the dorsal side of the tongue in amniotes and thus in man, too, is accordingly derived from the mandibular gill-cover, and this explains why this membrane is innervated by a branchial nerve (n. trigeminus). Another remarkable fact is that the sublingual rod is retained in all the descendants of the osteolepiforms. In man it is represented by a row of small cartilages, which is frequently found in embryos, and sometimes in the adult, in or just below the median septum of the tongue (*Slv*, Figure 5C).

In the porolepiforms (*Glyptolepis*) the sublingual rod is lacking, as in the urodeles. The subbranchial series consists only of the urohyal and, as pointed out above, this element and the overlying hyobranchial skeleton are developed fundamentally as in urodele larvae (Figure 4A, B). In these respects, there are thus very great resemblances indeed between the urodeles and the porolepiforms, and other most striking similarities are found farther forwards in the floor of the mouth cavity (Figure 6D, E). The anterior part of each of the jaws of the porolepiforms thus carries peculiar tooth-bearing structures (*Ps*, '*Op*'), which can easily be identified in urodele larvae but are lacking in all other tetrapods, and between the jaws there is a crescent-shaped field (*gl.f*) of dental plates. This field, the prolingual field, no doubt contained glands and undoubtedly it corresponds to the similarly situated, also crescent-shaped glandular field of KALLIUS, which is characteristic of the urodele larva and plays an important part in the formation of the tongue in this group of tetrapods (Figure 5 E1, E2). Fibres of one of the hypobranchial muscles, the genioglossus (a true m. hyoglossus is lacking in the urodeles) grow up into the glandular field and the floor of the mouth cavity in the area of that field rises and forms the tongue of the adult.

The tongue is thus formed in a different way in the urodeles, on the one hand, and in the anurans and the amniotes, on the other; and, as is now evident, this is due to the remarkable differences between the porolepiforms and the osteolepiforms in the structure of the floor of the mouth cavity (Figures 4, 6B, D). The fact that, in the detailed structure of this part of the head, the porolepiforms agree closely with larvae of urodeles —there are hardly any other differences than such as refer to the degree of ossification—whereas the osteolepiforms in all essentials are as anurans and amniotes, is in full accordance with the results gained by the studies of the snout[21, 25], and that the tetrapods are diphyletic in origin (Figure 1) cannot be doubted any longer.

Zusammenfassung. Kurzer Bericht über die dänischen Expeditionen nach Ostgrönland (LAUGE KOCH) 1929–1957. Die zoologische Bedeutung des fossilen Vertebratenmaterials (über 10000 Exemplare) wird angedeutet. Neuere Ergebnisse über die Evolution der Tetrapodenzunge werden besonders im Zusammenhang mit Grönlandmaterial besprochen. Damit wird die Ansicht bestätigt, dass sich die Urodelen selbständig aus porolepiformen Crossopterygiern entwickelt haben, während Anuren, Sauropsiden und Säugetiere von Osteolepiformiern abzuleiten sind. Die Auswertung des umfangreichen Fossilmaterials ergibt eine diphyletische Herkunft der Tetrapoden.

The Jurassic Ammonite-Faunas of East Greenland

By J. H. CALLOMON*

To those geologists primarily interested in the grander aspects of the science such as the tectonics of mountain-building, or the petrology of igneous and metamorphic processes, the Mesozoic era has relatively little to offer, for it marked a period of comparative calm in movements of the earth's crust. This quiescence is one of three main factors which make Mesozoic rocks particularly suited for stratigraphical studies. The second is that in two of the three systems which make up the Mesozoic, namely the Jurassic and Cretaceous, relatively shallow seas covered a considerably greater proportion of the earth's surface than they do at present, leaving widely-spread sheets of usually little-disturbed sediments now readily accessible and well exposed. The third factor is that the Mesozoic period marked the acme in development and abundance ot the ammonites.

The stratigrapher classifies rocks according to the fossils they contain. In correlating beds found at different places, and generalizing his finding into a standard succession, or geological column applicable to a whole area, he makes use of what we may call the first principle of stratigraphy: *rocks containing the same fossils are of the same age*, with the more trivial extension that in undisturbed sediments, the higher beds are the younger. The evolution of fossils is made the basis of

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stratigraphic subdivision, and the implied associated time-scale. It follows that the fineness of stratigraphical subdivision that can be achieved depends entirely on the habits of the available fossils. Different organisms evolved at widely differing rates, and it is immediately clear that some index-fossils are much better than others. It so happens that on the whole ammonites approached the ideal more closely than any other form: they evolved more rapidly than any other marine animal; they are of world-wide occurrence; they are very common, and usually well-preserved; they are readily identified and require no special technique of cleaning or development; and they are insensitive to facies—factors such as e.g. temperature and depth of water in which they lived, and lithology of the rocks e.g. limestone, clay or sand, in which they are now found. In fact the only deposits in which they are not found are those laid down in water of other than full marine salinity, and coralline limestones.

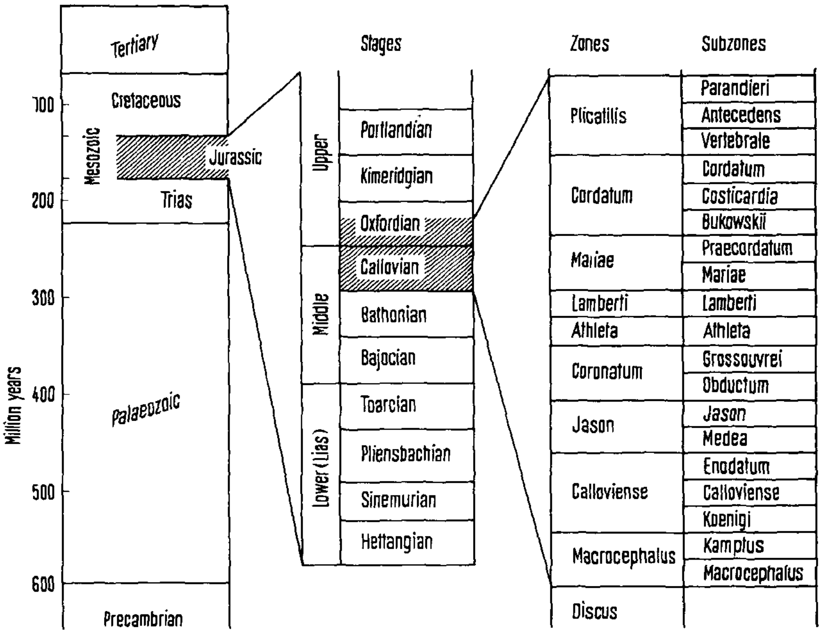

Fig. 1

Figure 1 shows how the standard geological column is subdivided into successively finer units, down in part to the level of subzones which are widely recognizable in northern-central Europe. Zones and subzones are labelled with the names of index-fossils, here in every case an ammonite species. The number of zones or subzones into which the Jurassic can thus be divided is about 120, and these are the basis of the geologist's time-scale. It is of interest to see roughly what this time-scale corresponds to in absolute terms, and through the advent of radioactive age-determinations this is now possible. Included in Figure 1 is a time-scale in millions of years put forward by HOLMES[1] which, although probably subject to future modification, is unlikely to be wrong by a factor of two; and if we accept for the Jurassic a time-span of 45 million years, a subzone is on the average equivalent to a period $\Delta t \sim$ 375000 years. Taking the mean age t of the Jurassic as 160 million years, we can define a *secular resolving-power* $t/\Delta t$ which in this case is then about 430. (This corresponds in more recent times to being able to distinguish, for example, an event in the year 1007 B.C. from one in the year 1000 B.C., a problem not without its difficulties even in historic times.) It exceeds by probably an order of magnitude anything that has so far been attained in any system outside the Mesozoic, and we see that ammonites, properly used, constitute an extremely sensitive clock.

The Jurassic System in East Greenland

Jurassic rocks were first recognized in East Greenland in 1870, and are now known to extend along a coastal strip some 700 km long (70°–77° N) and up to 130 km wide at its widest in the south, in Scoresby Sound, where the succession is at its most complete, best exposed and least disturbed. The total thickness of Jurassic observed is up to 1800 m (6000 feet), and although large parts of this consist of beds containing only plant remains, there are many fossiliferous horizons yielding extensive suites of marine fossils, including ammonites. In a typical section of 200 m of sediment up to 50 separate beds may be distinguishable without difficulty, of which up to 20 may yield ammonites. Some of the beds are shell-banks typical of shallow off-shore waters, packed with the remains of whole colonies of shells in their position of growth—a veritable out-door museum. But most remarkable are some of the ammonite-beds: perhaps 1 m thick, they are crowded with splendidly-preserved complete ammonites to the almost total exclusion of all other forms of life. When weathered out on gentle slopes, they can cover the ground in hundreds, sometimes even thousands, calling for scarcely more effort to collect than is required to lift them. To the palaeontologist such finds are an exhilarating experience.

Study of the ammonites shows that the Jurassic of East Greenland is probably largely complete. Representatives of most of the stages of classical Europe (Figure 1) are recognizable, and the Lower Jurassic

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[1] The geological time-scale is from: A. HOLMES, Trans. Edinb. Geol. Soc. *17*, 183 (1960).

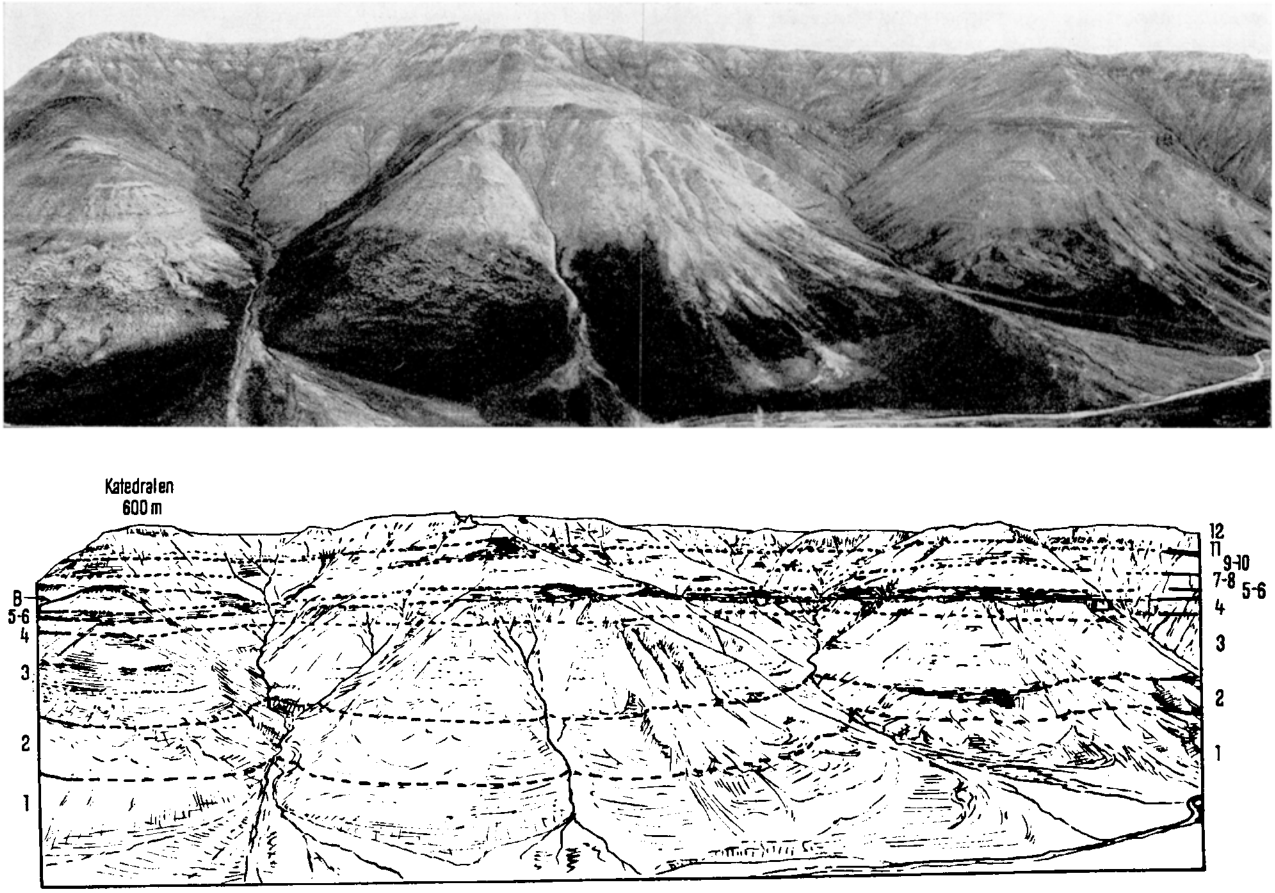

Fig. 2. View southwards across Ugle Elv, at the head of Hurry Fjord, Jameson Land. Height of plateau ca. 600 m, valley bottom at ca. 110 m above sea-level. 1, Upper Lias, Toarcian *Oyster Bed*. 2, *Lower Vardekløft Formation*, 50 m. 3, *Yellow Series*, Borealis Zone, 130 m. 4, Indistinctus Zone, 28 m. 5–6, *Upper Vardekløft Formation*, Pompeckji-Nudus Zones, 20 m. 7–8, Greenlandicus-Kochi Zones, ca. 70 m. 9–10, Variabile-Calloviense Zones, 55 m. 11, *Black Series*, Upper Oxfordian, 0–5 m. 12, *Koch Fjeld Formation*, Lower Cretaceous, Berriasian, 100 m. B, basalt dyke.

(Lias) ammonites differ so little from those of Europe that correlation at zonal level presents no special problems. In contrast, attempts to extend zonal correlation to higher beds immediately run into the most serious difficulties.

The faunal succession in the Middle Jurassic of Greenland is embodied in the nine ammonite zones shown in Figure 5. The lowest zone is separated from the underlying Lias (Toarcian) by a series of black shales which have so far yielded only plant remains, and about whose age one can therefore say very little. The topmost zone is immediately succeeded by beds containing Upper Jurassic ammonites (Oxfordian, Plicatilis Zone). Moreover, its ammonites are the same as those of the European Calloviense Zone. This therefore establishes both the presence of a large discontinuity in the Greenland succession, comprising in fact most of the zones shown in Figure 1, and the upper age limit of the beds actually present. The second topmost, Tychonis, zone correlates roughly with the European Macrocephalus Zone, for their faunas have some elements in common. The difficulty with the remaining seven Greenland zones is that they contain only ammonites which are quite unknown in Europe. There are many strong reasons against concluding that we have here in turn beds and faunas which span what marks a major non-sequence in the European record. The Middle Jurassic ammonite faunas of East Greenland in fact provide one of the earliest and clearest examples of what is now recognized to have been a not uncommon phenomenon, of ammonites restricting themselves in their habitats and separating into *fauna realms* and, more locally, *provinces*.

Similar factors govern the ammonite faunas of the Upper Jurassic beds of East Greenland, although to a lesser extent. Details remain to be worked out, but it is clear that they consist of a mixture of forms known hitherto either from England or Russia, but in only a few cases from both. They are therefore of particular interest in that they allow certain English and Russian faunas to be correlated whose relations had previously been in doubt. Also present are once again some forms peculiar to the area and unknown elsewhere. The Greenland succession is in places so abundantly fossiliferous, especially near the top, that not the least obstacle to precise correlations is now in fact the relative lack of knowledge of the European succession.

The Problem of Faunal Realms and Provinces

The standard zonal succession of Figure 1 represents the results of observations made in Europe north of the Alps. Attempts to extend the zones geographically meet with very varying success, for although the basic principle of stratigraphy continuous to hold, its converse need not: because of the existence of faunal realms, *rocks of the same age do not necessarily contain the same fossils.* The boundaries of a faunal province can be surprisingly sharp: for example, whereas the Enodatum Subzone of the Calloviense Zone has been recognized in an area lying between western France (Deux Sèvres), England, the Moscow basin and Mangyshlak, east of the Caspian Sea, a maximum distance of nearly 4000 km, its faunas have been replaced by others in only 300 km southwards, and the subzone is not recognizable in the south of France.

Fig. 3. Ammonites of the Pompeckji Zone on the slopes of Katedralen, the result of 5 min collecting.

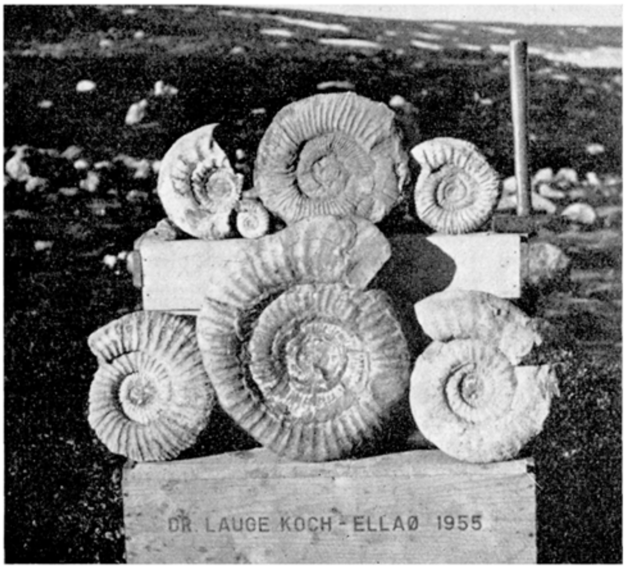

Fig. 4. Ammonites from the Upper Jurassic of Milne Land. Top centre: *Subplanites* sp. from the Pectinatus Zone, Upper Kimeridgian. The others: various Pavlovids and Dorsoplanitids from the Upper Kimeridgian-Portlandian.

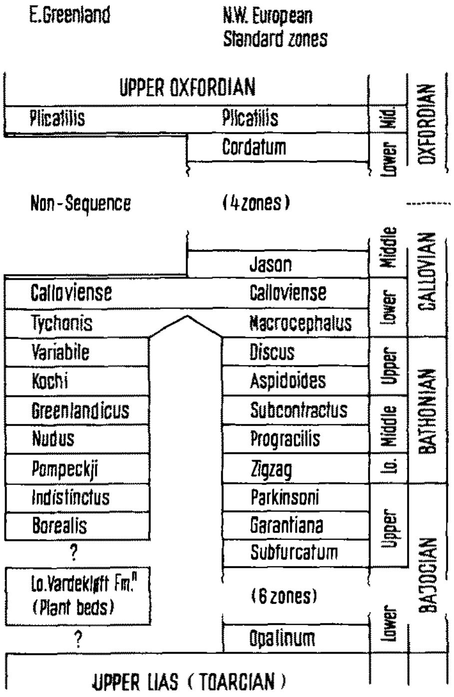

Fig. 5

Similarly the discoveries of recent years show that the Middle Jurassic ammonite succession of Greenland epitomizes a major circum-Arctic, or Boreal, faunal realm which first separated out in the Bajocian. The Greenland faunas are now also known in parts from Spitsbergen, north Russia (Petchora), Siberia, Alaska, and Arctic Canada (Prince Patrick Island), over distances of 5000 km, and yet are totally unknown among the Bathonian faunas of England, 2700 km from Scoresby Sound, of which they must largely be equivalents. The problem of the exact correlation of the Greenland zones with those of Europe remains and can only be solved if an area is found in which the faunal realms overlap.

We see, then, that whereas on the one hand some properties of ammonites give us the means for locally very precise stratigraphy, they had at the same time habits which create obstacles in trying to extend stratigraphical correlations round the world. This is perhaps unfortunate, but adds interest to the problem.

Faunal Realms and Ammonite Phylogeny

Apart from their uses in stratigraphy, the habits and evolution of the ammonites themselves are a subject of absorbing interest. One of the primary objectives is the study of their phylogeny—the reconstruction of an evolutionary tree. In trying to deduce such a tree from the fossil record we have to suppose that evolutionary changes were more or less uniform, and join into lineages those forms which seem to present morphological sequences with fewest discontinuities. Despite systematic collecting of over 150 years and the description of many thousands of species it has only relatively recently become possible to construct a phylogenetic classification of the Jurassic ammonites which one may view with any confidence. The difficulties are mainly twofold. Firstly, although as we have seen the ammonites evolved very rapidly, they did so repeatedly through the same morphological types. There are many examples of species of widely differing ages, and known to be not closely related, which yet are so similar as to be practically indistinguishable, i.e. homeomorphic. Secondly, the existence of faunal provinces means the evolution side by side of several lineages independently. Faunal provinces usually overlapped to some extent, and their boundaries were not stationary. In unravelling the phylogeny of ammonites in a region in which several faunal provinces touched, the problem is to distinguish those discontinuities in the record which may have represented genuine 'bursts' of evolution from those which arose merely from faunal migration. This problem is particularly common in just that area, i.e. N.W. Europe, in which, for historical reasons, our knowledge is most complete.

The ammonites of the Middle Jurassic of Greenland have helped to solve a particularly difficult example of such problems. The ammonite succession in the Lower Callovian of much of N.W. Europe, and particularly Great Britain, where it is best developed, is marked by two major breaks. The first, between the Discus and Macrocephalus Zones (Figure 1), forms the basis of the boundary between the Bathonian and Callovian. The faunas of the former are suddenly and almost wholly replaced by large numbers of the genus *Macrocephalites*. The second break lies between the Macrocephalus and Calloviense Zones. *Macrocephalites* suddenly becomes very rare and then disappears altogether from Britain, although it remains common further south, e.g. in the Jura. Instead there suddenly appear in the Calloviense Zone of Britain a profusion of forms of two new families, the Kosmoceratidae and Cardioceratidae, which continue to hold the field undiminished throughout the Callovian, although never penetrating much further south than the Alps. Two faunal realms, the Boreal (northern) and Tethyan (southern) are thus discernible in Europe from the end of the Bathonian onwards. The problem was, where did the two Boreal families originate? The solution almost universally adopted until quite recently rested on the observation that the first members in the Calloviense Zone had morphologically many points of resemblance to *Macrocephalites*, whose Bathonian ancestors are well known. This was specially the case in *Kepplerites*, the first of the Kosmoceratidae, rare examples of which had in fact been found in the Macrocephalus Zone. It was therefore assumed that both Kosmoceratidae and Cardioceratidae had evolved from *Macrocephalites*, and although the observed transition was not quite as smooth and continuous as one would have liked, this could be attributed to the incompleteness of the record.

In fact it is now quite clear that the faunal break at the Calloviense Zone in Europe merely marks a widespread faunal migration, with the arrival in force from the Arctic of faunas (Kosmoceratidae and Cardioceratidae) which had been evolving there independently long previously. The ammonites of the Borealis-Tychonis Zones of Greenland form a continuous series which can be joined smoothly on to the Cardioceratidae of post-Calloviense Europe and then followed uninterruptedly to the top of the Lower Kimeridgian, probably now the clearest example of ammonite evolution so far recognizable. Similarly, the finds in Greenland have shown the Kosmoceratidae to have had an extensive pre-Macrocephalus history, and for this reason alone (there are others) we must conclude that the extraordinarily close resemblance between *Kepplerites* and some *Macrocephalites* of the Macrocephalus Zone is coincidental, an example of synchronous, convergent homeomorphism.

It seems probable that the Upper Jurassic ammonites of Greenland will make similar contributions to the unravelling of the phylogeny of another family, the Perisphinctidae. These have always formed a proverbially difficult group to classify, for the range of morphological variation is rather narrow in the whole group, and homeomorphism accordingly more frequent and harder to detect. Differentiation into faunal provinces is in addition particularly common, making it more important than usual to establish the true 'home' of each group. The existence of a Boreal realm of Perisphinctidae is now clearly established, and its development well characterised by the Greenland succession[2].

Zusammenfassung. Die Juraformation von Ostgrönland ist reichlich fossilführend. Unter den marinen

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[2] For a comprehensive review of the Jurassic of East Greenland, see: D. T. Donovan, *The Jurassic and Cretaceous systems in East Greenland*, Medd. om Grønl. *155*, no. 4 (1957). – Addenda and modifications based on subsequent work are to be found in: J. H. Callomon, *The Ammonite Zones of the Middle Jurassic Beds of East Greenland*, Geol. Mag. *96*, 505 (1959); *The Jurassic System in East Greenland*, in *The Geology of* the *Arctic* (Ed. G. O. Raasch, University of Toronto Press, Toronto, Ontario, 1961). – For discussion of faunal realms and provinces in the Jurassic, see: W. J. Arkell, *Jurassic Geology of the World*, chapters 27, 28 (Oliver and Boyd, Edinburgh and London 1956). – The standard text on ammonite systematics is: W. J. Arkell et al., *Treatise on Invertebrate Palaeontology*, Part L, Mollusca 1: Cephalopoda-Ammonoidea (Ed. R. C. Moore, Geological Society of America and University of Kansas Press, 1957).

Tieren sind Ammoniten vorherrschend, und es liess sich eine breite und detaillierte Faunen- und Schichtgliederung durchführen. Die Bedeutung der Gliederung wird im Hinblick auf stratigraphische Zonenbildung und allgemeine Korrelation kurz besprochen. Die Gliederung der Schichtfolgen ist zur Aufklärung der Biologie und Evolution der Ammoniten brauchbar. Von besonderem Interesse erweisen sich die Ammoniten des mittleren und oberen Jura von Grönland, da sie ein klares Beispiel geben für die Tendenz einzelner Familien, sich in ihrer Ausbreitung auf begrenzte Faunengebiete zu beschränken. Die Grenzen solcher Provinzen blieben nicht dieselben und Unterbrechungen in den zu beobachtenden Faunen an bestimmten Stellen sind oft auf Auswanderungen der Faunen zurückzuführen. Unterbrechungen dieser Art dürfen keinesfalls übersehen werden, wenn eine phylogenetische Klassifizierung versucht wird. So haben die ermittelten Schichtfolgen von Grönland einige phylogenetische Ungewissheiten aufklären können.

Brèves communications – Kurze Mitteilungen – Brevi comunicazioni – Brief Reports

The Structure of Ocoteine (Thalicmine)

Ocoteine is an aporphine alkaloid which was isolated from the bark of *Ocotea puberula* Nees[1]. From its degradation products, it was suspected to be identical to thalicmine[2], an alkaloid isolated by YUNUSOV and PROGRESSOV from the bark of *Thalictrum minus* L.[3]. A direct comparison kindly performed by Prof. YUNUSOV confirmed the identity of both alkaloids[4].

Ocoteine has three methoxyls and one methylene dioxygroup. On the basis of the relation to cotarnine, the Russian workers proposed the structure of 5,6-methylenedioxy-3,4,7-trimethoxyaporphine (I)[3]. The partial structure (II) has been put forward to explain the isolation of 4,5-dimethoxy-N-methyl phtalimide (III) by oxidation of the base itself and of *m*-hemipinic acid by permanganate oxidation of the corresponding methylenedioxytrimethoxy-1-methylaminoethyl-9,10-phenanthraquinone[2]. The latter compound was also found in the bark of *Ocotea puberula*[1]. Structure (II) was suggested because no alkaloid was known at the time to have positions 1 and 7 substituted. Positions 2, 3 and 4 are the most commonly substituted besides C-5 and C-6 where all naturally occurring aporphines are substituted by oxygenated substituents.

Dr. S. GOODWIN of the National Institutes of Health (Bethesda) recorded a few years ago the proton resonance spectrum of ocoteine and she interpreted her results in terms of structures (IV) and (V), the former one being preferred[5].

By the courtesy of Dr. N. SHEPPARD (Cambridge University) we were able to record the spectra of several aporphine alkaloids and of ocoteine. When converted to the same units—τ units—our data correspond to those of Dr. S. GOODWIN.

Our results together with the rotatory dispersion curve of ocoteine[6] and the physical data previously published[2] support structure (IV) for ocoteine (thalicmine).

Evidence for structure (IV) is provided by the following facts: (a) the chemical shift data for the aromatic protons collected in the Table together with the N–CH_3 and O–CH_3 absorption values already published elsewhere[7] indi-

Table[a]

Name		Formula			O-CH_3						Aromatic protons			
		R^1	R^2	R^3	2[b]	3[b]	4	5	6[b]	7	1[b]	2[b]	4	7[b]
Dicentrine	VI	OCH_3	H	—	6.20	6.20	—	—	—	—	3.30	—	2.42	3.62
Bulbocapnine	VI	H	OH	—	—	6.20	—	—	—	—	3.25	3.25	—	3.45
o-Methylbulbocapnine	VI	H	OCH_3	—	—	6.18	6.28	—	—	—	3.07	3.07	—	3.32
Corydine	VII	H	OCH_3	—	—	6.18	6.35	—	6.18	—	3.12	3.02	—	3.35
o-Methylcorydine	VII	H	OCH_3	CH_3	—	6.18	6.32	6.37	6.18	—	3.15	3.15	—	3.35
Glaucine	VII	OCH_3	H	CH_3	6.20	6.25	—	6.45	6.20	—	3.42	—	2.00	3.55
Ocoteine (thalicmine)	IV	—	—	—	6.13	6.13	—	—	—	6.07	3.27	—	2.43	—

[a] In τ units.

[b] Assignments of resonance to these positions may be interchanged.

Measurements were made at 40 Mc using a Varian Associates 12″ electromagnet. Calibration of the peaks was made by using side bands generated by a decode oscillator. The substances were examined in chloroform solution and silicon tetramethyl used as an internal standard.

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[1] G. IACOBUCCI, Ciencia e Invest. *7*, 48 (1951); An. Asoc. Q. Arg. *42*, 18 (1954).

[2] M. J. VERNENGO, A. S. CEREZO, G. IACOBUCCI, and V. DEULOFEU Liebigs Ann. *610*, 173 (1957).

[3] S. YUNUSOV and N. N. PROGRESSOV, J. allg. Chem. *22*, 1047 (1952).

[4] Private communication from Prof. S. YUNUSOV to Dr. V. DEULOFEU.

[5] Private communication from Dr. S. GOODWIN to Dr. V. DEULOFEU.

[6] M. J. VERNENGO, Exper. *17*, 420 (1961).

[7] R. I. C. BICK, J. HARLEY-MASON, N. SHEPPARD, and M. J. VERNENGO, J. chem. Soc. *1961*, 1896.