Segregation and Migration Patterns in Some *Graphoceras* Populations (Middle Jurassic)

(Die Bedeutung einiger *Graphoceras*-Populationen (Mittlerer Jura) für Migration und Absonderung bei Ammoniten)

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With 2 Text Figures and 1 Table

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Abstract: Populations of the ammonite *Graphoceras* from the Aalenian (Middle Jurassic) of Bearreraig (Skye, N.W. Scotland) are dominated by juveniles of both sexes between 8 mm and 21 mm diameter (at end of phragmocone) and small adult microconchs with lappets, but larger and adult macroconchs are rare. In comparison *Graphoceras* faunas in several other localities in N.W. Europe show few specimens in this size range but are dominated by larger juveniles and adults, with slightly varying macroconch: microconch ratios. Palaeogeographically Bearreraig was a near-shore environment while the others were further off-shore. This suggests that there may have been a tendency to geographical segregation, with smaller juveniles of both sexes and adult microconchs inhabiting near-shore areas while larger juveniles and adult macroconchs and microconchs were mainly further off-shore.

In the Skye populations juveniles less than 7 mm diameter and larvae are rare and this deficiency may indicate an earlier phase, such as planktonic mode of life before migration to near-shore (? nektobenthic) environments in later juvenile stages.

Similar patterns of behaviour are known for some modern coleoids, but more information is needed about ammonite population structures in a variety of palaeogeographic settings and facies.

Kurzfassung: *Graphoceras*-Populationen aus dem Aalen (Mittlerer Jura) von Bearreraig (Skye, NW-Schottland) enthalten vorwiegend juvenile Formen beider Geschlechter (mit Phragmokon-Durchmessern zwischen 8 und 21 mm) und kleine adulte Mikrokonche (mit Ohren); größere und adulte Makrokonche sind dagegen selten. *Graphoceras*-Faunen anderer NW-europäischer Fundpunkte weisen dagegen wenige Exemplare dieser Größenfraktion auf, bestehen vielmehr überwiegend aus großen juvenilen und adulten Formen; dabei variiert die Makro/Mikrokonch-Ratio nur geringfügig. Paläogeographisch befand sich Bearreraig in küstennaher Lage, die übrigen Fundpunkte dagegen off-shore. Dies läßt vermuten, daß eine geographische Trennung erfolgte, wobei juvenile Formen beider Geschlechter und adulte Mikrokonche near-shore-Environments bevorzugten, adulte Makro- und Mikrokonche dagegen off-shore-Bereiche besiedelten.

Interessant ist, daß in den Skye-Populationen juvenile Formen unter 7 mm Phragmokon-Durchmesser selten sind. Dies könnte dafür sprechen, daß die Graphoceraten noch eine frühere, wahrscheinlich planktische Phase durchliefen, bevor sie zu einer (nektobenthischen?) near-shore-Lebensweise übergingen.

Ähnliche Verhaltensmuster sind von einigen modernen Coleoiden bekannt; von den Ammoniten sind weitere Informationen über die Populationsstrukturen in unterschiedlichen Milieus oder Fazies erforderlich.

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1. Introduction

There can be great variation in contemporaneous ammonite assemblages belonging to the same taxon in different localities and strata. Sometimes this is a result of taphonomic factors, but in other cases significant differences in the living ammonite populations available for fossilisation must have occurred.

Differences in size occur frequently, but more widely discussed in the past (e.g. see Kennedy & Cobban 1976, Lehmann 1981) are differences between localities in the ratio between sexual dimorphs (the macroconch : microconch ratio). Several authors (e.g. Westermann 1969) have suggested that these differences in sexual structure of populations may have been due to geographical segregation of the sexes during during much of the year outside a breeding season.

The purpose of this contribution is to raise some questions about the preservation of ammonites of different size ranges in different localities, and about possible habitat changes during the life cycle. It arises from analyses of populations of *Graphoceras* from the Concavum Zone (Aalenian, Middle Jurassic) at Bearreraig (Isle of Skye, N.W. Scotland) and comparison of these with *Graphoceras* collections of similar age from other localities.

2. Graphoceras populations at Bearreraig

Successive populations of *Graphoceras* have been obtained from nodules in the lowest 9 m of the Udairn Shale Member of the Bearreraig Sandstone Formation at Bearreraig, Isle of Skye, in the Hebrides Basin of N.W. Scotland (Morton 1976). The occurrence of pathological deformity in these populations has already been described and discussed (Morton 1983). The nodules formed rapidly near the sediment/water interface in an area with a high sedimentation rate, so that the ammonite assemblage obtained from each nodule approximates to a single biological population, possibly entombed catastrophically. There are no significant differences in the size or dimorphic structures of populations from different nodules or from different levels, so that the results of the analyses of each have mainly been aggregated for present purposes.

2.1 Dimorphic structure

The ammonites recovered from the nodules are predominantly of small to medium size. Large specimens (presumably adult macroconchs) are rare. The populations display marked dimorphism and individual specimens can be grouped into the following categories:

a) microconchs with lappets (m);

b) probable microconchs with similar morphology and evidence of closer final sutures (m ?);
c) probable juvenile macroconchs, with morphology similar to that of the rare large macroconchs (see below) but smaller in size and showing no evidence of adult character (M ?);
d) juveniles of uncertain dimorphic status — some more similar morphologically to microconchs (? (m)), others to macroconchs (? (M)), but most indeterminate (?).

The total numbers of specimens in each category for each sample (referring to nodules from a specific stratigraphical level) are summarised in Table 1.

Table 1 Dimorphic composition of *Graphoceras* populations from the Concavum Zone at Bearreraig, Isle of Skye. Stratigraphical level refers to height above (or below) the base of the Udairn Shale Member that the sample was collected; see text for explanation of column headings.

Sample no.	Strat. level	m	m?	M?	?(m)	?(M)	?	Total
75/8	8.8 m	21	12	47	13	2	54	149
75/5	8.0 m	15	8	19	2	-	36	80
NES-B8	c6.0 m	-	-	2	-	-	3	5
75/4	5.4 m	9	6	18	1	-	35	69
75/3	5.0 m	22	3	4	-	-	39	68
NES-B5	3.0-4.5 m	2	3	8	2	-	9	24
80/22	-1.5 m	1	2	-	-	-	6	9
Totals		70	34	98	18	2	182	404
Percentages		17.3	8.4	24.3	4.5	0.5	45.0	100

Within each population there is a great range of morphological variation. In general microconchs tend to be more evolute with rounded whorl shape and fewer ribs per whorl than macroconchs of similar size. The macroconchs become more involute with flatter whorl sides and closer, finer ribbing. However there is much morphological overlap, especially if the shell diameter is less than 15 mm. The microconchs are most similar to *Graphoceras* (*Ludwigella*) *carbatinum* (Buckman) and the macroconchs to *Graphoceras* (*Graphoceras*) *limitatum* Buckman (cf. Morton 1983).

Half of the specimens are juveniles of uncertain dimorphic status, while of these which can be allocated with more confidence to one or other dimorph there are approximately equal numbers of microconchs (25.7%) and macroconchs (24.3%). The main difference between the dimorphs is that large presumably more mature macroconchs (with diameter at end of phragmocone greater than 35 mm) are extremely rare (about 1%), whereas most of the recognised microconchs show evidence, in spite of their small size, of being mature adults or nearly so, with at least short lappets and the last two or three sutures closer.

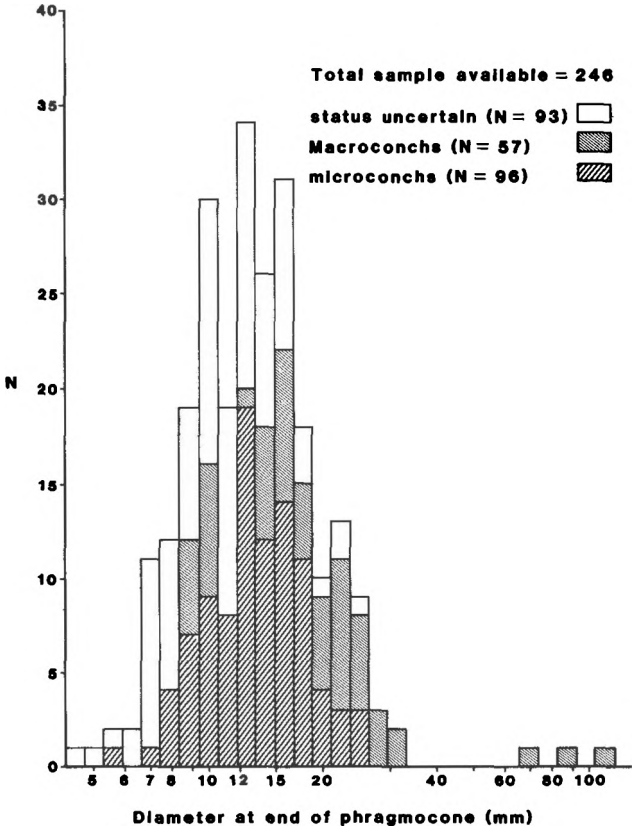
2.2 Size-frequency structure

In describing the size-frequency structure of a population it is advisable to use a standard measure of size. For ammonites the most widely convenient measure is the

diameter at the end of the phragmocone (beginning of the body chamber). The apertural end of the body chamber is too frequently broken or not preserved for this to be useful for comparison in most ammonite assemblages.

The size-frequency distributions showed little variation between samples, so that the data are combined in Text Fig. 1, which also shows the distribution of recognised dimorphs and indeterminate juveniles. Most of the specimens are between 8 mm and 21 mm diameter at the end of the phragmocone, with very few smaller than 7 mm or larger than 26 mm. There is a slight skewness in the distribution, but not enough to be significant, and there are no distinct size groups, such as might suggest separate generations. It is possible that each fossil population represents a single generation of juveniles, but it would be surprising for the same size range to be preserved repeatedly unless there is some other ecological factor.

The shortage of smaller and larger specimens is not due to taphonomic factors. The ammonites are extremely well preserved with mechanical damage to the shell (e.g. by transportation) rare and they are in fine-grained sediments associated with



Text Fig. 1. Size-frequency histogram for combined Concavum Zone *Graphoceras* populations from lower part of Udairn Shale Member at Bearreraig, Isle of Skye, N.W. Scotland.

small bivalves, gastropods and abundant land-plant debris. Therefore wave- or current-sorting cannot be a factor. Larger macroconchs occur in higher strata of similar facies (see Morton 1975 for Bajocian sonniniids) and lower in the Murchisonae Zone, and at least the body chambers would have been preserved if many large shells had been around. It must be concluded that large and adult macroconchs were rare in the living populations of ammonites in the area. Similarly the rarity of specimens below 7 mm diameter cannot be due to selective removal because the fauna includes other small organisms (both benthic and nekto-benthic) and small fragments of land plants (including notably frequent charcoal debris which would be very light) are abundant.

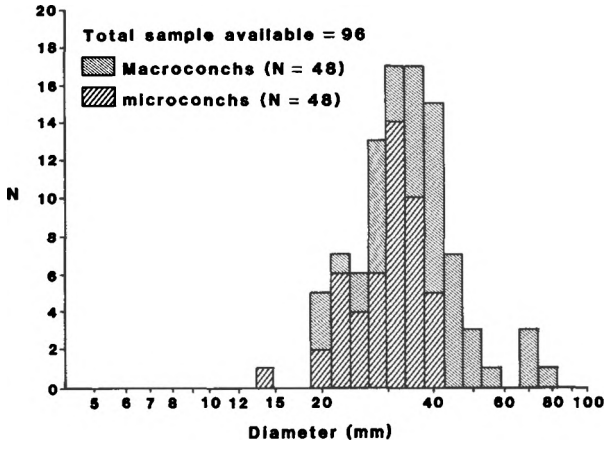
The living populations of ammonites from which the fossil *Graphoceras* assemblages were derived must have been lacking in very small juveniles and in larger and adult macroconchs. Incidentally the observation about abundance of juveniles also applies to the belemnites recovered from this part of the Udairn Shale Member, though large specimens are also common.

3. Comparison with other localities

Other localities from which assemblages of *Graphoceras* have been described are in general not comparable with those from Bearreraig in that the sequences are usually relatively condensed and the fossil assemblages are not derived from single biological populations. However they may be presumed to be representative of *Graphoceras* populations living in the area over a period of time, perhaps modified by taphonomic factors. Detailed comparisons are further hindered by the limited data available, so that only general discussion of dimorph ratios and size structures of most assemblages can be made.

3.1 Reugney, Jura Mts., France

Ammonites from the rich Concavum Zone assemblage at Reugney described by Contini (1969) are allocated to four "species" : two macroconchs *Graphoceras* (*Graphoceras*) *concavum* (Sowerby) (30 specimens) and *G.* (*G.*) *decorum* Buckman (20 specimens); and two microconchs *G.* (*Ludwigella*) *rudis* (Buckman) (24 specimens) and *G.* (*L.*) *cornu* (Buckman) (90+ specimens). Taken at face value this would imply a macroconch : microconch ratio of approximately 1 : 2, so that both dimorphs are well represented. From Contini's descriptions and figures (and from my own small collection made at the locality with the assistance of Dr. Contini) it is clear that medium to large (adult ?) specimens of both dimorphs are present, but there are few smaller juveniles of either dimorph. Specimen diameters given by Contini may not be strictly comparable with those given above for Bearreraig specimens because it is not specified where the measurements were made relative to aperture or end of phragmocone. A size-frequency histogram is shown in Text Fig. 2. The figure may be distorted by a bias towards larger specimens since only 37 out of 50 macroconchs and 41 out of 114 microconchs have been measured. However



Text Fig. 2. Size-frequency histogram for Concavum Zone *Graphoceras* at Reugney, Jura, France (data from Contini 1969, and my own collection). Note that the diameter is not measured at end of phragmocone, cf. Text Fig. 1.

my impression of the whole collection (kindly shown by Dr. Contini at the University of Besançon) is that there are few specimens with diameter less than 20 mm, and this is confirmed by measurements of specimens in my own collection. There are relatively few juveniles of the 8-21 mm range which are so abundant at Bearreraig. The Reugney specimens are preserved in an oolitic limestone and selective removal of smaller specimens is possible, but seems unlikely from the mixed size nature of the rest of the fauna.

3.2 Horn Park, Beaminster, Dorset

In the classic area for Aalenian and Bajocian ammonites of Dorset, the best available outcrop for Concavum Zone *Graphoceras* is the Inferior Oolite of Horn Park Quarry, near Beaminster. There have been no recent monographic studies so that the following general description is based largely on my own collection. The ammonite fauna is dominated by medium to large macroconchs with a smaller proportion of microconchs. The macroconch : microconch ratio is about 3 or 4 : 1. Most individuals are adults or large juveniles with a diameter greater than 50 mm, and smaller juveniles less than 30 mm in diameter are not common. The size range is generally greater than that at Reugney and there is a higher proportion of large adult macroconchs. The matrix is a coarse oolitic limestone (ironshot) and some winnowing of smaller sizes is possible but not wholly convincing as an explanation for the predominance of large sizes.

3.3 Schwäbische Alb, southern Germany

In this area Concavum Zone ammonites are found mainly in one limestone bed, the "*Concava*-Bank", at several localities and were described by Rieber (1963). From

Rieber's monograph the ratio of macroconchs (named as *concava, decora,* cf. *blanda*) to microconchs (*arcitenens, cornu, impolita* and *rudis*) is 24 : 10, that is approximately 2 : 1, with three specimens of uncertain status. Details of measurements are insufficient to give more than a qualitative account of size-frequency distribution, but from Rieber's descriptions and my own observations in Tübingen the assemblage is similar in character to that of Reugney with predominance of large juveniles (greater than 20 mm diameter) and adults of both dimorphs.

3.4 Bielefeld area, northern Germany

The graphoceratid ammonites of this area were described by Spiegler (1966) and Althoff (1940). From Spiegler's monograph there are in the Bethel section 10 macroconchs (*concavum*) and 15 microconchs (*cornu, rudis*) of *Graphoceras,* a ratio of 2 : 3. Only a few measurements are given but it would seem that most are medium to large sized juveniles with some adults of both dimorphs.

3.5 Conclusions

There are clear differences between the *Graphoceras* populations found at Bearreraig and those found at the other localities discussed. At Bearreraig the populations of *Graphoceras* are predominantly juveniles from 8 mm to 21 mm diameter (at end of phragmocone) with adult microconchs common but larger and adult macroconchs rare. The other localities have mostly larger juveniles and adult macroconchs and microconchs, in lithologies ranging from oolitic limestones to limestone-shale sequences deposited in mainly off-shore environments (see Ziegler 1982). Bearreraig also differs palaeogeographically in that the silty shales of the Concavum Zone were deposited in a near-shore environment in the rapidly-subsiding Hebrides Basin flanking the Scottish Highlands landmass which lay a short distance to the east.

This raises the possibility that there was geographical migration during the life-cycle of ammonites (or at least in *Graphoceras*), with small juveniles of both sexes and some adult microconchs inhabiting near-shore environments such as Bearreraig before migrating as larger juveniles and adults to more off-shore environments. However the data available at present on population structures and palaeogeographic settings are insufficient for this to be more than a speculative suggestion.

There are some differences in the macroconch : microconch dimorph ratios, but these are not very great between the localities discussed. Therefore no clear evidence has emerged in this study for significant segregation of the sexes in *Graphoceras* at any stage of growth.

4. Absence of larvae and very small juveniles

The absence in the Bearreraig populations of newly hatched larvae and of very small juveniles less than 7 mm in diameter is remarkable because they could have been

expected to be preserved if they had been present in the living populations. I do not know of any documented occurrence in *Graphoceras* but rare examples have been described for other ammonite groups (e.g. Kulicki & Wierzbowski 1983, Landman 1984), often in a preservation (in nodules in shales) not dissimilar from that at Bearreraig. This may mean that there is a still earlier stage of migration in the life-cycle.

5. Summary and comparison with living cephalopods

Comparison of the populations of *Graphoceras* from Bearreraig with collections of *Graphoceras* from other localities can be interpreted to imply migration during the life cycle. This and the absence of larvae at Bearreraig suggests that it may be possible to predict three distinct cases which may be represented in fossil occurrences of *Graphoceras*:

1. Larvae and very small juveniles up to 5-7 mm diameter (not yet found for *Graphoceras,* but documented for some other genera);
2. Small to medium sized juveniles from 8 mm to 26 mm diameter of both dimorphs, with some adult or nearly adult microconchs but rare adult macroconchs;
3. Larger juveniles greater than 25 mm diameter and adults of both dimorphs, in macroconch : microconch proportions which vary only slightly in *Graphoceras.*

In *Graphoceras* at least, stages two and three seem to represent migration from near-shore environments to more open off-shore environments. It remains to be seen whether similar patterns will emerge for other genera.

Comparing this migration pattern with those of living cephalopods shows no similarities with *Nautilus* in which juveniles are hardly ever found and are presumed to be deep pelagic in habitat. The same applies for fossil *Nautilus,* most of those found are more or less adult. In living coleoids there are two basic strategies of ontogenetic development (Boletzky 1977):

(a) Small eggs which hatch into larvae and small juveniles which are different in appearance from larger juveniles and adults and inhabit different environments (e.g. *Octopus* in which pelagic early stages settle to the bottom, at 6 mm mantle length in the English Channel, and are then nekto-benthic).

(b) Large eggs which hatch into larvae and juveniles which are not different in appearance or mode of life from adults (e.g. *Sepia*).

In terms of life cycle development and ecological adaptation perhaps ammonites were more similar to *Octopus* than to other coleoids or *Nautilus.*

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