

# ALLOPATRIC SPECIATION—AN EXAMPLE FROM THE MESOZOIC BRACHIOPODA

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**ABSTRACT.** The current debate on the processes of evolution is related to the author's knowledge of the phylum Brachiopoda in Mesozoic strata. An example is presented from the genus *Homoeorhynchia* in which marginal populations seem to have developed that eventually led to an ecological 'take-over' by a new species.

A GREAT deal of discussion has been going on during the past ten years about the processes of evolution. In particular there has been the alleged conflict between *phyletic gradualism* (the slow continuous process of change which has been in most palaeontologists' subconscious since the days of Darwin) and *punctuated equilibrium* (in which species are normally in a state of *stasis* or equilibrium, which is periodically punctuated or interrupted by sudden replacements of old species by new). An essential feature of the latter process is *allopatric speciation* in which the new species arise in marginal populations which have been isolated in some way from the main stable population.

Palaeontology cannot hope to tell us anything about gene flow, inherited immunities, and the rest of the matters which are under discussion at the moment, but it can provide a three-dimensional picture of evolving species which must be superior to the two-dimensional neontologists' view that has led to the current controversy over cladistics. Though I generally sympathise with the palaeontologists in this debate, I must ignore the political connotations as irrelevant and must also regret that so much emphasis has been placed on the fossil vertebrates.

Vertebrate fossils are inevitably very rare and it is unfortunate that their spectacular nature (notably among such groups as the dinosaurs) has led them to dominate the evolution debate. Even when they have been abundant enough to quantify, this has almost always been on the basis of a single unit character. Indeed, in the present debate on human evolution and the relationship between *Homo erectus* and *H. sapiens*, most of the arguments seem to concentrate on a single specimen—the Petralona skull from Greece. Not many invertebrate palaeontologists would nowadays accept a single specimen as representative of a population, let alone a whole species.

Invertebrates on the other hand, especially small marine invertebrates, are extremely abundant as fossils and in some cases are sufficiently widespread and well known to provide a meaningful picture of the nature of particular species at succeeding points in time. Thus in their survey of 'the state of the art' Gould and Eldredge (1977) could only find adequate examples of quantified evolutionary studies among the invertebrates.

Theoretically, planktonic foraminifera in continuously deposited deep-sea sediments should provide the examples needed to demonstrate such processes. My colleague Professor F. T. Banner assures me that this is so and that there is no doubt at all about phyletic gradualism in this group. He has cited numerous examples of lineages which show progressive, unidirectional, non-iterative changes (for example, in the genera *Globotruncana* and *Globorotalia*). Unfortunately few attempts seem to have been made to quantify such studies, though—as with all such studies—it would be necessary to study them throughout their area of occurrence to be sure one was dealing with evolution rather than migration. The well-known cases of reversal of coiling in *Globorotalia* as they are traced laterally across the North Atlantic provide a warning here, since clearly these are related to environmental controls. One very well-documented study has recently been published (Malmgren and Kennett 1981) in which the process of phyletic gradualism seems to be demonstrated in the lineage *Globorotalia conoidea*-*G. inflata*, though it must be noted that more than 30,000 measure-

ments of six characters were all based on material from one borehole and cannot exclude migrating factors.

If it is true that the planktonic foraminifera went on happily evolving in the open sea without punctuation and evidently without ecological isolation, then I suggest it is peculiar to planktonic forms and unlike almost all the examples I know from the fossil benthos. Presumably in their environment it is difficult to become isolated geographically or ecologically, but with the shallow water sessile benthos it is very easy.

#### EVOLUTION IN MARINE INVERTEBRATES

It is an elementary observation in palaeontology that some groups evolved more rapidly than others. Obvious examples of rapid evolvers are the graptolites, conodonts, and ammonoids. The most evident feature that these groups have in common is that they are all pelagic forms that moved about fairly easily in the water body. Comparable on land were the vertebrates which were equally mobile and equally rapidly evolving. On the other hand, the more slowly evolving groups in the sea were the benthos, especially sessile benthos such as brachiopods, bivalves, and corals.

Thinking in terms of allopatric speciation, the possible cause of this difference is not difficult to understand. The more mobile forms are more likely to enter marginal habitats and, given the right circumstances, to produce isolated populations in extreme conditions which may lead to the rapid evolution of new species.

If a population of giraffes is isolated in a valley where the only tree is a taller-than-average species of *Acacia*, then there will be strong selective pressure on that population to produce forms with longer necks. If circumstances change and the population is able to return to the plains from which its ancestors came, then this new stock may prove more successful in feeding than the main species and rapidly replace it. This is not Lamarckian giraffes stretching higher up the trees and passing on the ability to their offspring. It is not Darwinian giraffes all gradually evolving side by side into a new and 'better' giraffe. It is what may be called Gouldian giraffes that have done their evolving in private and then carried out a very successful take-over bid for the habitat of their ancestors. Such a process might have occurred in the Ngorongoro Crater in northern Tanzania had the giraffes been able to enter that steep-sided collapsed caldera.

Geneticists may then argue whether the rapid evolution of the marginal population was adaptation to different selective pressures or to a 'genetic revolution'. This need not concern us here since the necessary information is not available.

Gregarious sessile benthos with a short free-swimming larval stage, such as the brachiopods, are almost by definition slow evolvers. The young are of necessity adapted as closely as possible to the environment of their parents, otherwise they are very speedily selected out. There are no opportunities for 'hopeful monsters'. I cannot imagine anything in the Phylum Brachiopoda, for example, comparable to the octopuses with fifty-six and eighty-three tentacles respectively, which I have seen recently in the Toba Aquarium near Nagoya. Nevertheless, brachiopod populations are variable in their own quiet way, and this has led to a great deal of unnecessary taxonomic splitting among fossil forms. Thus Buckman (1907) created nineteen nominal species within the genus *Cincta* on the basis of material collected in one thin band in one quarry in Somerset. In my opinion, these are all referable to the species *C. numismalis* (Lamarck). Text-fig. 1 shows the variation (in one character only—that



TEXT-FIG. 1. Variation in *Zeilleria quadrifida* (Lamarck). Outline drawings of specimens in the British Museum (Natural History) from the upper Pliensbachian (*spinatum* Zone) of the Ilminster/South Petherton district of Somerset.

of valve outline) in the allied species *Zeilleria quadrifida* (Lamarck) from the Pliensbachian faunas being considered in this paper, also from Somerset. These variants range from 'typical' *Z. quadrifida* to 'typical' *Z. cornuta* (Sowerby) and both names are used equally commonly. Variation in zeilleriids generally was discussed at length by Delance (1974). He regarded *Cincta* as a subgenus of *Zeilleria*.

So far as rates of evolution are concerned these are, of course, relative. Mesozoic brachiopods are slow compared with ammonites. They are probably fast compared with fresh-water molluscs. Maynard Smith (1981) cited five species of molluscs in Lake Turkana which changed perceptibly in a period of 50,000 years when the lake was isolated. As he said: '... 50,000 years (2 m of sediment) is sudden to a palaeontologist but gradual to a geneticist.' This detailed demonstration of 'punctuated equilibria' has now been published (Williamson 1981). However, by using ammonites as a stopwatch, the rate of evolution of Mesozoic brachiopods makes them just about susceptible to study through the blurred fossil record. It is also possible to study them over a very wide area of well-documented strata.

#### HOMOEORHYNCHIA

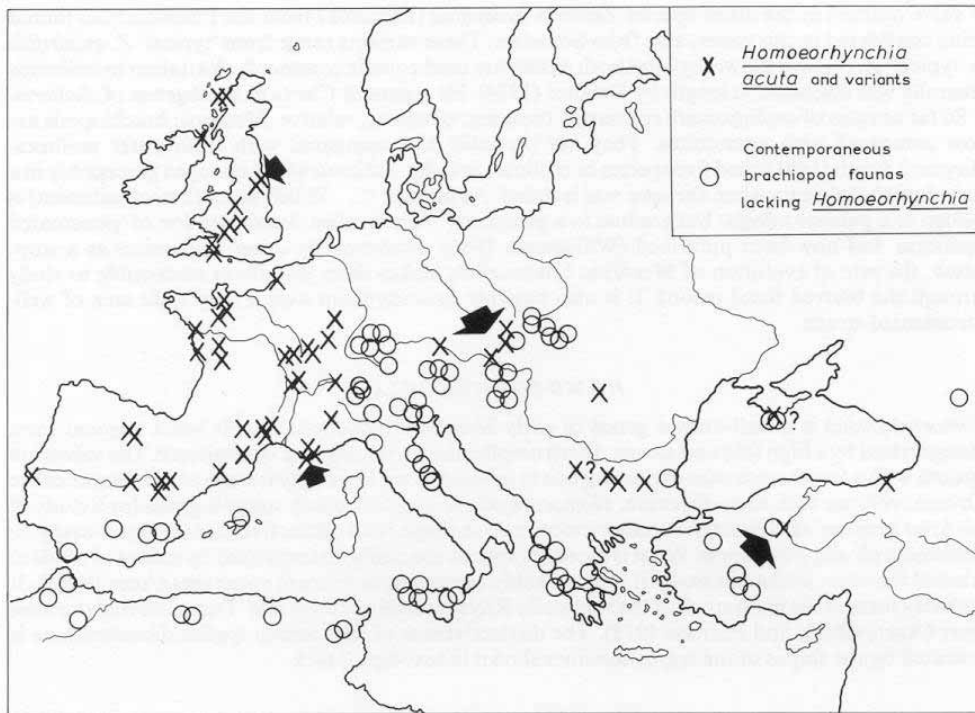
*Homoeorhynchia* is a well-known genus of early Mesozoic rhynchonellids. It has a trigonal form characterized by a high fold and strong, sharp uniplication in the anterior commissure. The valves are smooth with a few sharp costae appearing late in development. Internally it is a typical member of the Rhynchonellinae with radulifer crura. *Homoeorhynchia* is a particularly suitable genus for a study of this kind because its characteristically cynocephalous shape is so distinctive that it cannot easily be confused with any other form. What is more, its species are easily distinguished by means of obvious external features, whilst internally it is remarkably consistent in its main structures (Ager 1956a). It probably formed the main stock of the subfamily Rhynchonellinae from mid-Triassic to mid-Jurassic times (Ager, Childs and Pearson 1972). The distinctiveness of the various species discussed here is indicated by the slopes of the regression lines shown in text-figs. 3 to 5.

#### HOMOEORHYNCHIA ACUTA

*Homoeorhynchia acuta* (Sowerby) is a fairly uniform species, varying chiefly in lateral profile. Its outstanding characteristic is its sharp anterior plication containing a single costa. It is reasonably abundant in the upper Pliensbachian, especially in the *spinatum* Zone, right across Europe outside the Alps. It is not known outside Europe. However, it ranges from much lower in the Jurassic, notably in the Sinemurian and lower Pliensbachian, and has been recorded in the Rhaetian, though this record has not been confirmed. Closely similar earlier and probably ancestral forms are *H. ottomana* (Bittner) (e.g. specimens in the British Museum (Natural History) B 39223 from the 'Alpine Muschelkak' at Han Bulog near Sarajevo in Yugoslavia) and *H. subacuta* (Munster) (e.g. BM(NH) specimens 30646 from the 'Keuperian' of St. Cassian in Austria). It is therefore a long-ranging and stable species which virtually disappears abruptly at the top of the Pliensbachian. Text-fig. 2 shows its total known distribution. The figure also includes negative evidence in the form of records of contemporaneous brachiopod faunas where it is not known to occur.

Out of thousands of specimens I have studied of this species, I have only seen very rare variants (probably less than half a dozen) from the main populations in which a second costa is developed asymmetrically on the plication. These are so rare that they may be regarded as monstrosities, though (as is the custom) I did see fit to figure one in my monograph of British Liassic Rhynchonellidae (Ager 1956a, pl. iii, fig. 3a). This demonstrates the misleading nature of many monographs. It is probably significant, however, that it was only at the apogee of this species, when it was at its widest extent and greatest abundance at the end of Pliensbachian times, that significant marginal populations developed which were to prove its undoing.

I had no doubt until recently that *H. acuta* became extinct everywhere at the end of Pliensbachian times. I knew of no record of it anywhere in Toarcian rocks. However, in the British Museum (Natural History) I came across a small collection from the upper Toarcian that undoubtedly belongs



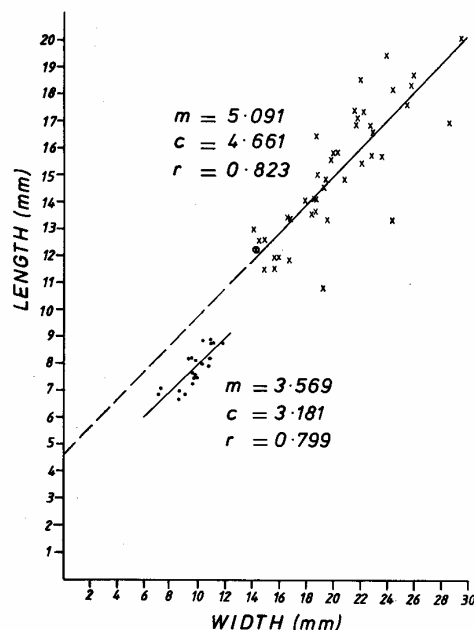
TEXT-FIG. 2. Geographical distribution of *Homoeorhynchia acuta* (shown by crosses) and contemporaneous brachiopod faunas lacking that species (shown by circles). Arrows indicate the marginal populations referred to in the text.

to this species. It was made a few years ago by Dr. M. K. Howarth and consists of twenty-three tiny specimens from the upper Lias, Moorei sub-zone of Frocester Hill, Gloucestershire (registered No. BB.45856). Dr. Howarth has confirmed (pers. comm. 1982) that there is no doubt whatever about the horizon of these specimens. Though all are very small (none larger than 9 mm in length) they are clearly adults with a well-developed unicostate plication. They do not plot in line with normal members of the species (text-fig. 3) and must be regarded as stunted survivors, living in an unfavourable environment. It is presumably significant that they occur beyond the known geographical range of *H. meridionalis*, which is not known north of Somerset.

Thus early members of *H. meridionalis* occurred in the south contemporaneously with the main body of *H. acuta* and later members of the latter species occurred in the north contemporaneously with the main body of *H. meridionalis*.

*Turkish variants.* These are an example of an earlier marginal population that did not get anywhere. I found this population at Yakaçik in central Anatolia, at the very edge of the known geographical range of the species. In it forms with two or three costae in the plication (the second developed asymmetrically) were not uncommon (Ager 1959, p. 1019, fig. 1). These were late Sinemurian in age and have no known descendants. All the forms here are small and poorly developed and it is reasonable to postulate marginal, rather unfavourable conditions. They fall within the normal range of variation of *H. acuta* (text-fig. 3). They appear to be very local in distribution. They were not mentioned by Vadasz (1913) who originally described Liassic brachiopod faunas from this region

TEXT-FIG. 3. Variation in *Homoeorhynchia acuta*, upper Pliensbachian Dorset and Somerset (shown by crosses) and the late Toarcian variants from Gloucestershire (shown by dots). A typical member of the Sinemurian population from Yakaçik, Turkey, is circled.  $m$  = slope of regression line;  $c$  = intercept on  $y$  axis (calculated);  $r$  = correlation coefficient. The extension of the regression line (dashes) in the upper scatter shows that the Toarcian forms are not juveniles of the normal *H. acuta*, but stunted variants. It should be noted that in this and subsequent scatter diagrams there is a slight allometry of growth which limits the significance of the regression lines.



and they do not occur in an otherwise very similar fauna I have described recently from Bilaçik, further south in Turkey (Ager *et al.* 1980).

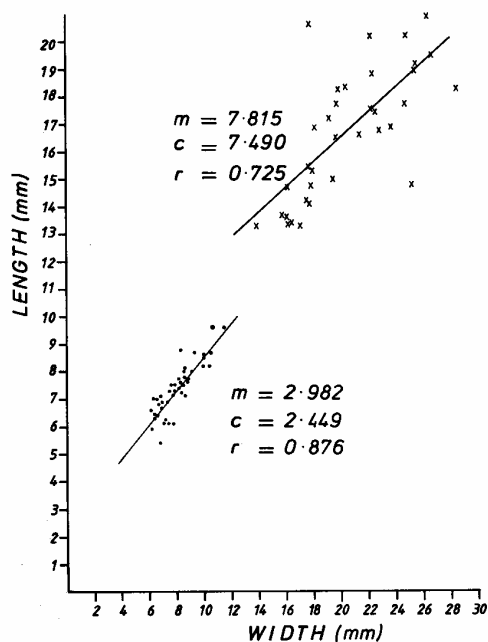
They may clearly be regarded as a marginal population, presumably at the edge of the species' range of ecological tolerance, that started to evolve in a particular direction but did not succeed. It is a clear example of an 'experiment that failed'. There may have been hundreds of such 'experiments' in the life of *H. acuta* but given the nature of the fossil record, it is fortunate that this particular one has been preserved.

*Yorkshire variants.* The Pliensbachian brachiopod faunas of Yorkshire have always been particularly interesting because they seem to have been cut off from the main stocks by the highly selective and probably unusual conditions of the English Midlands where ironstones were being deposited at this time. Thus the genus *Aulacothyris* is common in south-west England at this time, in the form of *A. resupinata* (Sowerby), but is completely absent from Oxfordshire up to the Humber. In Yorkshire, however, there are two further species which we may presume to have arisen through a process of geographical isolation. These are *A. pyriformis* (Tate) below and *A. fusiformis* (Rollier) above. This may also be an example of allopatric speciation (see Ager 1963, p. 258, fig. 15.5).

So far as brachiopods of a *Homoeorhynchia* type are concerned, they are virtually completely absent from the English Midlands (Ager 1956b). There are, however, two species which are—to all intents and purposes—restricted to Yorkshire. These are the tiny form of *H. capitulata* (Davidson) and the later larger form here called *H. lineata* (Young and Bird). The former may be regarded as a stunted population living in extreme conditions. It is multicostate (much more so than any of the other forms discussed herein) and only has a very short record.

The other Yorkshire species, however, was much more successful. It has commonly been placed in the genus *Rhynchonelloidea* (e.g. by Ager 1956a and 1956b) and it has differences in internal structures which make it more separate from *Homoeorhynchia* s.s. than the other populations discussed here. Nevertheless it is almost certainly not related directly to later species of *Rhynchonelloidea* (including the type species) and it seems more appropriate to link it with *H. acuta* as I did after an

'agonizing reappraisal' (Ager 1967, p. 161). It has the sharp cynocephalous fold, both in the bicostate and tricostate conditions (which were previously called '*Rhynchonella*' *bidens* and *triplicata* respectively). It is extremely common in the Yorkshire upper Pliensbachian and appears to have differed from *H. acuta* in having been able to prosper in clay ironstone depositing conditions. It does not appear to have left any descendants and the succeeding Toarcian deposits there are virtually devoid of brachiopods. Variation in *H. lineata* and *H. capitulata* is illustrated in text-fig. 4.



TEXT-FIG. 4. Variation in *Homoeorhynchia lineata* (shown by crosses) and *H. capitulata* (shown by dots), upper Pliensbachian, Yorkshire. Symbols as in text-fig. 3.

*Provençal variants.* Many years ago, Eudes-Deslongchamps (1863) commented that *H. acuta* was a northern form which was replaced to the south by *H. meridionalis* (a species first described by himself). When I quoted this remark in a paper (Ager 1961) I was criticized by the late and very knowledgeable specialist on Mediterranean Liassic brachiopods, G. Dubar. He did so on the grounds that Eudes-Deslongchamps had made an error in his stratigraphy and that whereas *H. acuta* was essentially a late Pliensbachian form, *H. meridionalis* belonged to the Toarcian. Dubar was, of course, basically correct, since the vast majority of the latter species—in France, in Spain, in Morocco, and even in England—belong to the early or mid Toarcian.

However, there were definite records of *H. meridionalis* in older strata in Provence. I am now told (pers. comm. Y. Almeras 1983) that all these records are incorrect and that all the Provençal forms are Toarcian in age. These again seem to be marginal populations since we are here already in the Alps and *Homoeorhynchia* is unknown in the deeper water facies not very much further east. What is more, these localities are not very far from the Toarcian localities in north-east Spain (such as Camarasa) where *H. meridionalis* becomes extremely abundant and variable.

*Slovak variants.* In 1964 I visited a unique locality in the Czechoslovak Carpathians with Milos Siblik. It was at Kostelec, where lower Jurassic limestones are thrust over the Cretaceous. Dr. Siblik had found an horizon, of undoubted late Pliensbachian age, with extremely abundant bicostate and tricostate cynocephalous forms. He subsequently described these as a new genus *Slovenirhynchia*

(Siblik 1967). In my view, previously expressed in a joint paper (Ager *et al.* 1972, p. 191), this is almost certainly a junior synonym of *Homoeorhynchia*. What is more, the new species named by Siblik, *S. maninensis* is, in my view, synonymous with *H. meridionalis* which does not otherwise occur in Czechoslovakia. This was also the view of Sučić-Protič (1969).

Here again we have a marginal population, close to the edge of the so-called Alpine 'trough' and indeed actually within the alpine belt, unlike any other members of the genus. What is more, it is extremely abundant, variable, and well developed. In text-fig. 2 the four localities mentioned above are all indicated with arrows and it will be seen that they are all marginal in the geographical sense. In the case of the last two localities, they are both actually in the alpine belt (where *H. acuta* does not occur) and close to much deeper water facies than those we associate with that species. It is conceivable that they represent deeper water brachiopod communities than those usually preserved in rocks of this age.

It is confidently suggested that the local, perhaps isolated, population of *Homoeorhynchia*, as seen at Kostelec gave rise to the new species *H. meridionalis* in the Toarcian, as suggested diagrammatically in text-fig. 6.

It is possible that another marginal population exists in Yugoslavia, since Sučić-Protič (1969) recorded *H. cynocephala* (Richard) and *H. crassa* sp. nov. from the middle Lias (Pliensbachian) of Serbia. These are almost certainly synonyms of *H. meridionalis* and it is noteworthy that she comments that the greatest development was in the Toarcian.

#### HOMOEORHYNCHIA MERIDIONALIS

As already mentioned and as implied by the specific name, Eudes-Deslongchamps regarded this species as a form of the warm south. It appears very widely in the western Mediterranean area in lower Toarcian strata. I have collected it in large numbers at such localities as Camarasa in the Spanish Pyrenees and in the Valley of Ziz in south-east Morocco. At these places it occurs in calcareous 'marls' which are quite unlike the black paper shales that one usually associates with the lower Toarcian in northern Europe. It is significant that other elements in the brachiopod fauna, such as *Spiriferina* and *Stolmorhynchia*, persist here in the south much later than they are found elsewhere. However, it is clearly not just a matter of latitude since, given the right circumstances, *H. meridionalis* can occur very much further north. The outstanding exception which proves this rule is the Ham Hill Stone in Somerset. This is a calcareous development within the Toarcian which yields abundant rhynchonellids. They were placed in a new species '*Rhynchonella*' *cynica* by Buckman (1895), by Kellaway and Wilson (1941) and by me (Ager 1956a), but again it was a matter of local specialists not recognizing a species that does not otherwise occur in their country. Variation in *H. meridionalis*, in this sense, is illustrated in text-fig. 5.

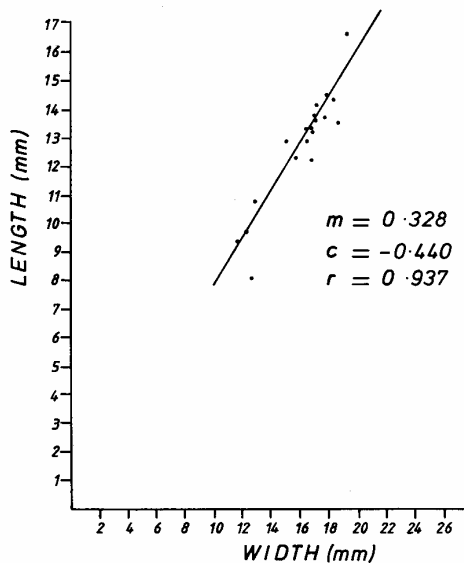
I later attributed this form to the southern species (Ager 1967, p. 161) and have no doubt that this is where it belongs. To all intents and purposes it is identical with the form found in southern Europe and northern Africa and is very well developed with no signs of stunting.

Whether or not it should be regarded as a subspecies of the better known species *H. cynocephala* (as I suggested in my recantation) is a matter of less certainty. I am persuaded by Dr. M. J. Clutson, who has worked extensively on the Toarcian and Aalenian forms, that the two are best kept separate. But I will leave him to discuss the taxonomy and variability of these later species such as *H. battalleri* (Dubar) (which he regards as a local subspecies of *H. meridionalis*).

#### THE TOARCIAN TAKEOVER

Looking at the genus *Homoeorhynchia* in general there is no doubt that, apart from the rare and local forms mentioned above, *H. acuta* is the dominant species of the Pliensbachian. When one comes to the Toarcian it is *H. meridionalis* that takes over almost everywhere that rich brachiopod faunas are found outside the alpine belt.

What then were the palaeogeographical events that accompanied this change? I have elsewhere



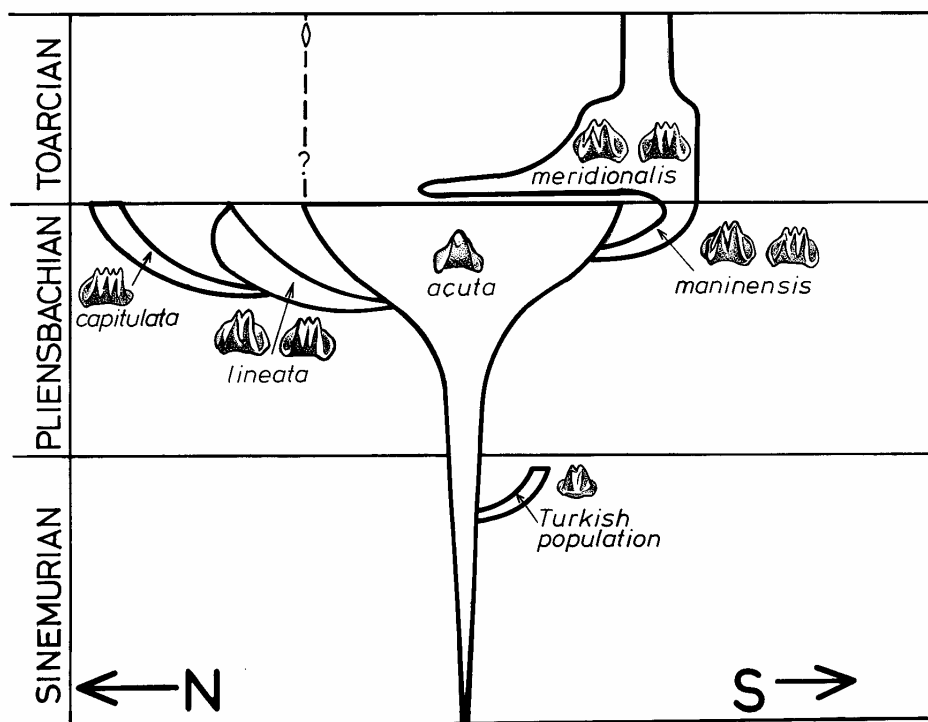
TEXT-FIG. 5. Variation in *Homoeorhynchia meridionalis*, Ham Hill Stone, Toarcian, Somerset. Symbols as in text-fig. 3.

suggested (Ager 1981) that the Toarcian transgression was one of the most important events of Mesozoic times. It was an episode of eustatic deepening on an almost world-wide scale with—for instance—the first Mesozoic flooding of the East African Seaway. Hallam (1981) has shown that episodic deepening of the sea was the leitmotif of early Jurassic history and that there was a major pulse in early Toarcian times. In Europe it was a time when shallow water carbonates and ironstones were generally replaced by black shale deposition and there was a general replacement of benthonic by pelagic faunas. Hallam (1967, 1972) has drawn attention to the 'profound turnover of the invertebrate fauna' with widespread extinctions of benthonic forms at this level.

It has earlier been hinted that marginal populations of *H. acuta* times might have been adapted to slightly deeper facies. It would therefore be logical to deduce that the spread of deeper water conditions favoured the marginal populations and enabled them to take over the regions previously occupied by the ancestral group. That it may not be as simple as that is suggested by the fact that the multicostate condition is 'normal' for Mesozoic rhynchonellids whereas the unicostate condition is decidedly 'abnormal'. It may therefore be that it was only rather special circumstances in the Pliensbachian that favoured *H. acuta* and with the return of 'normality' in the Toarcian (at least in its carbonate facies) the more usual and conservative *H. meridionalis* type reasserted itself. Clearly, however, there were advantages in the cynocephalous form since it was tried several times in the evolution of the Rhynchonellida, both in the Palaeozoic and in the Mesozoic (e.g. in *Pugnax*, *Ladogia*, and *Rhynchonella* s.s.).

The advantages of the *meridionalis* morphology are not easy to determine. It is conventional to associate multicostate shells with a sieving function when feeding (as originally suggested by Schmidt 1937). However, there seems to be no consistency in the lithologies associated with the contrasting morphological types. *H. acuta* occurs in calcarenitic type matrices (particularly ferruginous oolites) whereas its later homoeomorph *Rhynchonella loxiae* (Fischer de Waldheim)—the original type species—occurs in glauconitic clays. *H. cynocephala* occurs in sands and oolites, *H. lineata* in sideritic mudstones, and *H. meridionalis* is found in everything from lutitic calcareous marls to calcarenites (especially non-ferruginous oolites). What is more, in formations such as the Junction Bed on the Dorset coast, *H. acuta* is closely associated in the same thin bed with multicostate rhynchonellids such as *Quadratirhynchia crassimedia* (Buckman) and *Prionorhynchia serrata* (Sowerby).





TEXT-FIG. 6. Diagram showing the various populations of *Homoeorhynchia acuta* and its relations in the lower Jurassic and the suggested replacement of that species by *H. meridionalis* in the Toarcian.

CONCLUSIONS

*Homoeorhynchia* is the only genus I know, out of literally hundreds of genera of Mesozoic Brachiopoda, that appears to show good evidence of allopatric speciation. There may be hints of it elsewhere, for example in *Aulacothyris* (mentioned above), in *Plesiothyris verneulli* (Eudes-Deslongchamps), which may be the very local ancestor of the mid-Jurassic biplicate terebratellids, and in the southern *Quadratrhyrnychia* variants of *Tetrarhynchia*, but the general picture seems to fit in with the Gouldian doctrine of 'hardly ever'. Certainly there is no evidence in the group as a whole of phyletic gradualism happening throughout a species at any one moment in time. Species A never changes into species B everywhere simultaneously and gradually.

The pattern in any one place at any one time is of sudden replacement of one species by another. Thus, for example, in the lower Lias section at Hock Cliff (Gloucestershire), where the environment seems to be stable and the rest of the fauna (such as *Gryphaea arcuata*) is uniform, the rhynchonellid *Piarorhynchia juvenis* (Quenstedt) is replaced, from one bed to the next, by the closely related *Cuneirhynchia dalmasi* (Dumortier). The genera may be artificial but the distinctiveness of the two related species is indisputable and there are no gradations between them.

So far as *H. acuta* is concerned, there seem to have been several 'attempts' to return to the more conservative multicostate form. These 'attempts' were scattered both in time and space. Finally, however, populations appeared on the southern margin of the species' range, perhaps in slightly

deeper water, which then replaced the parent species with the coming of the Toarcian transgression (text-fig. 6). As Dodson and Hallam have pointed out (1977): 'a gradient can give rise to allopatric speciation and . . . it is not necessary to invoke the creation of geographic barriers or sharp environmental changes'.

In these marginal populations, phyletic gradualism must have taken place, though it cannot be recognized in the strata at present. What is seen more generally, with the degree of resolution that is available to us, is the punctuated equilibrium situation in the sudden take-over by *H. meridionalis* of most of the regime previously occupied by *H. acuta*.

In conclusion it may be said that phyletic gradualism must occur, but when it does, then paradoxically, it must happen very quickly.

*Acknowledgements.* I should like to express my thanks to Professor Akira Morishita and the University of Nagoya, Japan, where I was a guest when this paper was being written. I am grateful for discussions with Dr. J. Ferguson, Dr. M. J. Clutson, Dr. P. Styles, and Professor F. T. Banner and for guidance in the field to Dr. M. Siblik and the late Professor M. Gouvernet. Mr. J. U. Edwards kindly drew the diagrams and Mrs. V. M. Jenkins typed the manuscript.

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