AN ANALYSIS OF DEVONIAN GONIATITE DISTRIBUTIONS

by MICHAEL R. HOUSE

ABSTRACT. A review is given of the characteristics of Devonian ammonoid distributions inferred qualitatively in relation to proposed continental positioning. Since ammonoids were subject to post-morten drifting comments are made on this in the light of a review of post-mortem drifting in *Nautilus*. This introduces a substantial uncertainty limiting quantitative analyses of goniatite distributions. Gross analysis of latitude diversity of goniatite genera is given and this gives some support for a proposed palaeoequator position. Other analyses document data on the supposed migration routes.

SINCE goniatites were marine organisms, the evidence they contribute to establish past continental distributions is limited to inferences on faunal links and barriers and on gross diversity distributions. Since also goniatites were subject to post-morten drifting, which in the case of the living *Nautilus* approximately doubles its life area of distribution, much of the evidence obtained from them is uncertain. To these uncertainties must be added the usual cautions, when dealing with fossil material, resulting from uneven or unequal preservation, collection, and description of goniatite remains.

From a qualitative study of Devonian ammonoid distributions (House 1964, 1971), certain generalizations have emerged which may be summarized as follows:

1. The richest and most complete Devonian ammonoid record is in the area embracing Europe, North Africa, and the Urals. There is scarcely a genus known which does not occur in this area. It does not seem that the poorer record elsewhere is due wholly to collection failure.
2. From the Old World area there seems evidence for a strong faunal link which is trans-Arctic, linking the Ural faunas via Novaya Zemlya, and perhaps the north Siberian coast, to the Cordillera of western North America. This route apparently lay on the northern side of the Devonian Old Red Sandstone Continent.
3. The eastern North American faunas, on the other hand, are restricted in diversity, especially those from the well-known New York succession. Goniatites are there abundant in the Middle and Upper Devonian (Eifelian to earliest Famennian) but many common European genera are not known although a number of these occur in the Cordilleran area.
4. Southwards down the Appalachians, especially in the Middle and early Upper Devonian, a stronger European affinity is noticeable. It has been inferred that the link here was via North Africa.
5. No Devonian ammonoids at all are known from South America, Antarctica, Africa south of the Sahara, or from peninsular India.
6. A fauna of remarkable European affinity occurs in the Devonian of Australia. It is inferred that a faunal link with Europe ran along the proto-Tethys line, and there is some evidence of this in faunas known from the southern Urals and Kazachstan

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area, and the poorer recorded from Afghanistan, Burma, China, and Vietnam. The Asian part of this link is very inadequately documented.

7. Wide distribution of ammonoids is apparent even in the Lower Devonian (when the group first appeared). Maximum distribution appears to have been reached in the early Upper Devonian (Frasnian) and is exemplified by the distribution of the genus *Manticoceras* (text-fig. 1).

8. The evidence does not appear to indicate a separation into faunal provinces in the Devonian so far as the ammonoid evidence is concerned (House 1971).

No quantitative analyses of these distributions have been made and most specialists, including the author, have taken the view that little is to be gained from such analyses in view of the uncertain premisses outlined in the opening paragraph above. That this is not wholly so will be apparent below. But studies of other Devonian groups, particularly of benthonic brachiopods (Johnson 1971) have yielded more profitable results.

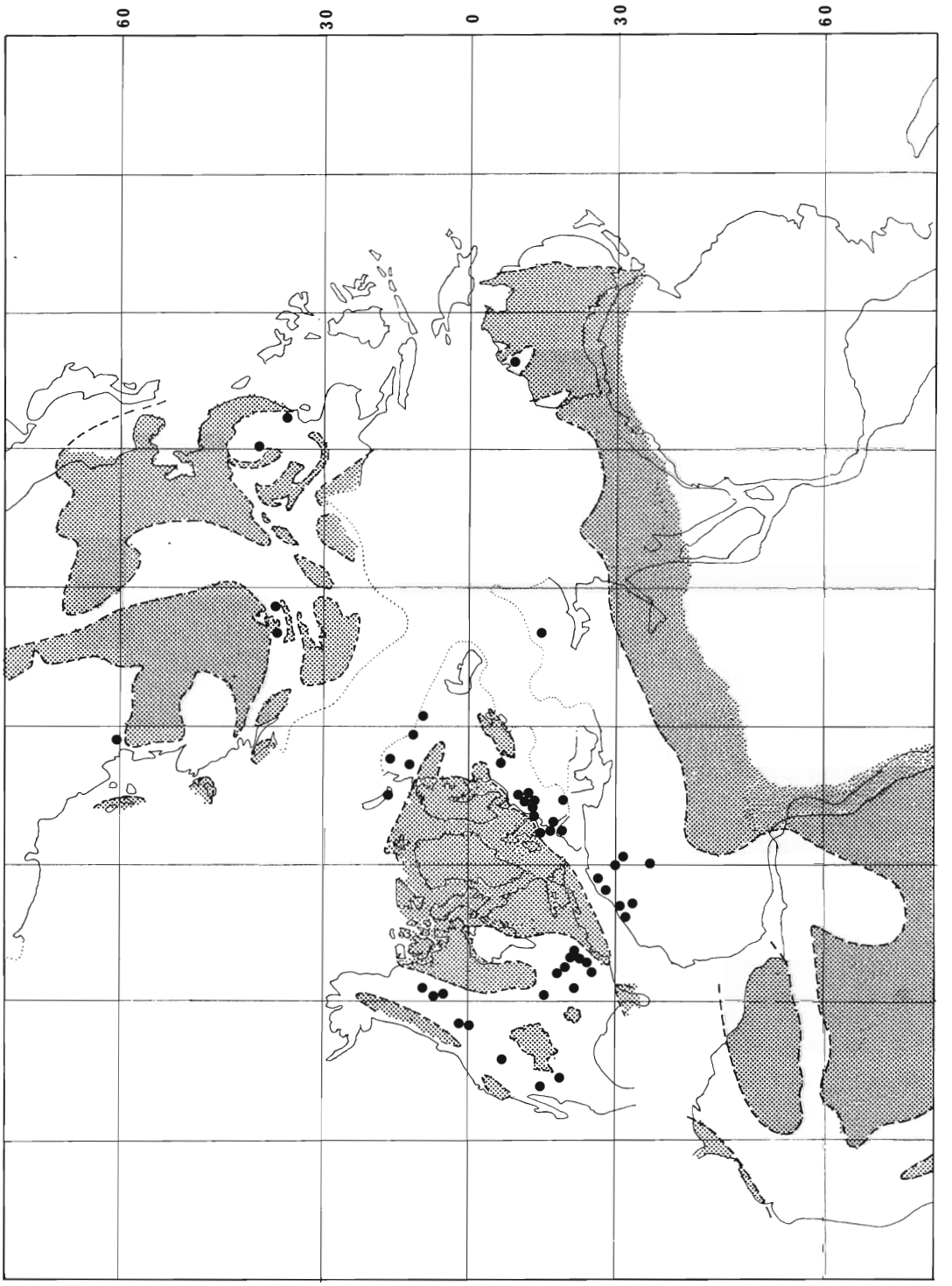
The value of such analyses essentially depends on the assumption that the fossil distribution bears some relation to the life distribution. Since it is only the known fossil distribution which can be used in analyses it is appropriate first to consider the affects of post-mortem drifting.

POST-MORTEM DRIFTING

With fossil benthonic organisms it is usually possible to determine whether or not an organism is preserved in its life position. With nektonic organisms this is usually impossible. In the case of chambered cephalopods determination of this is even more difficult since the shell was probably buoyant for long periods after death and hence capable of being transported substantial distances from the life habitat by current movement. Even an association of adults with young stages, which might be taken as an indication of a breeding area, does not dispel this problem since the protoconch probably provided some positive buoyancy immediately after the release of the larval cephalopod from the egg capsule, and even before the development of the chambered phragmocone.

The possible analogy with the living *Nautilus* is here instructive. In recent years attempts have been made to plot the distribution of living as well as of drifted *Nautilus* shells. The distribution map by Stenzel (1964, p. K90) was limited to the area between New Zealand and Japan. Subsequently new records by Hamada (1964, 1965, 1966), especially from the Thailand and Japanese coasts, led to the production of a very much more detailed map (Toriyama *et al.* 1965, p. 153) covering a similar area: in this paper those authors drew attention to records of living *Nautilus* on the western, southern, and eastern coasts of Australia.

TEXT-FIG. 1. Diagram showing the distribution of *Manticoceras* in the Frasnian. Sites plotted on the Lower Carboniferous symposium reconstruction with Africa brought close to North America and the Ural separation reduced as much as possible. Records not complete along the Alpine or Ural fold belts. Tentative Late Givetian or Frasnian palaeogeographic outlines of land areas stippled, based on published data as follows: North America (Johnson 1971), South America (Harrington 1968), Poland (Pajchlowa 1959), Russia (Rzhonsnitskaya 1968), China (Khyn-Yun 1962), and Australia (Johnstone *et al.* 1968, Hill 1968).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On the map of the distribution of *Nautilus* given here (text-fig. 2) the records from the Australasia area to Japan and Samoa are taken wholly from the work of Toriyama *et al.* (1965). Records given elsewhere are mainly from the review by Teichert (1970). The record shown here of a living specimen from the Andaman Islands is included on the evidence of Foord (1888, p. xi; Smith 1887). This record is perhaps uncertain and may refer to a drifted, ill, *Nautilus*. It may, on the other hand, when viewed in conjunction with the other records in the Bay of Bengal, and those inferred on the Indian coast (Teichert 1970, p. 1129), be taken to suggest that there is a breeding area thereabouts which has yet to be located precisely.

I am indebted to Dr. W. J. Kennedy for drawing my attention to information on the distribution of drifted *Nautilus* shells in the central and western Indian Ocean collated by Dr. J. D. Taylor, Department of Zoology, British Museum (Natural History). Dr. Taylor has kindly allowed me to report here that a *Nautilus* shell was found on an exposed shore beach at the extreme easterly end of Aldabra Island by Dr. C. J. R. Braithwaite during the course of the recent Royal Society of London scientific work there; that *Nautilus* shells collected on the coast of Kenya, 80 km south-west of Mombasa at Shimoni, Kenya, are in the collections of Mrs. M. Hemphill and Mrs. J. Jessop of Shimoni; and that Dr. Taylor has seen a *Nautilus* shell which had been found on a seaward beach at the northern end of the atoll at Diego Garcia in the Chagos Archipelago.

The extensive necroplanktonic distribution shown on the map bears a clear relation to ocean current patterns. The probable area where *Nautilus* remains will occur in bottom sediments is stippled on the accompanying distribution map (text-fig. 2). It will be noticed that the distribution area is more than doubled when drifted records are taken into account.

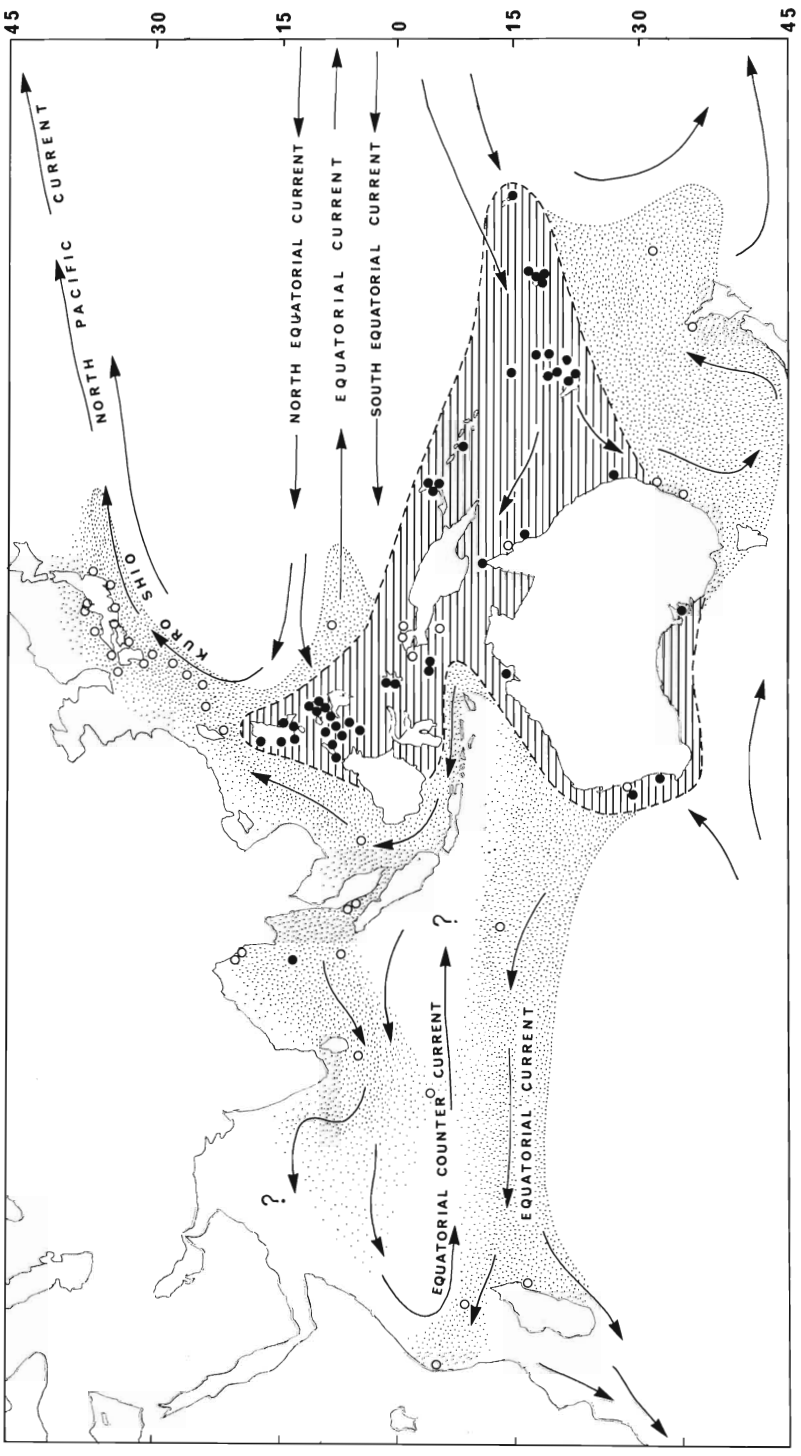
Even if the complete distribution of fossil goniatite shells were known it would also be composed of the same two components, one, the true life area, the other the post death drifted area. The first may bear some relation to latitude, in terms of greater equatorial diversity and marine links or migration routes, but the recognition of these will be masked by post-mortem drifting.

Recognition of the true life distribution area in the case of fossil ammonoids is extremely difficult. Characteristics of the area would probably include: a greater numerical abundance of goniatites; the presence of examples of all growth stages; the relative absence of epifaunal growths; and predominance of unbroken shells. But each of these characteristics need not be exclusive to examples from the life area. This problem is considered further in a paper by Hamada (1965).

It is with these uncertainties in mind, in addition to the usual problems inherent in fossil material of uneven or unequal preservation, collection, and description, that any comments on goniatites distribution must be viewed.

GROSS DISTRIBUTION OF TAXA

In a series of papers Stehli and others have developed techniques for analysing the distribution of taxon diversity (Stehli 1964, 1968; Stehli and Helsley 1963; Stehli, McAlester, and Helsley 1967). By analogy with Recent distributions, greatest diversity occurs near the equator and this declines poleward. The data which have been



TEXT-FIG. 2. Map showing the distribution of *Nautilus* shells at the present. Black dots show records of living specimens and horizontal ruling shows probable life distribution. Open circles show records of drifted shells and stippled area indicates the possible post-mortem distribution area. If the East African shells have drifted from the nearest known life areas, the current speeds recorded in the Indian Ocean suggest that they must have drifted for several years. Alternatively there is an undiscovered life area for *Nautilus* in the Indian Ocean. For sources see text.

used in the present contribution were assembled by the author during the revision of the Devonian goniatite section for a revised edition of the *Treatise on Invertebrate Paleontology, Part L.*

The distribution of eighty-eight Devonian ammonoid genera (excluding only Imitoceratidae and Clymeniina) were plotted on the symposium palaeogeographic reconstruction for the Lower Devonian. Generic tots in areas defined by fifteen degrees of longitude and ten degrees of latitude were used. The resultant raw data is shown on the accompanying map (text-fig. 3). These totals refer to records for the whole Devonian. A number of difficulties were encountered in making this collation. Uncertainty of treatment of the Alpine fold belt on the reconstruction was resolved by eliminating all but the clearest southern records. In a number of cases arbitrary boundary decisions were made. A number of speculations on poorly known faunas were necessary. In some cases, for example in the Great Khingan and Western Australia, Devonian records were known to be quite incomplete, but no allowance could be made for this.

From a general consideration of these results it is clear that there is greater diversity closer to the proposed palaeoequator and this would appear to decrease poleward. It is obvious that there is no such correlation with present continental distributions.

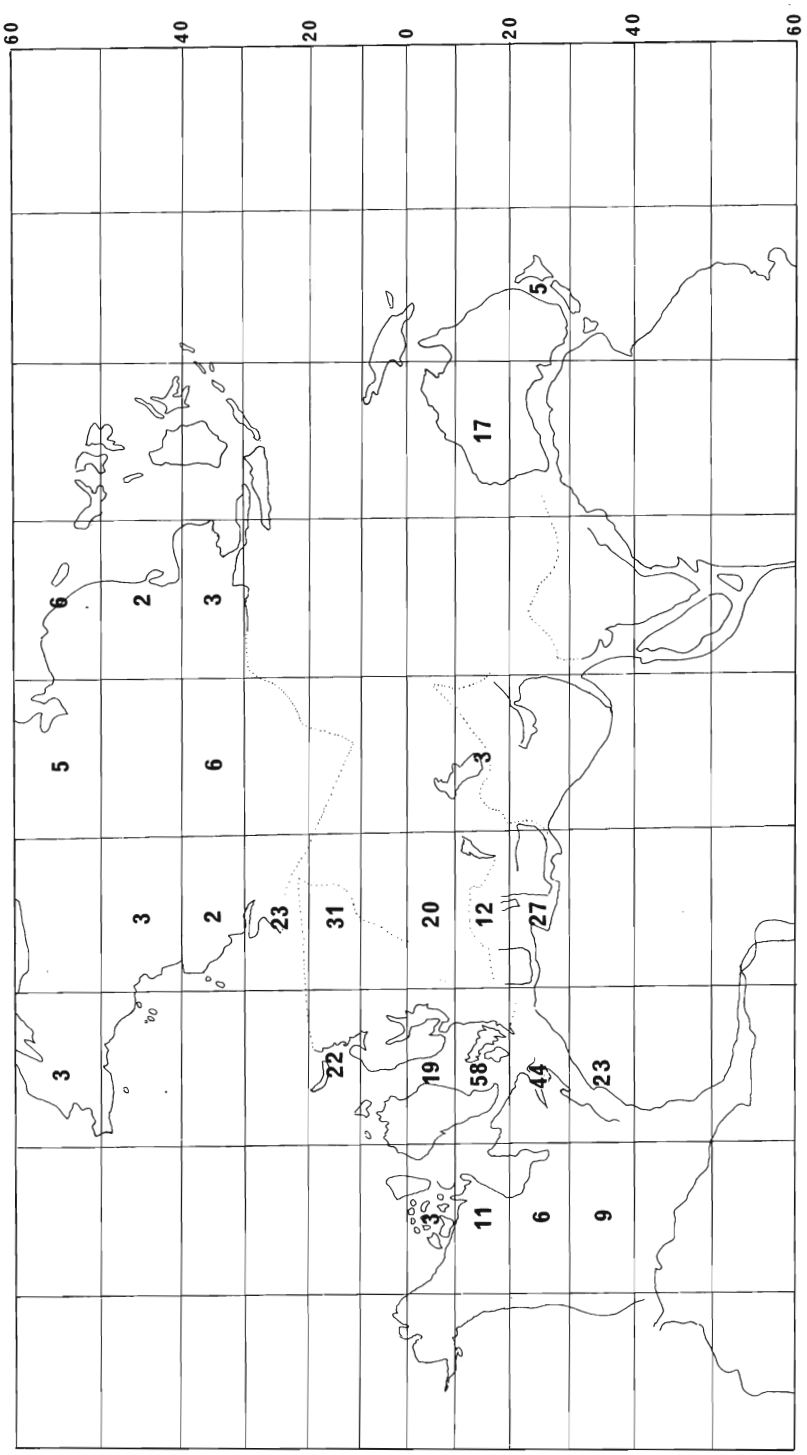
Mr. D. A. Wheeler of the Geography Department, University of Hull, kindly undertook a cubic trend surface analysis of this data (text-fig. 4). No corrections have been made for the several errors introduced either by using Mercator's projection in this way or for area differences of the graticule blocks used.

The Northern Hemisphere results here suggests a concordant latitude trend for poleward diversity fall. The Southern Hemisphere data is much less convincing. The very poor relative record of western North America and the Middle East results in a trend at right angles to that which might be desired. In part this would be corrected if a later position, for example, the Lower Carboniferous position (text-fig. 1) for the North American continent, had been used, for then the data would have been moved relatively north and appropriately rotated to some extent. Since most of the data is of late Middle and Upper Devonian generic distribution, this would perhaps have been more appropriate. Some will doubtless take this result to indicate correlation, not with any real distributions, but as indicating the areas where most workers have been engaged.

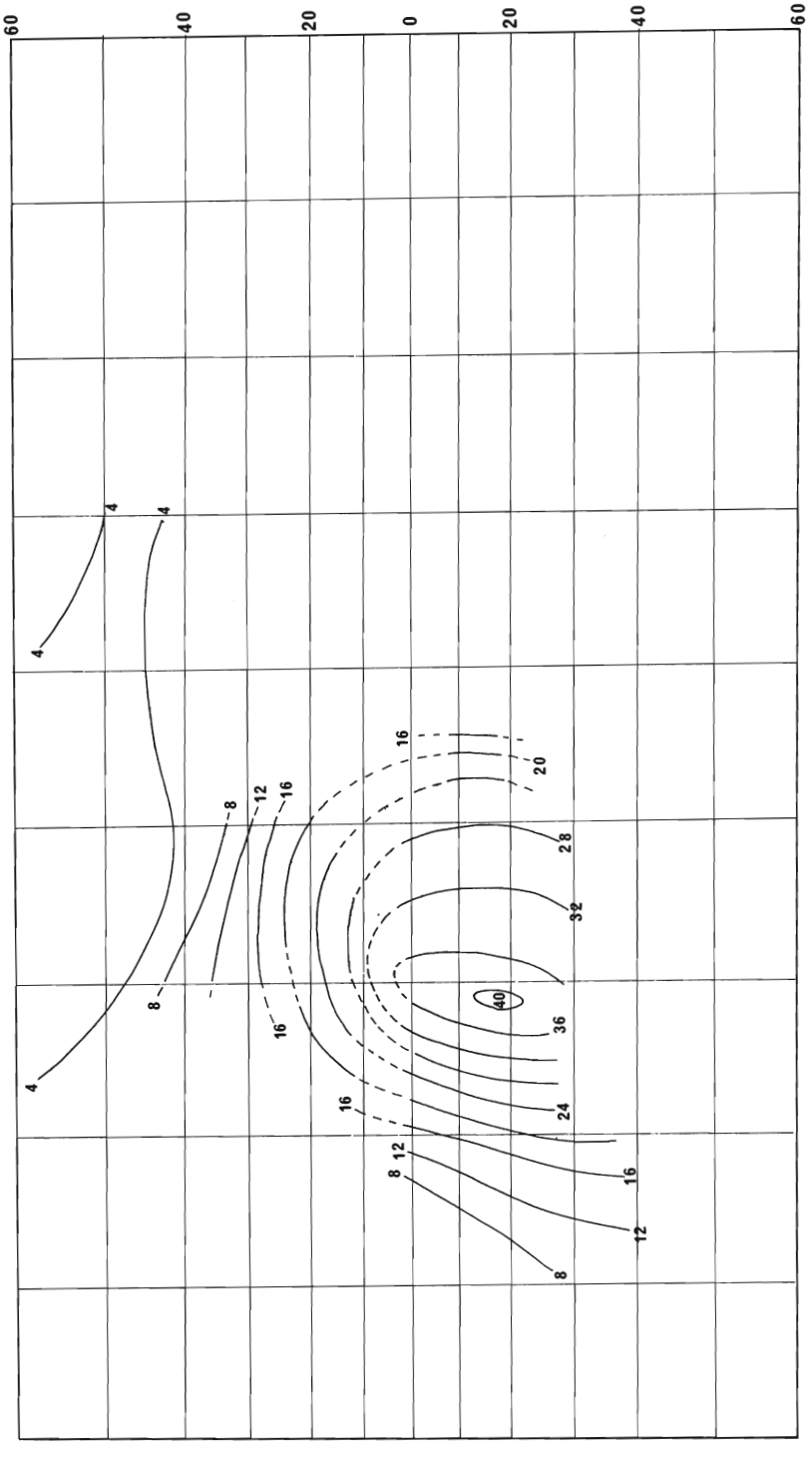
This analysis is a crude one, and the nature of the data allows only such broad generalizations as have been made. Stehli (1964) mentions an analysis of this sort for the Devonian using a collation of many groups. Were the data for this collated by specialists on a broader scale a much more discriminating tool for the Devonian would be forthcoming. But any analysis of this sort does not make allowance for the affect of the past pattern of continent distribution which may affect the result in a number of ways.

CENTRE OF EVOLUTION

'Supposing the exigencies of fossilization and preservation allow, a centre of evolution may be recognised by the occurrence in it of the fullest and most complete record of the group' (House 1964, pp. 268, 269). For the Devonian ammonoids the



TEXT-FIG. 3. Distribution of total Devonian ammonoid genera (excluding Imitoceratidae and Clymeniina) in areas defined by fifteen degrees of longitude and ten degrees of latitude using the Lower Devonian symposium reconstruction.



TEXT-FIG. 4. Cubic trend surface analysis of the data shown on text-fig. 3 prepared by D. A. Wheeler and using the same Lower Devonian reconstruction.

present evidence suggests this area embraced North Africa, Europe, and the Urals. Although the latter area was excluded in 1964 (House 1964), it is clear from recent work of Bogoslovski (1969) that the Ural faunas are very European in type throughout the Devonian. It is true that several genera, notably *Fasciculoceras*, *Laganites*, and *Parenites*, are not recorded from Europe and North Africa, but too much should not be read into this in view of the absence of detailed work on faunas around the Lower/Middle Devonian boundary. The lack of record from the Urals of *Cabrieroceras* and possibly *Holzapfeloceras*, *Maenioceras*, and *Wedekindella* suggests that the Givetian link was not as strong as that both earlier and later.

The faunas of the eastern slopes of the Urals show no distinction in this respect. Indeed those faunas are most noticeably European in character particularly in the Late Devonian. The reconstructions provided (text-fig. 1 and text-fig. 3) showing substantial separation in Devonian times along the present Ural line are not therefore confirmed by the ammonoid evidence if substantial geographical separation of elements of the Uralian geosyncline is envisaged. If such a separation is required a line east of the Urals is indicated.

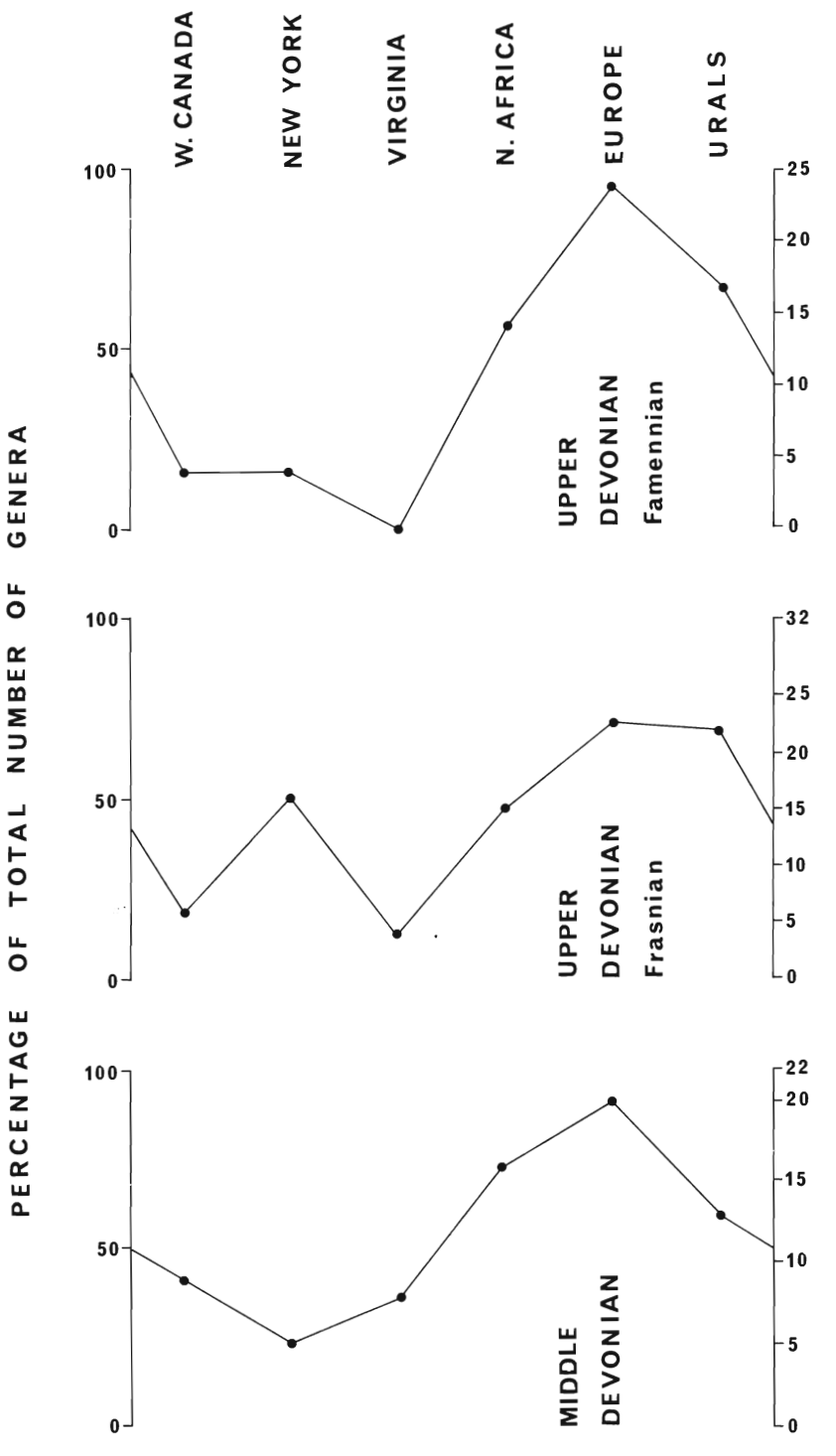
MARINE LINKS

The main evidence of marine migration routes established qualitatively for the Devonian ammonoids will now be considered. Three such routes have been thought to be important. Firstly a trans-Arctic link of present continental arrangement. Secondly a link between Africa and the southern Appalachians. Thirdly a link along the proto-Tethys line between Europe and Australia, tentatively linked with which are the records in China and south-east Asia.

Since all the genera known in North America (with one exception) and North Africa (with one exception) occur in Europe and western Russia percentages give some indication of faunal affinity. The accompanying graphs (text-fig. 5) illustrate the factual evidence of generic distributions relating to the first two of the marine links mentioned above. Since much of the documentation has already been presented (House 1962, 1964, 1971, 1972, in press; House and Pedder 1963) details of records are not given here and this account is limited to general conclusions and their bearing on the proposed palaeogeographic reconstructions provided for this symposium.

Trans-Arctic link. It has been supposed that this migration route lay north of the supposed Old Red Sandstone Continent which can be so clearly circumscribed using the Smith and Bullard pre-drift reconstructions of the North Atlantic (House 1968). The probability of such a link has long been recognized, first through the abundant occurrence in western North America of the Middle Devonian brachiopod *Stringocephalus* (Boucot *et al.* 1966), a typical form of Europe and the Urals but a genus which is absent from New York and the Appalachians. Secondly there is the similar evidence in the distribution of *Amphipora* (Duncan, in Cloud 1959). The wide distribution of continental Devonian deposits shows that the route must have lain in the region of the northern Canadian Arctic islands or further to the north-west.

The goniatite evidence for this link between the Urals and Western Canada ranges from the Lower Devonian, with the occurrence of the Emsian *Teicherticeras*, and



TEXT-FIG. 5. Diagram illustrating the occurrence of ammonoid genera (excluding Imitoceratidae and Clymeniina) in various areas around the supposed Old Red Sandstone Continent.

continues up to the Early Famennian with typical *Cheiloceras*, *Sporadoceras*, and other genera of Europe and the Urals (House and Pedder 1963).

So far as the provided reconstructions are concerned that of the Lower Devonian (text-fig. 3) retains the feature of close assembly of North America, Europe, the Urals, and Siberia which conveniently brings into proximity these faunas. This is not true of the Lower Carboniferous reassembly (used in text-fig. 1) which may more reasonably apply to the Late Devonian. The distribution of *Manticoceras* of the Frasnian would be more reasonable were northern Siberia closer to North America. This again emphasizes the unsatisfactory result of invoking too much separation along the present Ural line. The absence of Late Famennian Wocklumeria Stufe faunas, and the rarity of Mid-Famennian faunas, is not inconsistent with a later separation if that is required by other evidence.

Afro-Appalachian link. Eastern North America shows a number of faunal peculiarities, especially in the Mid and Late Devonian. The extremely well-known sequences of New York, which are as well exposed, searched, and monographed as any such area in the world, still have provided no evidence of a number of genera occurring in western North America and Europe.

So far as the goniatites are concerned, and particularly, but not wholly, with regard to the Givetian, a more European aspect becomes apparent southward in West Virginia and Virginia. Genera absent from New York but present farther south include *Sobolewia*, *Maenioceras* (House 1962, p. 255) and recent finds of earlier *Cabrieroceras*, *Foordites*, and ?*Gyroceratites* as well as of younger *Epitornoceras* and *Pharciceras* confirm this picture.

A migration route south of the source area of the Catskill delta and its inhospitable associated sediments is suggested. Since almost all the genera mentioned occur in North Africa (Petter 1959) and only one is known in central U.S.A., it seems reasonable to suggest that the link was to the east. A proximity of Africa to the Appalachians is therefore suggested. A similar view has been reached by Oliver (1973, this volume) on the basis of endemic coral genera restricted to eastern North America, North Africa, and Spain.

Proto-Tethys link with Australia. The Australian goniatite faunas known show remarkable affinity with those of Europe. This link was present in the Lower Devonian and is indicated by records from south-east Australia (Teichert 1948, Erben 1965). The Middle Devonian is poorly represented but the Frasnian faunas of Western Australia (Glenister 1958) are quite remarkable. The link continued in the later Upper Devonian, both in Western Australia (Delépine 1933, Teichert 1943, Glenister and Klapper 1966) and also New South Wales (Jenkins 1966, 1968; Pickett 1960). As in other parts of the world, it is the Frasnian faunas which are best represented.

There is no really convincing evidence on the precise course of the migration route or routes suggested by this evidence. So far as the better-documented Frasnian and Early Famennian faunas are concerned, the Famennian faunas of Iran (Walliser 1966), probably Middle Devonian faunas of Burma (Reed 1908) and the widespread Frasnian faunas of China (Chao 1956, Sun 1935), and rich Famennian faunas especially of the Great Khinghan (Chang 1958, 1960) suggest that the link may have been

a Proto-Tethys one, but the reconstructions provided for this symposium suggest other possibilities along the same general route. Teichert (1943) drew attention to the northern Siberian records of the Frasnian *Manticoceras* and suggested this was the faunal link between the Urals and Novaya Zemlya with China. It is clear, however, that during the Frasnian, goniatites were particularly cosmopolitan and hence they may not be a useful guide to migration routes of less prolific times. The variety of the poor record in China and the Great Khinghan suggests a more equatorial position than that envisaged in the reconstruction.

Acknowledgements. I am indebted to Mr. D. A. Wheeler for preparing the trend surface analysis used; to Dr. J. D. Taylor for permission to publish new records of *Nautilus* shells from the eastern Pacific; and to Dr. R. N. Whybray for help with Japanese literature.

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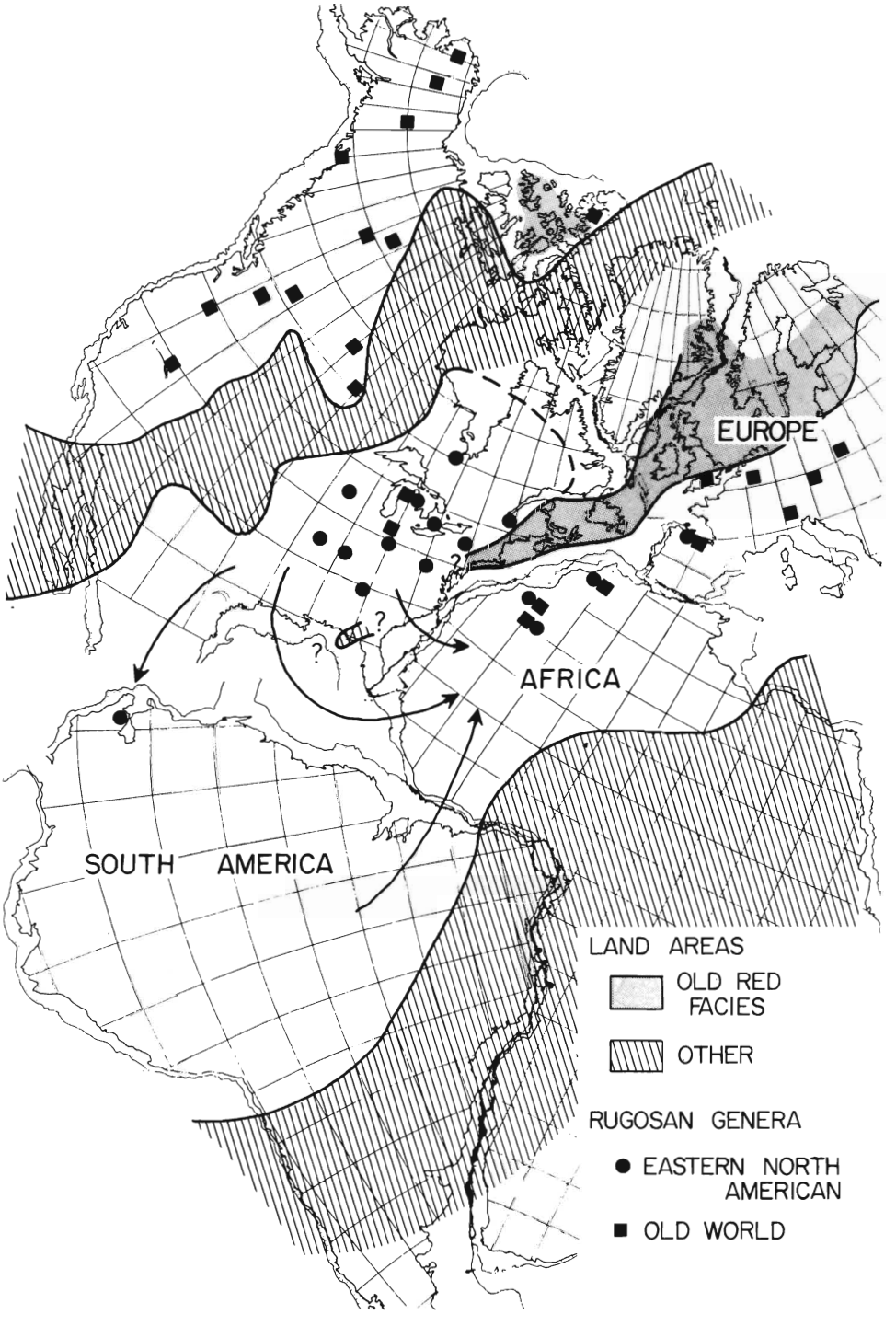

TEXT-FIG. 1. Palaeogeography of eastern North America and surrounding areas during the Middle Devonian. Base map from Bullard *et al.* (1965), by permission. Possible migration routes are indicated by the arrows.