zone of Scoresby Sound down to a bed transitional between this and the *Lepidopteris* zone. In Sweden, finds of strobili are only known from Hälsingborg harbour (basal Lias). At Svedala in S. W. Scania megaspores of *L. scottii* are associated with small cuticle fragments comparable with *Lepidopteris ottonis*; they are accompanied by cuticles similar to the Rhaetic conifer *Stachyotaxus septentrionalis* in a boring at Stabbarp. These observations are of interest as suggesting occasional overlapping of an important guide-fossil of the *Thaumatopteris* Assemblage-zone, comparable to that of *Thaumatopteris schenkii*, *Tb. brauniana*, and *Plebopteris angustiloba* mentioned on pp. 89—90.

<sup>1</sup> According to information in letter by Dr. J. ZNOSKO (Warsaw) the Polish spores figured by him in 1955 (see VIII, p. 8) do not belong to *L. scottii*. The new record by MARCINKIEWICZ (1957) from the Święty Krzyż mountains is not verified by illustrations.

Attention should be paid to the fact that megaspores of *Lycostrobus scottii* were found by the present author in certain strata of the "Höllviken II" boring in S. W. Scania previously referred by BROTZEN (1950) to the Wealden. The finding was interpreted as indicating "a Rhaetic-Liassic, possibly lias *a* age of the plant-bearing horizon referred to the Wealden" (VIII, p. 9). The interpretation is supported by the finding of the Rhaeto-Liassic species *Ricciisporites tuberculatus* ("spore tetrads") at the same horizon (XI), as well as by unpublished material of *Czekanowskia*. It should be noted, however, that the finds in the "Höllviken II" boring pointing to a Rhaeto-Liassic age of strata previously ascribed to the Wealden are restricted to the levels 1422.08—1428.08 m, and 1433.81 m. They do not invalidate BROTZEN's interpretation of higher horizons of the same boring as referable to the "Wealden."

The present author agrees with JUNG (1958) that the megaspores of *Lycostrobus* should have a generic and specific name of their own, but prefers to use the neutral denomination "megaspores of *Lycostrobus scottii*" in the present case. The reason for this is that the Swedish material of *L. scottii* cannot be referred to any of the species suggested by JUNG until its range of variation has been investigated statistically. It is moreover difficult to exclude the possibility that the differences in size between the material from N. Europe and E. Greenland and that from Central Europe might be influenced by different chemical treatment of the spores.

In contradistinction to the strongly sculptured megaspores of *Lycostrobus scottii* the megaspores named *Triletes pinguis* by HARRIS (1935) are smooth-coated, showing resemblance to those of the living *Selaginella martensii* (IV). The stratigraphical value of this type must therefore be rather low in the case of isolated spores. This is also suggested by the fact that the *Triletes pinguis* type of spores occurs in *Selaginella ballei* (IV, V), a herbaceous lycopsid similar to the sub-genus *Stachygynandrum* of the living genus *Selaginella*. That smooth-coated spores of *Triletes* must be used with discrimination for stratigraphical work is also suggested by the fact that a type of smooth-coated megaspores rather similar to *Triletes pinguis* is known in *Selaginellites polaris* from the Lower Triassic (Eotriassic) of Hold with Hope, East Greenland (I).

NILSSON (1958) has drawn attention to the fact that not only the megaspores of *Lycostrobus scottii* but also its microspores may be of considerable value in stratigraphical connections. Spores of the *Chasmatosporites* type, which includes the microspores of *Lycostrobus*, were found by him to have a rich occurrence in an oil-shale known from borings at Sandåkra in northern Scania. This represents according to him the uppermost Rhaetic. *Chasmatosporites* has been reported both from some Liassic localities in Scania, such as Höör, Pålshö, and Tosterup, and from the Rhaetic of Bjuv. As pointed out by NILSSON similar spores occur in the Lias of Poland. NILSSON (1958) includes ERDTMAN's *Monosulcites magnolioides* in *Chasmatosporites*. This form was compared by the present author (IV, p. 67) with Bennettitalean microspores. She has not yet been

in a position to restudy similar material in the light of the evidence brought forward by NILSSON. In this connection, attention should be called to the possibility of distinguishing between spores of *Pteridophyta* and pollen grains of gymnosperms by staining with fuchsin. This method was suggested for Mesozoic material by THIERGART in 1949, and was based on ZETZSCHE and KÄLIN's experience of the different staining of sporonin and pollenin [(1932); see JUST 1951]. A new way to identify different taxonomical units is study of the wall of the sporomorph by the aid of elaborate optical techniques (see, for instance, ERDTMAN 1959).

In the study of microfloras of spores and pollen grains in the Mesozoic the best stratigraphical results are obtained by a study of the whole assemblage of sporomorphs. Estimations of the percentage-proportions of components representing the main systematic groups (*Pteridophyta*, *Gymnospermae*, and *Angiospermae*) seem well justified (cf. THIERGART 1949, p. 27, and POKROVSKAJA 1950, pp. 358—370), and may in cases give valuable stratigraphical suggestions. The boundary between the Lower and the Upper Cretaceous may thus be well marked off stratigraphically by the appearance of pollen grains of angiosperms, reflecting the sudden rise of this group.

The proportions of spores and pollen grains comparable with different natural groups, such as various families of ferns, certain *Cycadophyta* and *Ginkgophyta*, or conifers, have been used for stratigraphical correlations of Triassic-Jurassic rocks by MAL'AVKINA (1953, 1956), who in particular studied the Emba and Akt'ubinsk regions to the south of the Urals. She was thus able to distinguish between various spore and pollen complexes representing the Rhaetic, the Lower Jurassic, and the Middle Jurassic. Moreover, pre-Rhaetic and Rhaetic complexes of the Emba district were separated by the complete absence of spindle-shaped pollen-grains (sporomorphs) similar to those of the *Ginkgophyta*, *Bennettitales* etc. in the former. The interpretation of the conditions in the Rhaetic and the Jurassic were complicated by the fact that the region studied by MAL'AVKINA lies in the border-land between two phytogeographical provinces (cf. VACHRAMEJEV 1957, p. 94, text-fig. 3).

Attention should be drawn to the fact that estimations based on comparisons with lower systematic groups always include considerable sources of error, due to the well-known fact that unrelated sporomorphs in many cases show a tendency to overlap. These difficulties were recognized by NILSSON (1958), who used a classification into artificial groups only for the stratigraphical comparison between the spore and pollen contents of the Swedish Rhaeto-Liassic and those of the Older Mesozoic as a whole (op. cit., Tables 2—3).

In addition to extended studies of the Swedish Lower Mesozoic rocks along the lines suggested above, where the whole assemblage of spores and pollen grains is taken into consideration, attention should be directed on the establishment of guide-forms, facilitating stratigraphical determina-

tions of samples of cores etc. A good example of work along this line is a study by KLAUS (1953) entitled "Mikrosporen-Stratigraphie der ostalpinen Salzberge". The Austrian author constructed "Sporen-Spektren" for the Upper Permian, the Triassic, and the Liassic, using a few dominant forms only. Of particular interest for a comparison with Swedish material is the Lower Triassic guide form "*Pityosporites ballstattensis*" (for its vertical distribution see KLAUS 1953, p. 168, Abb. 2), since a somewhat similar type occurs in the Triassic strata of the "Höllviken II" boring ("*Sporomorpha c*" in II, p. 13; for the stratigraphy cf. BROTZEN 1950, pp. 16—21.<sup>1</sup>)

My own work on isolated sporomorphs from the Rhaeto-Lias is, besides the studies of megaspores discussed above, mainly confined to the description of the tetrads named *Ricciisporites tuberculatus* (VI, XI; cf. also III, p. 5; Pl. 1, Fig. 13). Several kinds of spores (and pollen grains of gymnosperms) obtained by the preparation of sporangia and pollen-sacs, are described in IV (cf. also V). My own experience, as well as the collected information available from palynological studies of the Swedish Rhaeto-Lias, is not yet large enough to allow the definite establishment of a series of species suitable as guide-forms. Attention should be drawn, however, to some types which appear to be useful for this purpose. The above-mentioned *Ricciisporites tuberculatus* is a well-defined species not known outside the Rhaeto-Lias, and appears to be a good guide-fossil in the Swedish Mesozoic (XI, p. 8). Since it occurs both in the Rhaetic and in the basal Lias, it cannot be used for the determination of the Rhaeto-Liassic boundary. The species is known only from the Rhaetic strata of Scoresby Sound, but its vertical distribution in East Greenland has not yet been systematically studied. *Eucommiidites troedssonii* (ERDTMAN) COUPER (see NILSSON pp. 63—65) may be mentioned among forms that may prove useful for the determination of the Rhaeto-Liassic boundary in Sweden. In the *Pteridophyta* schizeaceous ferns may be pointed out as having a prominent exine sculpture, which makes them likely to be of use for stratigraphical purposes. The genus *Corrugatisporites*, which is represented by two species in the Liassic of Scania (NILSSON 1958, pp. 43—45), has been compared with the *Schizæaceae*. Among the pollen grains compared with the *Coniferae*, *Cerebropollenites mesozoicus* (COUPER) NILSSON is characterized by a well-defined exine sculpture. The grains have been compared with *Tsuga* by COUPER but according to FLORIN (1958, p. 382), no forms which could be expected to have produced such pollen grains are known as yet from the Jurassic. The species extends downwards to

<sup>1</sup> According to information in a letter from Dr. KLAUS, who kindly undertook an investigation of a sample from the "Höllviken II" boring in 1955 at the author's suggestion, the "*Sporomorpha c*" is not identical with the Austrian form. A somewhat similar sporomorph has recently been described from the Keuper of Swierczyna in Poland by PAUTSCH (1958, p. 323, Pl. 1, Fig. 6). The Triassic forms mentioned are all distinguished from accompanying ones by their large sizes, but the Polish and Austrian sporomorphs are more roundish in shape than the Höllviken one. The resemblance may imply that the sporomorphs in question represent systematically related plants.



the Rhaeto-Liassic boundary. This is also the case with *Classopollis torosus* (REISSINGER) COUPER (see NILSSON, op. cit., pp. 74—76), in which may be included the microspores of the conifer *Cheirolepis muensteri* from the Lias of Franconia (cf. KLAUS 1953, p. 166). The last-mentioned forms are therefore regarded as being of potential stratigraphical value for the determination of the boundary between the Triassic and the Jurassic.

For a review of cuticular analysis from a taxonomic point of view the reader is referred to HARRIS 1947, and to JUST 1951; general information on this subject may also be obtained in II, pp. 3—4, 7—9. It will be evident from the information provided by these sources that material of detached leaf-cuticles from the Older Mesozoic may easily be classified into two groups on the base of the structure of the stomatal apparatus, corresponding to the haplocheilic and syndetocheilic types of FLORIN (1933). In Lower Mesozoic deposits nearly all cuticles with syndetocheilic stomata may be identified with the *Bennettitales*. Bennettitalean cuticles are also in general characterized by having sinuous cell-outlines, or walls with jagged thickenings, but this is not a constant feature of the group.

Haplocheilic stomata occur in the *Cycadales*, *Ginkgoales*, *Coniferae*, and in Mesozoic Pteridosperms. Forms which to some extent appear "transitional" occur in the latter group and in the *Pentoxylales* (II, pp. 8—9; cf. TOWNROW 1957, and SAHNI 1948). The orders may as a rule be distinguished from each other by the characters of the leaf-cuticle, but this does not exclude the occasional presence of atypical cases causing uncertainty. The worker carrying out identifications from cuticles obtained by maceration in bulk, and similar methods, will in practice not always have to rely on microscopical characters alone. The determination may be facilitated by the circumstance that many fragments will provide some suggestions of the external shape of the leaf, as, for instance, whether it was needle-shaped or not, or whether the margin was entire or dentate (cf. the Höllviken material of *Lepidopteris* published in II, and SZE 1953). Suggestions concerning the kind of venation of the leaf may even be obtained from small cuticle fragments, and this will in cases provide useful information about the affinities of the plant (cf. X pp. 6, 20).

The genera *Nilssonia* and *Doratophyllum* are both well characterized by the epidermal structure of the leaf. The stomata are haplocheilic, and suggest affinity with the *Cycadales*. The close relationship between *Nilssonia* and the said group was proved from a study of the reproductive organs corresponding to the leaves, whereas *Doratophyllum* is still only tentatively compared with the true cycads. The leaves of both are hypostomatic, and the cuticles show in places more cutinized cells with trichome scars (cf. IV, pp. 40—47). Polymorphism and intergrading occur in the Rhaeto-Liassic species of *Nilssonia*, and are likely to make them less useful for stratigraphical work than *Doratophyllum*, which is represented by three well-defined species in the Rhaeto-Lias of Scania. According to HARRIS (1937, p. 29), *Doratophyllum astartensis*, which is hitherto known only from



the Rhaetic, may be a satisfactory species as a zone fossil. This applies also to detached leaf fragments.

The epidermal structure of the *Bennettitales* appears to be of little use for the generic distinction of sterile leaves, since the genera based on leaf form may be expected to be heterogeneous with regard to their natural affinities. Nevertheless the group includes characteristic species, which may be identified from their cuticles alone. To these belong, for instance, *Pterophyllum compressum* and *Pt. ptilum*, which were used by the author for establishing the Rhaetic age of certain strata of the Höllviken boring (III, IV; it should be noted that *Pt. compressum* LUNDBLAD in IV is identical with *Pt. aequale* (BRONGNIART) NATHORST in III).

The possibility of using the epidermal characters of the *Ginkgoales* for the determination of cuticles in borings has been mentioned in X (p. 6). This paper contains a review of the microscopical characters of members of the genera *Ginkgoites* (pp. 8, 10), and *Sphenobaiera* (pp. 29—31). Attention should be drawn to the fact that remains of the genus *Czekanowskia* HEER (see FLORIN 1936), which seems to occupy a more isolated position from a systematic point of view, are as a rule easy to determine generically from fragments since the cuticle is uniform, and the shape of the leaf is indicated even in small portions. Similar material occurs in a layer with megaspores of *Lycostrobus scottii* in the "Höllviken II" boring mentioned in VIII.

The *Coniferae* (and the *Taxales*) are of great potential significance for stratigraphical determinations. The diagnostic value of the epidermal structure of various recent genera was treated in a monograph by FLORIN in 1931, which greatly facilitates the interpretation of the fossil material. FLORIN has published numerous papers on the epidermal structure of the *Coniferae* in connection with his studies of evolution in *Cordaites* and conifers. Attention should here in particular be called to his recent paper on Jurassic taxads and conifers of N. W. Europe and E. Greenland (FLORIN 1958). It contains information on the appearance of different genera during the Jurassic, and includes descriptions of several well-defined species from the Rhaeto-Lias of N. W. Scania, which are of value also for future identifications of detached cuticles.

A fragmentary cuticle compared with the genus *Voltzia*, which is common in the Triassic of Central Europe, was figured from pre-Rhaetic strata of the "Höllviken II" boring in II. Attention should be called to the resemblance between my figures (II, Pl. 2, Figs. 1—2), and the *Voltzia* stomata figured by KRÄUSEL in 1955 (p. 12; text-fig. 7). The descriptions of pre-Rhaetic material from the Mesozoic published after 1949 support on the whole the suggestions as to the age of the "Höllviken II" strata studied in II (see TOWNROW 1957, and the papers on sporomorphs mentioned on p. 94).

The Mesozoic pteridosperms are a probably heterogeneous group of considerable interest also from a stratigraphical point of view. The genus

*Lepidopteris*, which had a wide distribution in the Triassic (see, for instance, III, SZE 1953, and TOWNROW 1956) belongs here. It occurs both in the northern and the southern hemispheres; the value of *Lepidopteris ottonis* as a guide-fossil for the Rhaetic has already been mentioned. Other important genera referred to this group are *Thinnfeldia* (IV, pp. 34—35), *Stenopteris* (IV, pp. 35—38), *Ptilozamites* (IV, pp. 38—39), and *Dicroidium* (see in particular TOWNROW 1957). The cuticle characters of several members of these species are well known. *Ptilozamites* appears to be useful for the correlation of the Rhaeto-Lias of Scania [for instance the Rhaetic *Pt. nilssonii* (IV, pp. 38—39), which has a well-defined cuticle], and this applies also to members of the genera *Thinnfeldia* and *Stenopteris*, of which the Swedish material needs further study. *Thinnfeldia* and *Dicroidium* have their main distribution in the southern hemisphere (cf. HARRIS 1937, and JUST 1951).

The Mesozoic *Caytoniales* have been compared both with angiosperms and with Mesozoic pteridosperms; their gymnospermous affinities seem now unquestionable. The cuticle of the leaf, *Sagenopteris*, is very characteristic, not the least as regards the shape of the stomatal apparatus. The Rhaeto-Liassic species will probably be of use for determining the Rhaetic-Liassic boundary in material from Scania.

HARRIS published in 1937 a table of the vertical distribution of plant species in the Rhaeto-Liassic of Scoresby Sound, which represents a selection of the stratigraphically more useful forms. It is significant that about fifty per cent of these consist of gymnospermous leaves, to a great extent defined by their cuticles; these may in the majority of cases be specifically determined from isolated fragments, at least when both sides of the leaf are present. This circumstance gives an idea of the usefulness of cuticle determinations in stratigraphy. The disadvantage in using cuticles instead of sporomorphs for stratigraphical determinations is the fact that the former cannot be expected to suffer transport over such great distances as the latter, and to be distributed so widely. Although their horizontal ranges may thus be smaller, cuticles on the whole are not inferior to sporomorphs for stratigraphical purposes.

The successful stratigraphical employment of "cuticular analysis" depends at present mainly on the extension to which plant-remains preserved as compressions have been studied microscopically from the districts and strata concerned. From the review given in pp. 84—87 it will be evident that conditions for this kind of work are particularly favourable in N. W. Europe and E. Greenland. This has also been proved by stratigraphical correlations in Scania carried out by the present author, for example the establishment of the Rhaetic at a depth of 1.450—1.485 m (III) in the "Höllviken II" boring. The chances for the determination of pre-Rhaetic material from Europe are improving, mainly owing to our increasing knowledge of the floras of the Keuper. The possibility of correlating the Middle Jurassic rocks of Europe is becoming greater, but stratigraphical

work is handicapped by our insufficient knowledge of the floras of the Upper Jurassic. The simplest way for palaeobotanical correlation of Middle and Upper Jurassic rocks is probably by the study of megaspores. It is remarkable that the microscopical study of compressions and correlation in Triassic-Jurassic rocks by the aid of "cuticular analysis" have not yet received much attention in certain countries with good possibilities for this kind of research, such as the U.S.S.R. and China; this line of study has been almost entirely disregarded in the U.S.A.

### RÉSUMÉ

After a general consideration of the status of our knowledge of Rhaetoliassic floras, the correlation and vertical distribution of similar floras from N. W. Europe and E. Greenland are reviewed with special reference to the investigations of some localities in N. W. Scania carried out by the present author. Correlation by plant microfossils in Lower Mesozoic rocks is discussed with regard to experiences from the study of Rhaetoliassic floras, and is exemplified i. a. by the author's studies of material from borings. The leaf-cuticles of the gymnosperms are briefly reviewed with regard to their value for stratigraphical determination and the possibilities of using identifications from cuticles on a larger scale in correlating Triassic-Jurassic rocks are particularly emphasized.

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<sup>1</sup> The transliteration of the Cyrillic alphabet in the present paper has been carried out in conformity to the official Russian system (reviewed in an article by G. NORSTRÖM in the Swedish journal Ymer 1958, p. 157).

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