Foraminiferal morphogroups, paleoenvironments and new taxa from Jurassic to Cretaceous strata of Thakkhola, Nepal

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ABSTRACT

The foraminiferal assemblages of the Upper Jurassic Nupra Formation and Lower Cretaceous Tangbe Formation in Thakkhola, Nepal are documented and a morphogroup analysis is carried out. Fifty-five agglutinated and four calcareous species are identified from a shale-siltstone-sandstone succession which was originally deposited on the northern Gondwana margin (southern hemisphere). Four new species are described: *Tolypammina undosa*, *Thalmannammina glomata*, *Parvigenerina mucromata* and *Trochammina nupraensis*.

The distribution of agglutinated foraminiferal morphogroups and the variations in species diversity are important indicators of environmental changes. The Oxfordian to Kimmeridgian black shales contain well diversified assemblages which are dominated by epifaunal morphogroups, but include also a large infaunal component. These shales are interpreted as slightly dysaerobic deeper shelf deposits. The Tithonian dark silty shales are typified by low diversity assemblages and by the predominance of elongate infaunal morphotypes; these shales are taken to represent a prodelta facies. The Lower Cretaceous consists of alternating shales, siltstones and sandstones with foraminiferal assemblages of very low diversity, dominated by flattened spiral epifaunal morphotypes. These shales are attributed to shallow prodelta shelf to delta plain environments. The study demonstrates that the morphogroup distribution pattern of the Thakkhola succession shows strong analogy with modern distribution trends. The Jurassic assemblages recorded from the prodelta to delta plain deposits of the North Sea Basin and those from corresponding facies in the Thakkhola succession display similar morphogroup patterns.

INTRODUCTION

The Upper Jurassic to Lower Cretaceous succession of Thakkhola was deposited in the southern hemisphere, on the northern continental margin of Gondwana. Previous studies of agglutinated assemblages have been heavily biased towards northern faunas, and relatively little is known about the agglutinated foraminifera of the southern hemisphere. The Late Jurassic was a period of extensive organic-rich shale deposition which led to the accumulation of important hydrocarbon resources. Agglutinated foraminifera can, therefore, provide very useful tools for palaeoenvironmental and palaeoecological studies of these deposits.

The material studied in this paper was collected in 1988 and 1991 in the Thakkhola area of northern Nepal, located immediately north of the central Himalayan range. The field area is accessible through the Kali Gandaki River valley, and is delineated by the villages of Jomosom, Tangbe, Chhukgaon, and Muktinath at approximately 29°N and 84°E (Fig. 1). The Upper Jurassic to Lower Cretaceous succession of the region has a minimum thickness of 1100 m, and consists mainly of shales, siltstones and sandstones deposited under deltaic to deeper shelf conditions. The sediments were strongly lithified during diagenetic processes, and were, to a varying degree, folded and faulted during the Himalayan collision.

The geology and stratigraphy of the Mesozoic of the Thakkhola region was recorded in detail by Gradstein et al. (1989; 1992). Both papers also include preliminary reports of the Upper Jurassic to Lower Cretaceous foraminifera. The Lower Cretaceous stratigraphy of the region was emended by Gibling et al. (1994). The foraminiferal succession of Thakkhola is discussed by Nagy et al. (in press), with regard to stratigraphy, depositional facies and regional affinities. The main objectives of the present study are: 1) to use a morphogroup analysis

Figure 1. Map of the Thakkhola area with location of the studied sections marked. Inset map shows India and Nepal with position of Thakkhola.

for the environmental interpretation of the succession, 2) to describe new taxa present at this mid-latitude site in the southern hemisphere.

Depositional setting
The Mesozoic deposits of northern Nepal are the remnants of the sedimentary cover of the Tethyan lithosphere consumed at a northward-dipping subduction zone, when oceanic ridge-spreading led to the northward drift of India and the opening of the Indian Ocean. The formations studied are part of a Triassic-Lower Cretaceous sedimentary succession representing a detached sliver of the ancient Gondwana margin, which was obducted onto the Eurasian plate during ocean closure and continental collision in the mid-Tertiary.

The deposition of the Thakkhola succession took place on the southern margin of the Tethys Ocean (Powell et al., 1988), when Thakkhola lay at mid latitudes, 30°-41°S (Gradstein et al., 1992). The Thakkhola region was then located on the northern continental margin of India, which was part of eastern Gondwana, also including Madagascar, Antarctica and Australia (Fig. 2). This passive margin formed part of an extensive continental shelf to slope area where organic-rich deposits accumulated in Late Jurassic time. The Nupra Shale belongs to this facies, and similar deposits can be traced westwards in the Northern Himalayas where the well-known Spiti Shale represent this facies.

Figure 2. Paleo eographic reconstruction of circum-NeoTethys landmasses in Late Jurassic and Early Cretaceous time (modified after Sengör, 1985, and other sources). Th=Thakkhola, Nepal.

Stratigraphical framework
A compilation of age significant fossil occurrences in the Oxfordian to Albian succession of Thakkhola is given in Table 1 and Fig. 3. Detailed discussions of the stratigraphy and age relationships are provided by Gibling et al., (1994) and Nagy et al., (in press). The lithostratigraphic scheme proposed by Gibling et al. (op.cit.) is followed in this paper.
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Figure 3. Generalised columnar section of Upper Jurassic and Lower Cretaceous deposits in Thakkhola showing position of the analysed sections. The age relationships are indicated by showing position of dated horizons. Numbers in brackets refer to Table 1, where further details about datings are listed.

TABLE 1. List of age significant biostratigraphic events in Oxfordian to Albian formations of Thakkhola. Events are plotted stratigraphically in Figure 3.

<table>
<thead>
<tr>
<th>BIOSTRATIGRAPHIC EVENT</th>
<th>AGE</th>
<th>REFERENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 A Parawedekindia sp.</td>
<td>Early Oxfordian</td>
<td>Bordet et al. (1971)</td>
</tr>
<tr>
<td>2 A Perisphinctes (Subdiscosphinctes) sp.</td>
<td>Middle Oxfordian</td>
<td>Gradstein et al. (1992)</td>
</tr>
<tr>
<td>3 A Astrapoceras sp.</td>
<td>Middle Kimmeridian</td>
<td>Bordet et al. (1971)</td>
</tr>
<tr>
<td>4 A Karolicaeus-Aulacosphinctoides assemblage</td>
<td>Early Tithonian</td>
<td>Gradstein et al. (1992)</td>
</tr>
<tr>
<td>5 A Virgatospinctes-Lemencia assemblage</td>
<td>Middle Tithonian</td>
<td>Gradstein et al. (1992)</td>
</tr>
<tr>
<td>6 BF Epistomina uberti</td>
<td>Upper Tithonian</td>
<td>Nagy et al. (in press)</td>
</tr>
<tr>
<td>7 A Blanfordiceras-Haplophylloceras assemblage</td>
<td>Upper Tithonian</td>
<td>Gradstein et al. (1992)</td>
</tr>
<tr>
<td>8 D Kalyptea wisemaniae etc.</td>
<td>Early Berriasian</td>
<td>Gibling et al. (1994)</td>
</tr>
<tr>
<td>9 D Egmonrodinium rorynum</td>
<td>Berriasian</td>
<td>Gibling et al. (1994)</td>
</tr>
<tr>
<td>10 BF Cribrostomoides canui</td>
<td>Middle Valanginian</td>
<td>Nagy et al. (in press)</td>
</tr>
<tr>
<td>11 BF Trochammina ficta</td>
<td>Valanginian</td>
<td>Nagy et al. (in press)</td>
</tr>
<tr>
<td>12 A Deshayesites cf. pygmaeus</td>
<td>Early Early Aptian</td>
<td>Gibling et al. (1994)</td>
</tr>
<tr>
<td>13 A Deshayesites sp., Tropaeum hillsi</td>
<td>Middle Early Aptian</td>
<td>Gibling et al. (1994)</td>
</tr>
<tr>
<td>14 A Dufrenoyia mackesoni, D. sp. juv.</td>
<td>Late Early Aptian</td>
<td>Gibling et al. (1994)</td>
</tr>
<tr>
<td>16 PF Ticinella primula assemblage</td>
<td>Late Albian</td>
<td>Premoli Silva et al. (1992)</td>
</tr>
<tr>
<td>17 PF Planomalina butzori assemblage</td>
<td>Latest Albian</td>
<td>Gradstein et al. (1992)</td>
</tr>
</tbody>
</table>

Numbers refer to position of event in diagram. A = ammonite, D = dinocyst, BF = benthic foraminifera, PF = planktonic foraminifera.
Lower Nupra Formation: The Nupra Formation is a succession of rather homogeneous dark to black marine shales. Its thickness is difficult to assess owing to tectonic deformation, but a reasonable estimate is a minimum of 250 m. The Nupra Formation rests disconformably on oolitic sandy limestones from the Bagung Formation with an intervening hiatus spanning the Callovian, and at least part of the lower Oxfordian. It is convenient to divide the Nupra Formation into a lower and upper part.

The lower part of the Nupra Formation contains relatively rich middle Oxfordian ammonite assemblages. Rare ammonites indicate that lower Oxfordian strata might be present at the base of the formation, and that Kimmeridgian occurs at higher levels. This stratigraphical interpretation is confirmed by the composition of the benthic foraminiferal assemblages.

The lower Nupra Formation has been sampled for foraminifera in the J02 section, located approximately 3 km north of Jomosom, on the western side of the Kali Gandaki valley (Fig. 1). The sampled interval is 86 m thick (Fig. 4). Its lower part is tectonically little disturbed, while its upper portion shows strong tectonic deformation.

Upper Nupra Formation: In the upper Nupra Formation, each of the three substages of the Tithonian is represented as shown by the ammonite occurrences. The samples analysed for foraminifera from these strata were collected in the JKI section located on the northern bank of Kag Khola north of Jahrkot and from the MUI section, situated ca. 1 km southwest of Muktinath.

The Nupra shales are overlain by a succession of deltaic sandstones, siltstones and shales which make up the Chukh Formation. Dinocyst evidence suggests that the lower part of the Chukh Formation is of early Berriasian age. This formation was not sampled for foraminifera.

Tangbe Formation: The Tangbe Formation consists of a series of interbedded sandstones, siltstones and shales (up to 500 m thick); it has been interpreted as a shallow shelf to deltaic environment. The lower half of the formation was sampled for foraminifera in the CHH1 section, exposed on the eastern side of Kali Gandaki, south of Chhukgaon. The presence of Valanginian and probably Hauterivian strata in this part of the formation is indicated by benthic foraminifera. In the upper part of the Tangbe, early Aptian and late Albian ages are given by ammonites and planktonic foraminifera, respectively.

METHODS
The Mesozoic shales of Thakkhola are strongly consolidated by diagenetic processes. The foraminiferal samples were processed following the kerosene method, in a version modified by Nagy et al., (in press) for the disintegration of highly indurated...
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sediments. Important steps of the procedure are: 1) Boiling of the sample in sodium hydroxide. 2) Addition of a basic cleanser containing a soft abrasive to the sample in the sieve. 3) Washing through the sieve by means of a brush, with very small amounts of water at the beginning. 4) Repetition of the procedure after drying the sample, if required.

The >63µm fraction was used for the foraminiferal analysis. At least 300 identifiable specimens were picked from each sample, except for eight relatively poor samples from which only 157 to 263 specimens were picked. The number of species is given (where possible) for a sample size of 300 identifiable specimens. The Fisher α-index, used for regional comparisons of species diversity is described by Murray (1991). Open nomenclature sp. (or spp.), without number designates forms with poorly defined morphology. Numbered sp. designates morphologically well-defined forms, which could not be more closely identified at the species level.

Description of morphogroups
The idea behind combining foraminiferal taxa into morphotypes based upon their overall morphology rests on the assumption that there is a relationship between "form and function" of the agglutinated foraminiferal test. The approach adapted here follows that of Nagy (1992), used for analysis of Toarcian and Bajocian faunas of the North Sea Basin. Though differing in details, this approach is based upon the same principles as morphogroup analyses of Severin (1983), Jones & Charnock (1985), Bernard (1986), and Koutsoukos et al. (1990).

Modern agglutinated foraminifera partition their environment vertically into a number of separate niches based upon feeding strategy. The relative importance of a given niche changes depending upon environmental factors such as water depth, oxygenation, environmental stability, presence or absence of currents and, in particular, the availability of food.

For the purpose of interpreting the paleoenvironments of the Thakkhola succession, the foraminiferal species data from the four studied sections have been combined into seven morphogroups. The morphogroup classification of agglutinated foraminifera adapted here as well as the inferred microhabitats are discussed below and summarised in Fig. 5. The morphogroup affiliation of the species is indicated in Fig. 6, while taxa characterising the various morphogroups are illustrated on Plates 1-3.

<table>
<thead>
<tr>
<th>MORPHOGROUP</th>
<th>TEST SHAPE</th>
<th>POSITION WITHIN SEDIMENT</th>
<th>FEEDING STRATEGY</th>
<th>MAIN GENERA</th>
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<tr>
<td>1-a</td>
<td>TABULAR</td>
<td>ERECT EPIFAUNAL SEMI-INFANAL</td>
<td>SUSPENSION FEEDER DETRITIVORE</td>
<td>Rhizammina Silicotuba Jaculella Hyperamminoides</td>
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<td>2-a</td>
<td>GLOBULAR</td>
<td>SURFICIAL SEMI-INFANAL</td>
<td>DEPOSIT FEEDER</td>
<td>Thuramminoides Placentammina Thurammina Recurvoides Repmanina Thalmannammina</td>
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<td>2-b</td>
<td>PLANOCNVEX</td>
<td>SURFICIAL SEMI-INFANAL</td>
<td>HERBIVORE DETRITIVORE</td>
<td>Trochammina Arenobulimina Recurvoides</td>
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<tr>
<td>3-a</td>
<td>ROUNDED planispiral</td>
<td>INFAUNAL TO SURFICIAL</td>
<td>DETRITIVORE</td>
<td>Cribrostomoides Haplophragmoides Recurvoides</td>
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<td>3-b</td>
<td>ELONGATE subcyldrical tapered (mixed growth)</td>
<td>INFAUNAL</td>
<td>DETRITIVORE</td>
<td>Scherchorella Bulbobaculites Spiroplectammina Textulariopsis Parvigenerina Vermeulinoides</td>
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<tr>
<td>4-a</td>
<td>FLATTENED planispiral trochospiral</td>
<td>EPIFAUNAL</td>
<td>HERBIVORE ACTIVE DEPOSIT FEEDER</td>
<td>Ammodiscus Glomospirella Trochammina Trochamminella</td>
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<td>4-b</td>
<td>FLATTENED irregular</td>
<td>EPIFAUNAL</td>
<td>PASSIVE DEPOSIT FEEDER</td>
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Figure 5. Foraminiferal morphogroups distinguished in the Thakkhola assemblages, with inferred microhabitats and feeding strategies.
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<tr>
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<td>Verneuillonioides cf. neocomensis</td>
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**ASSEMBLAGE**

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<th>EOMAR</th>
<th>VERNEUIL</th>
<th>SGI</th>
<th>SPIRO</th>
<th>TROCHAM</th>
<th>TROCH, AFF</th>
<th>SCHAM</th>
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<td>4</td>
<td>5</td>
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**Figure 6.** Stratigraphic distribution of foraminiferal taxa in the lower Nupra, upper Nupra, and Tangbe formations, with subdivision into assemblages. For agglutinated species the morphogroup assignments are indicated.
Morphogroup 1-a (Pl. 1, figs. 1-6) comprises all tubular forms, belonging to the genera *Rhizammina*, *Jaculifera*, etc. These forms are interpreted as being erect suspension feeders. An example is the modern species *Saccorhiza ramosa*, which builds a pseudo-podal net in order to feed above the sediment/water interface (Altenbach, 1988). These forms are found mainly in deep-water environments, beyond the shelf break (Jones & Charnock, 1985).

Morphogroup 2-a (Pl. 1, figs. 7-16) consists of globular forms which often live at or just below the sediment surface. Modern representatives of *Saccammina*, for instance, live with the test partially exposed, and the aperture submerged in the sediment (Hedley, 1962; Christiansen, 1971). The modern globular species *Astrammina rara* lives just below the sediment/water interface and extends its pseudopodia up to the sediment surface, where it feeds (DeLaca, 1986).

Morphogroup 2-b (Pl. 1, figs. 16-23) includes slightly elevated, planoconvex to concavoconvex species with rounded periphery, belonging to *Trockammina*, *Arenoturrispirillina* and *Recurvovidae*. For these forms an essentially surficial microhabitat is indicated by their planoconvex shape and downward oriented aperture. These features combined with the rounded periphery indicate a vagrant mode of life, partially immersed in the upper part of the surficial fluvoculent layer (Nagy, 1992).

Rounded planispiral forms such as *Haplophragmoides* and *Cribrostomoides*, and subsymmetrical representatives of *Recurvovidae* belong to Morphogroup 3-a (Pl. 2, figs. 1-4). These are probably shallow infaunal forms moving and feeding just below the surface of the sediment. A modern example is *Cribrostomoides globosus* which was found in the upper 2 cm of the sediment in box cores collected from the Panama Basin (Kaminski et al., 1988).

Subcylindrical or tapered, elongate forms which make up Morphogroup 3-b (Pl. 2, figs. 15-23) tend to live infaunally under normal conditions. A good example is the genus *Reophax*, which has been found burrowing to a sediment depth of 15 cm in the deep Panama Basin (Kaminski et al., 1988). *Karrerulina conversa* has also been observed in an infaunal life position on the Hatteras Abyssal Plain (W. Kuhn, pers. comm. to M.A.K.).

Morphogroup 4-a (Pl. 3, figs. 1-6) comprises flattened and watchglass-shaped forms. These are planispiral or trochospiral, and live on the surface of the sediment, or are epiphytal on algae or sea grass. Living species of *Ammodiscus* from the continental margins of North America, for instance, have been observed in culture to be mobile epifaunal detritivores. They can graze along the surface mud in a petri dish while holding their test erect and can also climb along the sides of the dish. (B.H. Corliss, pers. comm. to M.A.K.). Low spired trochamminids have an active or passive herbivorous feeding habit, and are most common today in high-energy environments of the photic zone. Some *Trockammina* species may, however, also occur in deeper water where they may live attached to erect metazoan or *Rhabdammina* tubes (M.A.K. 1993, personal observations).

Morphogroup 4-b (Pl. 3, figs. 7-12) includes two irregularly coiled species referred to *Tolypammina*. The modern *Tolypammina vagrans* (Brady) is a surficial attached form. Although the Thakkhola species of this genus have a much more compact shape, their morphology suggests that they were also surface dwellers. One side of their test is usually more flattened than the other, implying an epifaunal, essentially sessile mode of life.

**MAJOR FAUNAL TRENDS**

**Foraminiferal stratigraphy**

The foraminifera studied originate from the Oxfordian to Tithonian Nupra Formation of dark shales, and from the Valanginian to Albian Tangbe Formation of interbedded shales, siltstones and sandstones. The assemblages of both formations consist exclusively of agglutinated taxa, or contain in addition a subordinate calcareous component. The stratigraphic distribution of the species is presented in Fig. 6.

The lower Nupra Formation is characterised by the consistent occurrence of *Bulbobaculites pokrookaensis*, *Tolypammina confusa*, *T. undosa*, *Thurammina papillata*, *Parvigenerina mucronata*, *Trockammina omksensia*, *T. kumaensis* and *Cribrostomoides dolininae*. A total of 44 species were recognised in this unit, of which only three belong to the calcareous benthic group. Many of the agglutinated taxa recorded in our samples were first described from boreal deposits of Western Siberia.

The following common genera typify the lower Nupra shales by being restricted to, or occurring mainly in this strata: *Tolypammina*, *Parvigenerina*, *Bulbobaculites*, *Textulariopsis*, *Verneuilinoides*, *Spirolectammina*. The dominant genus both in the lower Nupra and Tangbe formation is *Trockammina*. The foraminiferal succession of the lower Nupra Formation can be subdivided into three assemblages named after the characteristic species (in ascending order): *Eomassonella paraconica*, *Verneuilinoides graciosus* and *Spirolectammina suprajurassica*. The base of each assemblage is defined by the first occurrence of its nominate species.

A major faunal disconformity is observed between assemblages of the lower Nupra Formation and those of the upper Nupra Formation. Only one species, *Haplophragmoides canu* is common to both. The upper Nupra contains an assemblage characterised by *Trockammina annae*. Other characteristic taxa restricted to this subunit include: *Epistomina uhligi*, *Recurvovidae stschekuriensis*, *Trockamminella* sp. 1 and *Verneuilinoides cf. neocomensis*. The subunit contains totally 16 agglutinated and four calcareous benthic species.
The foraminiferal assemblages occurring in the Tangbe Formation are characterised by *Trochammina aff. schaimica* associated with *T. ficta*, *T. aff. mugiensis* and *Recurvoides excellens*. Two species, *Ammobaculites aff. gerkei* and *Scherochorella sp.1* dominant in the upper Nupra Formation continue into this unit. The diversity in the Tangbe Formation is low, with 10 agglutinated and five calcareous benthic species in total, recovered in our samples.
Morphogroup distribution

Two main morphogroups dominate the JO2 section of the lower Nupra Formation: the surficial planococonvex (2-b) and the infaunal elongate (3-b), which represent 35-65% and 30-50%, respectively, of the assemblages (Fig. 7). The other five morphogroups (1-a, 2-a, 3-a, 4-a, and 4-b) remain minor constituents of the assemblages amounting each to about 1% to 10%.

In the two sections JK1 and MU1 of the upper Nupra Formation only four morphogroups are present (Fig. 7): the surficial planococonvex (2-b), the shallow infaunal rounded (3-a), the deeper infaunal elongate (3-b) and the epifaunal flattened (4-a). In the JK1 section the elongate morphogroup remains consistently dominant (representing between 60-75% of all morphogroups), while the planococonvex and the flattened morphogroups each form about 10 to 25% of the assemblages and the rounded morphogroup makes up only a negligible proportion. By contrast, in the MU1 section the planococonvex morphogroup is dominant (composing 60% of the assemblage) with the elongate morphogroup representing about 30%, the rounded morphogroup about 8% and the flattened morphogroup only about 2%. The plot of epifaunal to infaunal components (Fig. 10) illustrates the main difference between the two sections.

The Tangbe Formation contains the same four morphogroups (2-b, 3-a, 3-b and 4-a) found in the upper Nupra Formation but their distribution pattern in the two units is different (Fig. 7). In the Tangbe Formation the abundances vary considerably, and there are significant changes in morphogroup dominance throughout the section as the epifaunal planococonvex (2-b) and flattened (4-a) morphogroups, and the infaunal elongate (3-b) morphogroup alternatively dominate at various levels.

PALEOECOLOGICAL SIGNIFICANCE OF MORPHOGROUPS

Lower Nupra Formation - paleoecology

The foraminiferal assemblages of the lower Nupra Formation consist almost exclusively of agglutinated taxa. Calcareous species are observed in 8 of 20 samples, and their frequency does not exceed 0.6% (Fig. 8). By this feature the assemblages differ from normal marine Jurassic shelf faunas which consist predominantly of calcareous taxa (mainly Lagenina). Development of faunas consisting entirely or dominantly of agglutinated forms is attributed to brackish environments or to stagnant conditions by Lefaldli & Nagy (1980) and Nagy et al. (1988; 1990) in the Jurassic of the North Sea and Svalbard.

Ammonites and belemnites are observed throughout the lower Nupra Formation; rather sporadically in the lower 20 m, but commonly at higher levels. The presence of this fossil group suggests normal marine salinity conditions at least in the deeper parts of the water column. The comparatively high diversity displayed by the foraminiferal assemblages (number of species varying from 16 to 25, main 21.7) also rules out brackish conditions (Fig. 9).

The lower Nupra shales are extremely fine-grained, and contain no sandy or silty beds, suggesting deposition in a deep, low-energy setting. In spite of this, the organic content of the shales is dominated by terrestrial plant debris indicating that the depositional area was located near to an extensive land mass, eastern Gondwana, with high organic productivity. The total organic carbon content (TOC) of the lower Nupra shales (Fig. 8) varies from 1.5 to 2.3% (main 1.7%). The shales are, however, overmature, and their original TOC content may have been twice as high as that measured (Gradstein et al., 1992).

The increased TOC values, together with the virtually agglutinated nature of the assemblages imply that the depositional area of the lower Nupra experienced dysaerobic bottom conditions with lowered pH. Such conditions would have excluded calcareous assemblages which were presumably less tolerant of dysoxia and low pH than agglutinated faunas.

The degree of dysoxia was, however, moderate as suggested by the relatively high species diversities (Fig. 9). Further evidence for this is provided by observation of bioturbation preserved in concretions, indicating the presence of a burrowing infauna. In the shale itself bioturbation has not been observable, which might be more apparent than real. The homogeneous composition and diageneric compaction of many shales make recognition of bioturbation difficult. The absence of textural lamination in the Nupra shales provides further evidence for the absence of bioturbation.

The high frequency of both the planococonvex (2-b) and the elongate (3-b) morphogroups, together with the presence of five other morphogroups, and the relatively high species diversity indicate intensive exploitation of both the epifaunal and infaunal niches. It is of interest to note, that the infaunal component (morphogroups 3-a and 3-b) makes up 30 to 50% of the assemblages (Figs. 7, 10). This component suggests that the redox boundary was situated below the sediment-water interface, which is in accordance with the presence of bioturbation in concretions and probably also in the shales.

The deep water morphogroups (tubular erect, 1-a; globular, 2-a) occurring in low amounts in the lower Nupra, suggest a deeper shelf depositional facies in accordance with the extremely fine-grained lithology. From the bathymetrically shallower upper Nupra and Tangbe formations these morphogroups are absent. In the lower Nupra, typical deep-water taxa such as Pseudoreophax sp. or Trochammina quinqueloba and morphotypes typical of deep-sea dysaerobic sediments such as Glomospira and Ammodiscus ("Biofacies B" of Kuhnt & Kaminski, 1989) are rare or not observed.
When the ratio of epifaunal to infaunal morphogroups is plotted (Fig. 10) some fluctuations become apparent which may be related to cyclic changes in productivity. In the depositional environment of the lower Nupra, where persistent influx of organic matter was apparently an important factor, the infaunal morphogroups would probably decrease during periods of enhanced productivity which should correspond also to increasingly dysaerobic conditions. Seen as a whole, the environment must have remained relatively stable and favourable during the deposition of the lower Nupra Formation (from the lower or middle Oxfordian to the Kimmeridgian) to allow rich and diverse agglutinated assemblages to flourish. This is further supported by the small size of the foraminiferal tests suggesting early reproduction in favourable conditions.

The dominant genus in the lower Nupra Formation is the epifaunal *Trochammina*, which is also abundant in the overlying more marginal marine deposits of the upper Nupra and Tangbe formations (Fig. 9). This wide distribution reflects the opportunistic nature of *Trochammina*, a feature clearly apparent from the modern occurrence of the genus spanning a range from intertidal through estuarine, and shelf to deep oceanic environments (Scott et al., 1983; Murray, 1991).

**Upper Nupra Formation - paleoecology**

In the JKI section the upper Nupra Formation reveals a generally coarsening upwards lithology from its lower 10 m of somewhat silty shales, through thin sandstone beds to the massive delta front and delta plain sandstones of the overlying...
Jurassic - Cretaceous foraminiferal morphogroups, paleoenvironments, and new taxa from Nepal

<table>
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<tr>
<th>FORMATION</th>
<th>SECTION</th>
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<th>DOMINANT GENERA</th>
<th>DEPOSITIONAL CONDITIONS</th>
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<td></td>
<td>152</td>
<td></td>
<td>Spiroplectammina</td>
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Chukh Formation (Fig. 4). It is natural to assume that this coarsening upwards development reflects deltaic influence during deposition of the upper Nupra Formation.

The shales of the upper Nupra Formation contain mainly agglutinated taxa with a small calcareous component (of Lagenina and Robertinina) attaining in average 3%. The number of species varies from 7 to 13 (mean 11.3), and is considerably less than in the lower part of the formation (Fig. 9). It seems highly probable that this diversity reduction is a response to brackish conditions developed periodically during the early progradation phase of the Chukh deltaic system. Although a small degree of stagnation can not be excluded as the TOC content of the shales is around 1.2%. Bioturbation has not been observed in the shales, but its common occurrence in the concretions indicates the presence of a metazoan infauna.

The dominant species of the upper Nupra is Ammobaculites aff. gerkei composing up to 60% of the fauna. Ammobaculites is a common constituent of low diversity assemblages of modern marginal marine, brackish environments (Buzas, 1974; Haman, 1983). Other species abundant in the upper Nupra include Trochammina annae, Scherochorella sp.1 and Trochamminella sp.1 (Fig. 6). The common occurrence of Trochammina is consistent with brackish conditions, as is probably the case with Scherochorella and Trochaminella, which are closely related to Reophax and Trochammina, respectively.

There is a decrease in diversity from the lower to the upper Nupra shales both at the specific and generic level (Figs. 6, 9). Several of the genera common in the lower part of the formation are absent from the upper part (i.e., Thurammina, Tolypammina, Parvigerina, Bulbobaculites), while others occur only sporadically (Textulariopsis, Verneulinoides, Spiroplectammina). This distribution pattern implies that the mentioned genera were not, or only poorly adapted to brackish, marginal marine conditions. The upper Nupra Formation also

Figure 9. Number of foraminiferal species and distribution of dominant genera characterising the lower Nupra, upper Nupra, and Tangbe formations. The depositional conditions are outlined on the basis of lithological and faunal features.
displays lower TOC values and more bioturbation (observed in concretions) compared to the lower part of the formation, indicating more oxygenated conditions.

The prodeltaic upper Nupra shale represents a transitional facies between the deeper shelf lower Nupra shale and the delta plain Chukh Formation. The prodelta environment would have been subjected to higher energy and increased fluctuations in salinity, temperature, oxygenation, etc. Such fluctuations are suggested by the intermittent occurrences of ammonites and belemnites around the top of the upper Nupra shale. It is reasonable to assume that the cephalopod horizons reflect periods with normal marine salinity conditions in the prodelta area. A closer assessment of the environment requires, however, bed by bed sedimentary and paleontological analyses.

The main differences in foraminiferal distribution between the lower and upper Nupra Formation are illustrated by the diversity curves (Fig. 9) and the ratio of epifaunal to infaunal morphogroups (Fig. 10). In the upper Nupra (JK1 section), the diversity decreased considerably, fewer morphogroups are present, and there is a very strong dominance by the infaunal elongate morphogroup (3-b).

The elongate morphogroup (3-b) is dominant in the lowermost sample of the Tangbe Formation (CHH1/143) where it consists of Ammobaculites, common in some modern estuaries. The overlying samples are dominated by the planconvex (2-b) and the flattened (4-a) morphogroups. Both consist almost exclusively of Trochammina, a genus occurring in a wide variety of modern environments including brackish marginal marine waters and marches. The most abundant species of the Tangbe Formation include: Ammobaculites aff. gerkei, Trochammina aff. schaimica, T. ficta and T. aff. mugiensis.

The Tangbe Formation (section CHH1) represents a shallow, delta influenced environment experiencing frequent changes in salinity, oxygenation, temperature, organic input, energy, etc. Few species are tolerant of such extreme conditions, except for
opportunistic forms which are able to exploit resources at the limit of their range. The alternation in morphogroup dominance (Fig. 7) reflects changing depositional environments (prodelta, lagoon, estuary, etc.) normally associated with deltas where foraminifera exploit very different types of food: infaunal detritus feeders dominate environments rich in particulate matter such as estuaries while epifaunal grazers colonise environments with abundant vegetation in shallow, marginal marine waters. These variations are also reflected in the plot of epifaunal to infaunal morphogroups (Fig. 10).

**Paleoproductivity**
The number of foraminifera per gram of sample (FN) attains very high values in the lower Nupra Shales. It varies from 232 to 1794 with a mean of 828. In the JO2 section there are three pulses with increased FN, with maxima of 1794, 1586 and 1613, respectively (Fig. 8). The lithology is uniform, so there is reason to believe that the FN reflects ecological conditions rather than changing influx of clastic sediments.

The FN in the upper Nupra Formation shows low to intermediate values. In the JK1 section the FN of the lowermost analysed sample is 747, and from there decreases upwards to 13 near the top of the upper Nupra (Fig. 8). This decreasing trend is associated with a generally upward coarsening lithology connected to the progradation of the Chukh delta. In the Tangbe Formation the FN varies from 63 to 563 with a mean of 251.

The initial increase of FN in the JO2 section (early-middle Oxfordian) can be correlated with a steep third-order sea level rise and a shoreward shift in the coastal onlap curve of Haq et al. (1988). This implies that foraminiferal populations on the Nepalese margin in the early-middle Oxfordian may have been responding to the world-wide eustatic influences. The triple sawtooth aspect of the FN curve invite comparisons with the three early-middle Oxfordian third-order coastal onlap cycles (3.2; 4.1; 4.2) of Haq et al. (1988).

The reasons for fluctuating foraminiferal numbers are complex. There is no doubt that FN can be correlated with the flux of marine organic matter to the sea floor (Herguera & Berger, 1991), and is a proxy for marine productivity. However, this effect is too small to account for the magnitude of FN fluctuations observed in our data. The TOC contents of the Nupra Shales do not fluctuate greatly (even taking diagenesis into account), and the paleoproductivity equations of Herguera and Berger are probably better suited to fully oxic environments.

A more plausible explanation for the cyclical variations in FN can be found by comparing the benthic ecology of some modern seasonally anoxic basins. With decreasing levels of bottom water oxygen, metazoan activity (as well as the amount of bioturbation) successively decreases. At the onset of anoxic conditions at a monitored station in the Adriatic Sea, infaunal metazoans first exhume themselves and then perished. Some species of benthic foraminifera, however, can tolerate severely dysaerobic and even fully anoxic conditions. In a recent experiment, Bernhard (1993) demonstrated that certain low oxygen-tolerant species can survive month-long periods of total anoxia.

Extremely high FN has been observed in partially laminated surficial sediments from a 550 m deep station in the Santa Barbara Basin off southern California (Bernhard & Reimers, 1991), an area strongly affected by coastal upwelling and seasonally dysaerobic bottom water. The numbers of living foraminifera at this station (>1100/cm³) are one to two orders of magnitude higher than values found in well-oxygenated, open marine environments, and compare well with the high values found in the lower Nupra Shales.

In the absence of grazing pressure by metazoan predators, benthic foraminiferal populations can increase dramatically. In the case of the lower Nupra Shales, the initial increase in FN at the base of the JO2 section probably reflects the prolonged submergence of this area of the Nepalese margin into an oxygen minimum zone. Abrupt declines in FN may have been caused by the tentative return of metazoan predators during lowstands, when the most severely dysaerobic environments moved to a more distal location farther offshore.

As mentioned previously, the FN of the upper Nupra Formation (JK1 section) shows an upward decrease. We cannot exclude that this reflects a decrease in productivity. It seems more probable, however, that this feature is the product of dilution of foraminiferal tests by upward increasing sedimentation rates; an interpretation supported by the coarsening upward nature of the sediments.

**PERSISTENCE OF THE MORPHOGROUP DISTRIBUTION**

**Analogy with modern distribution trends**
The morphogroup distribution pattern of the Thakkholo succession is summarised in Fig. 11 by showing mean and maximum values within the various biostratigraphic units. This pattern is compared with modern distribution trends of morphological categories derived from the literature; mainly from Scott et al. (1983), Jones & Charnock (1985) and a review published by Murray (1991).

The tubular erect (1-a) and globular (2-a) morphogroups are restricted to the lower Nupra Formation where they occur with maximum frequencies of 5.4% and 11.1%, respectively. In modern oceans, these surficial forms are significant in upper bathyal and deeper environments, being abundant in middle bathyal to abyssal waters. These distribution trends are in accordance with an inferred deeper shelf environment of the lower Nupra shale.

The surficial planoconvex morphogroup (2-b) consists mainly of trochantinids, and is dominant through the lower Nupra Formation, but occurs with
strongly varying quantities in the upper Nupra and Tangbe units as well. In modern environments this group is most common in shelf and marginal marine waters. The infaunal elongate morphogroup (3-b) is strongly dominant in the prodeltaic upper Nupra Formation with *Ammobaculites*, but is also richly represented in the deeper shelf lower Nupra Formation mainly with *Verneuilinoides* and *Bulbobaculites*. In modern faunas, elongate forms are particularly abundant in inner shelf to upper bathyal areas, but are also significant in lagoonal and marsh environments. The surficial flattened spiral morphogroup (4-a), consisting mostly of *Trochammina*, is strongly dominant in the prodelta to delta top deposits of the Tangbe Formation. Significant quantities of this group are present in the upper Nupra Formation, while in the lower Nupra it is rather rare. In modern faunas, flattened planispiral forms are most abundant in marginal marine environments, particularly in marshes, lagoons, and estuaries. The flattened irregular morphogroup (4-b, composed of *Tolypaminina*) occurs in small amounts in the lower Nupra. In modern seas, this group is significant at upper bathyal and greater depths.

Analogy with Cretaceous assemblages of Portugal

Wightman's (1990) study of estuarine and marsh foraminifera from the Lower Cretaceous of the Lusitanian Basin of West Portugal shows that dominance is very high in marginal marine environments, and that the distribution of epifaunal and infaunal morphogroups is related to food resources as these two groups have very different feeding strategies. Monospecific infaunal *Ammobaculites* assemblages are interpreted as opportunistic colonists in estuarine environments where particulate food was abundant. High dominance of *Ammobaculites* and low species diversity in the upper Nupra Formation reveal analogy with these assemblages. *Trochammina* dominated assemblages of Portugal were typical of marsh environments with large amounts of vegetation.

Analogy with Jurassic North Sea assemblages

Foraminiferal distribution data from three formations deposited under varying degrees of deltaic influence in the Jurassic North Sea Basin are included in this study for comparative purposes. The analyzed samples are located as follows. 1) Drake Formation: 32 samples from well 33/9-3 (Statfjord Field), through interval 2609.7 m to 2620.1 m, upper Toarcian. 2) Rannoch Formation: 15 samples from well 34/10-1 (Gullfaks Field), through interval 1937.3 m to 1946.8 m, lower Bajocian. 3) Yons Nab Beds (Cloughton Formation): 14 samples from a coastal outcrop at Yons Nab, Yorkshire, middle Bajocian. Details about the facies-related distribution of Jurassic North Sea morphogroups are
Jurassic - Cretaceous foraminiferal morphogroups, paleoenvironments, and new taxa from Nepal


Comparisons of morphogroup characteristics of the Thakkhola and North Sea assemblages are presented graphically in Fig. 12, and summarised in Fig. 13. The infaunal component in this illustration includes the rounded planispiral (3-a) and elongate (3-b) morphogroups. The other five morphogroups are referred to as a single epifaunal component.

Based on sedimentological and faunal evidence the Drake Formation is interpreted to have been deposited under distal prodelta conditions. The foraminiferal faunas of the formation consist almost exclusively of agglutinated taxa and show intermediate diversities with a mean value of 2.7. The TOC content of the sediments is significant (with a mean of 1.6%); suggesting that the reason for development of agglutinated assemblages was probably somewhat dysaerobic bottom conditions eventually associated with lowered pH.

The morphogroup distribution of the lower Nupra Formation reveals important affinities with the Drake Formation in being dominated by the planocoynv epifaunal morphogroup (2-b) followed by the elongate infaunal morphogroup (3-b). In both formations the epifaunal component is chiefly Trochammina. The main differences between the two units are the higher species diversity and lower infaunal content of the lower Nupra Formation (Fig. 12). Furthermore, the infaunal component of the lower Nupra is dominated by Bulbobaculites, Textulariopsis and Verneuilinoides occurring roughly in equal amounts. The infaunal component of the Drake is dominated by Verneuilinoides followed by Reophax and Ammobaculites.

<table>
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<tr>
<th>Table 2. Main paleoecological features inferred for foraminiferal assemblages of Oxfordian to Albian formations of Thakkhola.</th>
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<td>Shallow-water taxa</td>
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<td>Microhabitat</td>
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Figure 12. Infaunal frequency (morphogroups 3-a, 3-b) against α-diversity index to compare major faunal features of various Jurassic and Cretaceous formations and facies of Thakkhola and the North Sea Basin. (D: dominant morphogroup).

Figure 13. Average values of infaunal frequency (morphogroup 3-a, 3-b) and α-diversity characterising three groups of facies in the Jurassic and Cretaceous of Thakkhola and the North Sea Basin. (D: dominant morphogroup).
The most obvious feature of the marine shelf to deltaic Tangbe Formation is its high content of epifauna and low species diversity. The epifaunal component consists predominantly of flattened spiral forms belonging to morphogroup 4-a. These features are typical also of the Rannoch Formation and Yons Nab Beds ascribed to delta front and interdistributary bay, respectively. It is of interest to note that the later two lithological units are dominated by *Ammodiscus*, while the most common genus of the Tangbe Formation is *Trochammina*.

**CONCLUSIONS**

The Oxfordian to Albian succession of Thakkhola (Nepal) is more than 1100 m thick, and consists of shales, siltstones and sandstones deposited in marine shelf and deltaic environments. The foraminiferal assemblages found in these strata are composed almost entirely of agglutinated species. A total of 59 species are identified, of which only 4 belong to the calcareous benthic group. The faunal diversity in the individual samples is usually intermediate to high throughout the studied succession.

The agglutinated species are arranged in seven morphogroups according to test shape, inferred life position and microhabitat preferences. The distribution of the various morphogroups fluctuates considerably in the formations studied, and the changes in distribution pattern reflect important environmental differences. The main characteristics of the assemblages are summarised in Table 2 and Fig. 14.

The lower Nupra Formation (Oxfordian to probably Kimmeridgian) consists of dark shales, moderately rich in organic matter. The foraminiferal assemblages occurring in these strata are virtually entirely agglutinated, and show intermediate to high species diversities. The assemblages are dominated by the surficial planoconvex morphogroup (2-b) and the infaunal elongate morphogroup (3-b), but the other five morphogroups are also present, in smaller quantities. The nature of the assemblages points to a deeper shelf environment with dysaerobic conditions in agreement with the geochemical, sedimentary and macrofossil based depositional interpretation.

The upper Nupra Formation, mainly of dark silty and sandy shales, forms part of a coarsening upward sequence deposited in a prodelta environment. The foraminiferal assemblages typical for these strata show low diversity and high dominance, and consist generally of agglutinating taxa with a small calcareous component. The salient feature of these assemblages (JK1 section) is the high dominance of the elongate infaunal morphogroup (2-b) composed chiefly of *Ammobaculites* followed by *Scherochorella*. It is inferred that the dominantly infaunal nature of the assemblages represents an adaptation to exploit the food resources in areas with high sedimentation rates.

The analysed interval of the Tangbe Formation consists of alternating shale and sandstone packages deposited under changing environmental conditions including shallow prodelta shelf, lagoon, estuary and delta plane. In these deposits the foraminifera are mainly agglutinated. The most common morphological unit is the flattened epifaunal group (4-a).

![Figure 14. Model summarising the relationships between morphogroup distribution and depositional environments in the Thakkhola succession.](image)
But in addition, the planoconvex epifaunal morphgroup (2-b) and, more locally, the infaunal elongate morphgroup (3-b) are also abundant. The low diversity, high dominance and variable morphgroups are in accordance with the stressed, marginal nature of the environments.

The morphgroup distribution pattern of the Thakkhola succession reveals significant analogies with morphgroup characteristics of modern shelf to marginal marine environments. A comparison of the Thakkhola formations with Toarcian to Bajoian deposits of the northern North Sea with regard to morphgroup distribution shows marked similarities.

**SYSTEMATIC DESCRIPTIONS**

Order FORAMINIFERIDA Eichwald, 1830
Suborder TEXTULARIINA Delage & Herouard, 1896
Superfamily AMMODISCACEA Reuss, 1862
Family AMMODISCIIDAE Reuss, 1862
Subfamily TOLYPAMMININAE Cushman, 1928
Genus *Tolypammina* Rhumbler, 1895

*Tolypammina undosa* sp. nov.  
(Pl. 3, Figs. 12-21)

**Diagnosis.** A very small species of *Tolypammina* with irregularly winding second chamber that is densely curved and forms a flattened but compact test with a strongly variable outline.

**Derivation of name.** Latin, *undus* = wave-like, with reference to the densely curved second chamber of the species.

**Holotype.** Pl. 3, fig. 18, to be deposited in the British Museum (Natural History), London.

**Description.** Test small, consisting of proloculus followed by an elongate tubular undivided second chamber; tubular chamber irregularly coiled and densely oscillating; coils are in contact with each other, forming a compact and slightly flattened test with a usually somewhat elongate but strongly varying peripheral outline; test surface is irregular, but one of the sides is more convex than the other, forming a compact and slightly flattened test surface. Attached tests have not been observed in the lower Nupra Formation containing this species. It is important to note here, that the lower Nupra shales are extremely fine-grained and contain very little silt and virtually no sand-size particles. Consequently, the substrate did not provide any firm surface for attachment of foraminifera. The tests are commonly compressed by diagenesis.

*Tolypammina undosa* is similar to the Oxfordian *T. confusa* Dain, 1966 in general shape, but differs by its densely winding second chamber, finely undulating test surface and much smaller size. In the lower Nupra Formation the length of *T. confusa* is 0.30-0.44 mm while its breadth is 0.26 to 0.36 mm, Thus, it is usually almost twice as large as *T. undosa*.

Superfamily HAPLOPHRAGMIACEA Eimer & Fickert, 1899
Family AMMOSPHAEROIDINIDAE Cushman, 1927
Subfamily RECURVOIDINAE Alekseychik-Mitkevich, 1973
Genus *Thalmannammina* Pokorny, 1951

*Thalmannammina glomata* sp. nov.  
(Pl. 4, Figs. 1-8)

**Diagnosis.** A small species of *Thalmannammina* consisting of relatively few subglobular chambers separated by depressed sutures, and with plane of coiling showing abrupt changes of 90° in later whorls.

**Derivation of name.** Latin, *glomus* = ball; with reference to the subspherical test and rounded chambers of the species.

**Holotype.** Plate 4, fig. 6, to be deposited in the British Museum (Natural History), London.

**Description.** Test small, involute, subspherical in shape, streptospirally enrolled with 5-6 chambers per whorl; later whorls show sharp change in plane of coiling of 90° from previous whorls; chamber subglobular, separated by strongly depressed sutures; wall thin, smooth, translucent, brownish in color, agglutinated by very fine quartz grains; aperture an oval slit at the base of the apertural face.

**Dimensions.** Measurements of 14 specimens show: diameter 0.11-0.22 mm, mean 0.14 mm

**Remarks.** By its small size and general appearance, this species is comparable to *Recrvooides paucus* Dubrovskaya, 1962, ranging in age from Volgian to Ryazanian. The later species has, however, a less globular test outline, almost flush sutures, and more numerous chambers which are subtrapezoidal in lateral aspect. Tests of *T. glomata* are with few exceptions diagenetically compressed.

Superfamily SPIROPLECTAMMINACEA Cushman, 1927
Family PSEUDOBOLIVINIDAE Wiesner, 1931
Genus *Parvigenerina* Vella, 1957

*Parvigenerina mucronata* sp. nov.  
(Pl. 4, Figs. 9-17)

**Diagnosis.** A species of *Parvigenerina* characterized by slightly twisted and rapidly expanding biserial test with a tendency to uniserial growth in the final
5 chambers; chambers flattened but with slightly peripheral outline and strongly expanded final one. Diagnostically, the test is somewhat convex-concave, exposing only the final whorl of chambers, umbilical side approximately of three whorls; spiral side somewhat convex, showing all chambers, umbilical side.

Derivation of name. From the occurrence of this species in the Nupra Formation of the Thakkhola region, Nepal.

Holotype. Plate 4, figs. 24-25, to be deposited in the British Museum (Natural History), London.

Description. Test low-spired trochoid, consists approximately of three whorls; spiral side somewhat convex, showing all chambers, umbilical side slightly concave, exposing only the final whorl of 4-5 chambers; chambers flattened but with slightly convex surface both on the spiral and umbilical sides; size of chambers increases rapidly, and the final one is strongly expanded giving the test a subovate peripheral outline; sutures depressed, inclined backward on the spiral side and straightly radiating on the umbilical side; peripheral margin of the outer three chambers strongly lobate; wall medium to finely arenaceous with granular surface; aperture obscure, thought to be an umbilical extrumbilical slit at base of final chamber.

Dimensions. Measurements of 12 specimens show: diameter 0.14-0.28 mm, mean 0.22 mm; breadth 0.09-0.14 mm, mean 0.11 mm.

Remarks. The twisted biserial chamber arrangement of Parvigenerina mucronata reveals that this species is close to Pseudobolithina, e.g. the modern form P. antarctica Wiesner, 1931. The tendency of P. mucronata to uniserial growth, and particularly its rounded terminal aperture are, however, diagnostic features of Parvigenerina and are the main reasons for its attribution to this genus.

The late Jurassic Pseudobolithina? acutata Komissarenko (in Bulyminova et al., 1990) differs from P. mucronata by its subcylindrical apertural neck with a well-defined base, and less elongate chambers. Flaring variants of the Valanginian Pseudobolivin(?o) jamalica Rylkova, 1986 are comparable to the present species in test outline, but these also have distinctly shorter chambers.

Superfamily TROCHAMMINACEA Schwager, 1877
Family TROCHAMMINIDAE Schwager, 1877
Subfamily TROCHAMMININAE Schwager, 1877
Genus Trochammina Parker & Jones, 1859

_Trochammina nupraensis_ sp. nov. (Pl. 4, Figs. 18-25)

**Diagnosis.** A low-spired species of _Trochammina_ characterised by its convex-concave shape, subovate peripheral outline and strongly expanded final chamber.

**Derivation of name.** From the occurrence of this species in the Nupra Formation of the Thakkhola region, Nepal.

**Holotype.** Plate 4, figs. 24-25, to be deposited in the British Museum (Natural History), London.

**Description.** Test low-spired trochoid, consists approximately of three whorls; spiral side somewhat convex, showing all chambers, umbilical side slightly concave, exposing only the final whorl of 4-5 chambers; chambers flattened but with slightly convex surface both on the spiral and umbilical sides; size of chambers increases rapidly, and the final one is strongly expanded giving the test a subovate peripheral outline; sutures depressed, inclined backward on the spiral side and straightly radiating on the umbilical side; peripheral margin of the outer three chambers strongly lobate; wall medium to finely arenaceous with granular surface; aperture obscure, thought to be an umbilical extrumbilical slit at base of final chamber.

**Dimensions.** Measurements of 14 specimens show: diameter 0.18-0.33 mm, mean 0.24 mm.

**Remarks.** The most diagnostic feature of _T. nupraensis_ is its strongly expanded final chamber. In the richly varied Upper Jurassic trochamminid faunas of Western Siberia, _T. quinquelocularis_ Dain, 1972 is most similar to _T. nupraensis_. Important distinguishing features of the two species are the more ovate and less coarse-grained test of _T. nupraensis_ having a more dominant final chamber.

The Lower Cretaceous species _Trochammina ficta_ Romanova (in Glazunova et al., 1960), also present in the Tangbe Formation, is typified by its strongly expanded last chamber. This species has, however, flush sutures on the spiral side and a smooth periphery. Furthermore, its spiral side is more elevated than that of _T. nupraensis_.

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**REFERENCES**


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Jaculella

SUBORDER TEXTULARIINA

The following list includes the 55 agglutinated and four calcareous species recognised in the study. A few poorly defined taxa designated by un-numbered sp. (or spp.) are not listed. The references are restricted to the original description. The genera are arranged in accordance with the classification proposed by Loeblich & Tappan (1987).

APPENDIX

SUBORDER TEXTULARIINA

Rhizammina sp. 1
Silicotuba sp. 1
Thuramminoides sp. 1
Placentamina sp. 1

Thurammina papilata = Thurammina papillata Brady, 1879, p. 45, pl. 5, figs. 4-8.

Jaculella depressa = Hippocrepina depressa Vasicek, 1947, pl. 1, figs. 1, 2.

Hyperamminoides sp. 1

Ammodiscus tenuissimus = Spirillina tenuissima Gümbel, 1862, p. 214, pl. 4, figs. 12a, b.

Ammodiscus cf. tenuissimus: Spirillina tenuissima Gümbel, 1862, p. 214, pl. 4, figs. 12a, b.

Tolypammina confusa = Tolypammina confusa Dain, 1966, p. 230, pl. 2, figs. 1-4; pl.3, fig. 8.

Tolypammina undosa sp.nov.

Glomospirella semiaffixa = Glomospirella semiaffixa Sharovskaya, 1966, p. 54, pl. 2, figs. 7-9.

Repmanina variabilis = Cornuspira variabilis Kübler & Zwingli1870, p.33, pl. 3, fig. 50.

Scherochorella sp. 1

Cribrostomoides dolininae = Cribrostomoides dolininae Bulynnikova in Dain, 1972, pl. 7, figs. 1, 2.

Cribrostomoides canui = Haplophragmoides canui Cushman, 1930, p. 133, pl. 4, figs. 1a,b.

Haplophragmoides globigerinoides = Trochammina globigerinoides Haeusler, 1882, p. 352, pl. 15, figs. 8, 9.

Haplophragmoides aff. umbonatus: aff. Haplophragmoides umbonatus Romanova in Glazunova et al., 1960, p. 52, pl. 3, figs. 2a-b.

Haplophragmoides sp. 1


Sengör, A.M.C. 1985. The story of Tethys: how many wives did Okeanus have? Episodes, 8, 1-12.


Lsfaldli, (1987). Four new species are described in the systematic chapter.


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Ammobaculites aff. gerki: aff. Ammobaculites gerki Sharovskaya, 1966, p. 65, pl. 7, figs. 1, 2, 4-5, 7, 8.
Ammobaculites tobolskensis = Ammobaculites tobolskensis Levina in Dain, 1972, pl. 15, figs. 3, 7.
Ammosphaeroidina sp.1
Recurvoides disputabilis = Recurvoides disputabilis Dain, 1972, pl. 10, figs. 6, 7; pl. 11, figs. 1-4; pl. 19, fig. 1.
Recurvoides stschekuriensis = Recurvoides stschekuriensis Dain, 1972, p. 58, pl. 13, figs. 5, 6a, b.
Recurvoides sp.1
Thalmannamnina glomata sp.nov.
Bulbobaculites aff. elongatulus: aff. Haplophragmium elongatum Dain, 1972, p. 69, pl. 18, figs. 8-10.
Bulbobaculites pokrovkaensis = Haplophragmium pokrovkaensis Kosyreva in Dain, 1972, p. 68, pl. 18, figs. 1-7.
Sprioplectammina suprajurassica = Spiroplectammina suprajurassica Kosyreva in Dain, 1972, pl. 20, figs. 7-16.
Spiroplectammina cf. suprajurassica: cf. Spiroplectammina suprajurassica Kosyreva in Dain, 1972, pl. 20, figs. 7-16.
Textulariopsis jurassica = Textularia jurassica Gümbel, 1862, p. 228, pl. 4, figs. 17a, b.
Textulariopsis sp.1
Parvigerina mucronata sp.nov.
Trochammina annae = Trochammina annae Levina in Dain, 1972, pl. 26, figs. 1-4; pl. 29, fig. 10.
Trochammina aff. composita: aff. Trochammina composita Bulynnikova, 1987, p. 26, pl. 9, figs. 1, 2.
Trochammina aff. elevata: aff. Trochammina elevata Kosyreva in Dain, 1972, p. 88, pl. 23, figs. 8-11, 13.
Trochammina ficta = Trochammina ficta Romanova in Glazunova et al., 1960, p. 66, pl. 10, figs. 2a, b.
Trochammina cf. ficta: cf. Trochammina ficta Romanova in Glazunova et al., 1960, p. 66, pl. 10, figs. 2a, b.
Trochammina kosyrevae = Trochammina kosyrevae Levina in Dain, 1972, p. 83, pl. 22, figs. 5-9; pl. 24, fig. 4.
Trochammina kumaensis = Trochammina kumaensis Levina in Dain, 1972, p. 91, pl. 25, figs. 4, 5, 7, 8; pl. 29, figs. 5-7.
Trochammina minutissima = Trochammina minutissima Dain, 1972, p. 86, pl. 24, figs. 1-5.
Trochammina aff. mugiensis: aff. Trochammina mugiensis Dain & Bulynnikova in Bulynnikova et al., 1990, p. 95, figs. 1, 2.
Trochammina nupraensis sp.nov.
Trochammina omksensis = Trochammina omksensis Kosyreva in Dain, 1972, p. 84, pl. 23, figs. 1-7; pl. 24, fig. 9.
Trochammina aff. schaimica: aff. Trochammina schaimica Kisseleva in Bulynnikova et al., 1990, p. 101, pl. 94, figs. 9, 10.
Trochammina quinqueloba = Trochammina quinqueloba Geroch, 1959, p. 118, pl. 12, figs. 1a-c, 2a, b, 3a, b.
Trochammina sp.1
Trochamminella sp.1
Eomarssonella paraconica = Eomarssonella paraconica Levina in Dain, 1972, p. 102, pl. 32, figs. 1-11.
Verneuilinoides graciosus = Verneuilinoides graciosus Kosyreva in Dain, 1972, pl. 30, figs. 2-4.
Verneuilinoides cf. neocomensis: cf. Verneuilinoides neocomensis Myatlyuk, 1939, p. 50, pl. 1, fig. 13.
"Dorothia" sp.1
Arenobulimina sp.1

SUBORDER LAGENINA
Lenticulina dofleini = Cristellaria dofleini Kazancev, 1936, p. 18, pl. 2, figs. 35-37.
Astacolus aleskerovae = Cristellaria aleskerovae Romanova in Glazunova et al., 1960, p. 69, pl. 11, figs. 4, 5a, b.

SUBORDER ROBERTININA
Epistomina aff. caracolla: aff. Gyroidina caracolla Roemer, 1841, p. 97, pl. 15, figs. 22a-c.
Epistomina uhligi = Epistomina uhligi Myatlyuk, 1953, p. 219, pl. 2, fig. 2.
PLATE 1.
Species arranged in morphogroups

Figs. 3-4.  *Silicotuba* sp.1: 3, sample JO2/102, x170; 4, sample JO2/106, x170.
Fig. 5.  *Hyperamminoides* sp.1: sample JO2/106, x140.
Fig. 6.  *Jaculella depressa* (Vašiček): sample JO2/111, x170.

Figs. 7-16.  Morphogroup 2-A, (globular).
Fig. 7.  *Thuramminoides* sp.1: sample JO2/109, x120.
Fig. 8.  *Placentammina* sp.1: sample JO2/111, x120.
Figs. 9-10.  *Thurammina papillata* Brady: 9, sample JO2/114, x110; 10, sample JO2/114, SEM, x110.
Fig. 11.  *Repmannina variabilis* (Kübler & Zwingli): sample JO2/104, x160.
Fig. 12.  *Ammosphaeroidina* sp.1: sample JO2/123, x140.
Fig. 13.  *Recurvoides* sp.1: sample JO2/110, SEM, x140.
Figs. 14-16.  *Trochammina quinqueloba* Geroch: 14, umbilical view, sample JO2/2, SEM, x180; 15, spiral view, sample JO2/2, x160.

Figs. 16-23.  Morphogroup 2-B, planoconvex (trochospiral, streptospiral):
Figs. 16-18.  *Trochammina minutissima* Dain: 16, spiral view, sample JO2/104, x170; 17, 18, spiral and umbilical views (respectively) of same specimen, sample JO2/105, SEM, x220.
Figs. 19-20.  *Trochammina kumaensis* Levina: spiral and umbilical views (respectively) of same specimen, sample JO2/126, SEM, x160.
Fig. 21.  *Arenobulimina* sp.1: spiral view, sample JO2/108, x160.
Figs. 22-23.  *Recurvoides disputabilis* Dain: 22, spiral view, sample JO2/111, x160; 23, spiral view, sample JO2/123, x140.
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PLATE 2.
Species arranged in morphogroups

Figs. 1-4. Morphogroup 3-A, rounded (planispiral).
Fig. 1. *Cribrostomoides canui* (Cushman): sample JO2/106, x160.
Fig. 2. *Cribrostomoides dolininae* Bulynnikova: sample JO2/10, x160.
Fig. 3. *Haplophragmoides globigerinoides* Haeusler: sample JO2/10, x160.
Fig. 4. *Recurvoideae* cf. *excellens* Rygina: spiral view, sample CHH1/154, x160.

Figs. 6-14. Morphogroup 3-B, elongate (subcylindrical).
Figs. 5-6. *Scherochorella* sp.1: sample JO2/2, x200.
Figs. 7-9. *Ammobaculites aff. gerkei* Sharovskaya: 7, planispiral stage, sample JKl/192, SEM, x160; 8-9, edge and lateral views of same specimen (respectively), sample JKl/l, x100.
Fig. 12. *Bulbobaculites aff. elongatulus* Dain: sample JO2/114, x160.

Figs. 15-23. Morphogroup 3-B, elongate (tapered).
Fig. 17. *Textulariopsis* sp.1: sample JKl/2, x170.
Fig. 18. *Eomarssonella aff. doneziana* Dain: sample JO2/117, x160.
Fig. 19. *Eomarssonella paraconica* Levina: sample JO2/102, x160.
Fig. 20. *Verneuilinoides* cf. *neocomensis* Myatlyuk: sample JKl/l, x160.
Fig. 23. "*Dorothia*" sp.1: sample JO2/111, x110.
PLATE 3.
Species arranged in morphogroups

Figs. 1-4. Morphogroup 4-A, flattened (trochospiral).
Fig. 1. *Trochammina aff. schaimika* Kisseleva: spiral view, sample CHH1/154, x160.
Fig. 2. *Trochammina aff. mugiensis* Dain & Bulynnikova: spiral view, sample CHH1/143, x140.
Fig. 3. *Trochammina sp.*: spiral view, sample JO2/106, x160.
Fig. 4. *Trochamminella sp.*: spiral view, sample JK1/192, x180.

Figs. 5-6. Morphogroup 4-A, flattened (planispiral).
Fig. 5. *Glomospirella semiaffixa* Sharovskaya: sample JO2/106, x140.
Fig. 6. *Ammodiscus tenuissimus* (Guembel): sample JO2/110, x120.

Figs. 7-21. Morphogroup 4-B, flattened irregular.
Figs. 7-12. *Tolypammina confusa* Dain: 7, sample 119, x140; 8, sample JO2/110, x160; 9, sample 109, x140;
10, sample JO2/123, SEM, x140; 11, sample JO2/102, x140.

Illustration of new species.
Figs. 12-21. *Tolypammina undosa* sp. nov.: 12, sample JO2/111, x180; 13, sample JO2/102, SEM, x180; 14, sample JO2/115, SEM, x180; 15, sample JO2/115, SEM, x180; 16, sample JO2/102, x180; 17, sample JO2/111, x180; 18, holotype, sample JO2/110, x180; 19, sample JO2/110, x130; 19, sample JO2/110, x180; 19, sample JO2/110, x180; 20, sample JO2/104, x180; 21, sample JO2/102, x180.
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Plate 4.
Illustration of new species

Figs. 1-8. *Thalmannammina glomata* sp. nov.: 1, sample JO2/123, x250; 2, sample JO2/123, x250; 3, sample JO2/123, x250; 4, sample JO2/123, x180; 5, sample JO2/108, x180; 6, holotype, sample JO2/123, x250; 7, sample JO2/123, SEM, x360; 8, sample JO2/106, x170.

Figs. 9-17. *Parvigenerina mucronata* sp. nov.: 9, sample JO2/102, x190; 10, holotype, sample JO2/109, x190; 11, sample JO2/126, x190; 12, sample JO2/106, x190; 13, sample JO2/109, x190; 14, sample JO2/106, x190; 15, sample JO2/102, x190; 16, sample JO2/106, SEM, x230; 17, sample JO2/106, x190.

Figs. 18-25. *Trochammina nupraensis* sp. nov.: 18, spiral view, sample JO2/113, x180; 19, spiral view, sample JO2/111, x160; 20-21, spiral and umbilical views (respectively) of same specimen, sample JO2/117, SEM, x120; 22, spiral view, sample JO2/2, x170; 23, spiral view, sample JO2/111, SEM, x200; 24-25, holotype, spiral and umbilical views (respectively) of same specimen, sample JO2/113, SEM, x200.
Jurassic - Cretaceous foraminiferal morphogroups, paleoenvironments, and new taxa from Nepal