

Early Permian glacio-marine thecamoebian assemblages from the northwest Himalayas, India

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ABSTRACT – Diverse assemblages of thecamoebians are reported here from the Early Permian Manjir Formation of the northwest Himalaya in India. These thecamoebian tests were found in palynological preparations and are assigned an Early Permian age based on co-occurrence of age-diagnostic palynomorphs. Several of them show very close morphological affinity with extant thecamoebian genera, such as *Amphitrema*, *Arcella*, *Centropyxis*, *Cyclopyxis*, *Cucurbitella*, *Diffugia* and *Trinema*. This fauna lived in shallow-marine environments during the Early Permian deglacial phase of the widespread Late Carboniferous–Early Permian glaciation of Gondwana. The extant forms used for morphological comparison with the fossil forms were recorded from lakes and ponds in various parts of India. This study supports the current hypothesis of minimal evolution in thecamoebian lineages through geological time, and this group of protists has survived through long geological time and several mass extinction events without any significant morphological change. Stratigraphical and palaeontological evidence indicates that this fauna lived in the shallow-marine environments along the northwestern margin of Indian Gondwana during the deglacial phase of Late Carboniferous–Early Permian glaciation. *J. Micropalaeontol.* 30(1): 75–89, May 2011.

KEYWORDS: Permian, glaciomarine, thecamoebians, Himalayas, India

INTRODUCTION

Thecamoebians characterize a special group of testate protists (agglutinated or autogenous) which belong to the Subphylum Sarcodina (Medioli & Scott, 1988). These are an important component of aquatic and terrestrial ecosystems and also occur in marginally brackish environments (Charman *et al.*, 2000; Patterson & Kumar, 2002). They are characterized by a sac-like cap-like test, with a simple aperture known as a pseudostome through which extrude pseudopods of the amoeba dwelling inside it. They are consumers of bacteria, fungi and different algal groups and are thus important for the energy flow and nutrient cycles in these ecosystems (Medioli & Scott, 1983, 1988; Beyens & Meisterfeld, 2002). Most of the known fossil thecamoebians are agglutinated by calcareous or siliceous grains and/or diatom frustules (Medioli *et al.*, 1990a, b). They are known from lake sediments from the tropics to the Arctic (see references in Patterson & Kumar, 2002; Boudreau *et al.*, 2005), peat bogs (Woodland *et al.*, 1998; Charman *et al.*, 2000) and salt marshes (Charman *et al.*, 2002; Roe *et al.*, 2002; Riveiros *et al.*, 2007). Published thecamoebian studies are mainly from the lakes and bogs in Europe and North America and there are relatively fewer thecamoebian studies from the tropical regions (Hoogenraad & Groot, 1940, 1946; van Oye, 1949; Sudzuki, 1979; Dalby *et al.*, 2000; Roe & Patterson, 2006; Farooqui & Gaur, 2007). Some of the earliest thecamoebian studies from India include brackish-water lakes and ponds of nineteenth-century Mumbai (Carter, 1856, 1864).

PRE-QUATERNARY OCCURRENCES OF THECAMOEBIANS

Distribution of fossil thecamoebian tests ranges from the Neoproterozoic through to the Holocene but their occurrence is patchy with wide gaps in the fossil record. The oldest undisputed record of thecamoebians is described as vase-shape microfossils (VSMs) from the Neoproterozoic rocks of Grand Canyon,

USA by Porter & Knoll (2000) and Porter *et al.* (2003). A diverse group of vaseform forms is known from Neoproterozoic sediments from various parts of the world, and a critical morphological evaluation about their possible affinity with thecamoebians is provided by Porter & Knoll (2000). Well-preserved and diverse VSMs were reported from carbonate nodules in 742 ± 6 Ma old black shales of the Chuar Group, Grand Canyon, USA, and nine new species belonging to eight new genera were described by Porter *et al.* (2003) using the taxonomy of modern testate amoebae. This assemblage also includes eight species belonging to two genera already known.

Medioli *et al.* (1990a) critically reviewed reports of pre-Quaternary thecamoebians published between 1930 and 1990. These included 26 species of agglutinated forms whose thecamoebian affinity was questioned. The oldest Phanerozoic record of thecamoebians is from Cambrian organic residues from Nova Scotia, Canada (Scott *et al.*, 2003). Other Palaeozoic finds are from the Carboniferous (Vasicek & Ruzicka, 1957; Wightman *et al.*, 1994; Wolf, 1995) and a short report on Early Permian material of the Himalayas of India (Farooqui *et al.*, 2010). The present paper is an expanded version of Farooqui *et al.* (2010), which discusses the geological and evolutionary significance of the reported assemblages. Reports of thecamoebians from the Mesozoic include forms isolated from amber and sediments reported by Schönborn *et al.* (1999), Poinar *et al.* (1993), Medioli *et al.* (1990b), Waggoner (1996a), Schmidt *et al.* (2001, 2004), van Hengstum *et al.* (2007), Bassi *et al.* (2008) and Martin-González *et al.* (2009). There are also a few scattered reports of Tertiary thecamoebians (Bradley, 1931; Frenguelli, 1933; Kövály, 1956; Waggoner, 1996b; Schiller, 1997, 1998, 1999; Boeuf & Gilbert, 1997; Foissner & Schiller, 2001).

Patterson & Kumar (2000, 2002) and Schmidt *et al.* (2004) have summarized fossil records and evolutionary history of the Testate Amoebae. More recently, van Hengstum *et al.* (2007) provided a stratigraphical summary of the distribution of

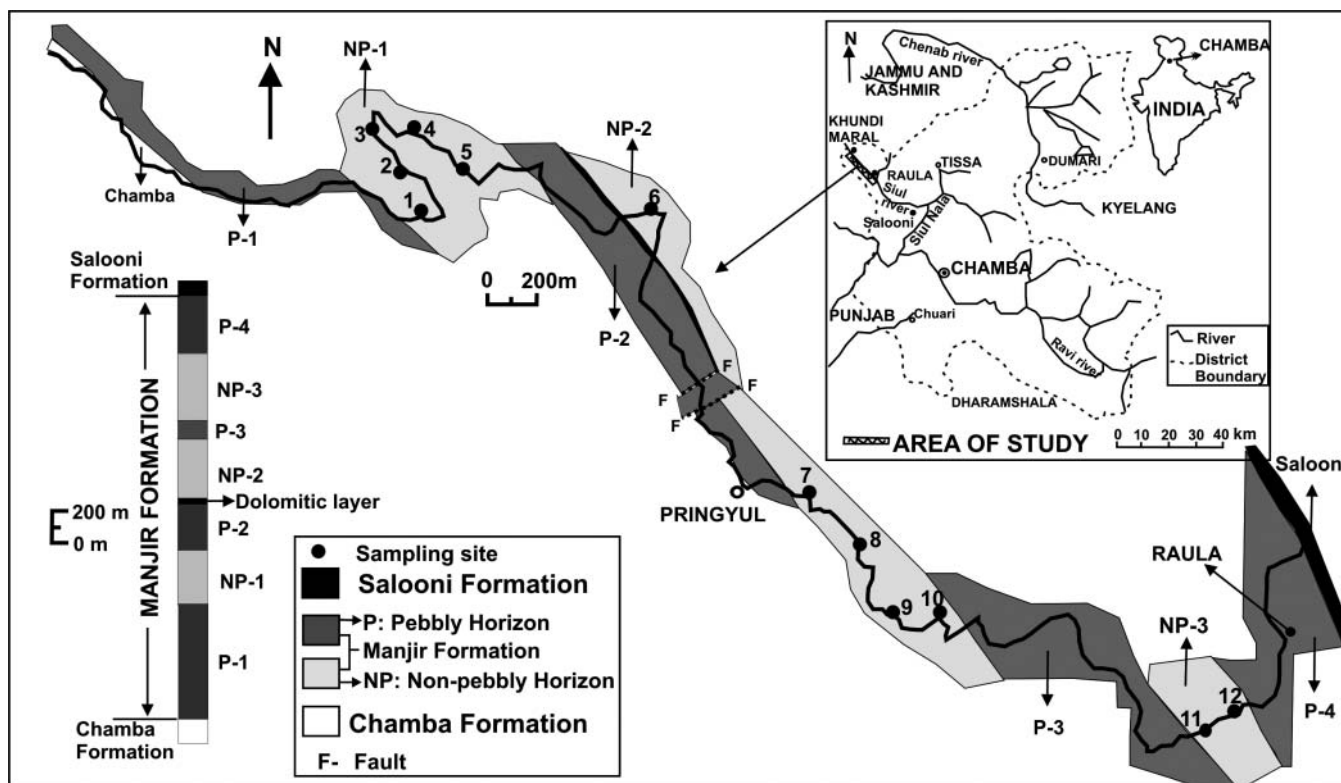


Fig. 1. Location map of the Khundi–Maral–Raula section in Chamba District, Himachal Pradesh, India.

thecamoebian families. These studies clearly demonstrate that despite a long geological history, thecamoebian lineages as seen in their test morphology have shown minimal evolution and display close resemblance to their Holocene forms.

THECAMOEBIANS IN PALYNOLOGICAL PREPARATIONS

Since thecamoebian tests are secreted (autogenous) and are proteinaceous, they are acid-resistant and have been reported in palynological preparations by Kumar & Patterson (2002), Farooqui & Gaur (2007) and Farooqui *et al.* (2010) plus in many other publications. Srivastava & Bhattacharya (1998) reported an assemblage of Early Permian age palynomorphs from coal balls of Arunachal Pradesh, northeastern Himalayas, India. A specimen referred to as “?Chitinozoa like vesicle” (their pl. 1, fig. 11) is most likely a specimen of *Diffugia*. Likewise, Pande *et al.* (2004) published a palynomorph assemblage from the Manjir Formation (Early Permian) of Himachal Pradesh in north India. They too reported an ‘unidentified specimen’ (their pl. 2, fig. 6), which is a well-preserved specimen of *Centropyxis*. There are significant opportunities for discovering thecamoebian assemblages from Phanerozoic sediments world-wide that may occur in palynological preparations (Kumar, 2011). The present paper also deals with Permian thecamoebians observed in palynological preparations. This method was applied in the present study because samples from the Manjir Formation are hard sedimentary rocks, and acid treatment was essential for retrieving the palynomorphs and other organic matter embedded within them.

STRATIGRAPHY AND AGE

The Chamba Basin (Himachal Pradesh) (Fig. 1) represents the Tethyan realm in the northwest Himalayas and the Manjir Formation is a major stratigraphic unit of this basin. Lithologically the Manjir Formation includes both arenaceous and calcareous rocks that are foliated, moderately metamorphosed and are represented by heterogeneous, poorly sorted pebbly horizons separated by non-pebbly horizons (diamictites). The section of the Manjir Formation studied constitutes three non-pebbly units (NP-1, NP-2 and NP-3) separated by four pebbly units (P-1, P-2, P-3 and P-4). Samples for the present study were collected from the dark grey to black shale/slate units of the non-pebbly horizons. The Manjir Formation is overlain by the Salooni Formation and underlain by the Chamba Formation (Table 1). Most early work on the geology of this region considered the Manjir Formation to be of Late Proterozoic age on the basis of its lithology and regional stratigraphy (Sehgal, 1965; Rattan, 1973). Later, well-preserved and stratigraphically significant palynomorphs were discovered from this formation. A rich assemblage of palynomorphs dominated by monosaccate pollen *Barakarites*, *Parasaccites* and *Plicatipollenites*, some non-striate disaccates *Scheuringipollenites*, *Platysaccus* and striate disaccates *Striatopodocarpites*, *Faunipollenites* and *Striatites* gave a definite Early Permian age to the Manjir Formation (Pande *et al.*, 2004).

Some samples from the pebbly units were also macerated for thecamoebians but were found to be barren. The present study is based on twelve samples that were collected along the Khundi–Maral–Raula section along the Siul River (Fig. 1).

Sample number (Fig. 1)	Formation		Lithology	Thickness (m)
	Salooni		Black pyritized shale, carbonaceous shale, minor siltstone bands	Not measured
	MANJIR FORMATION	Pebbly Unit P-4	Foliated calcareous, matrix-supported, bluish-grey pebbly horizon, matrix dominantly arenaceous, clasts of quartzite, shale and carbonate range from granular to small-pebble size.	341
12–11		Non-Pebbly Unit NP-3	Non-pebbly, non-calcareous, greyish-black slate and phyllite with occasional siltstone bands	428
		Pebbly Unit P-3	Foliated calcareous, bluish grey matrix-supported pebbly slate/phyllite, clasts often have sericitic envelope ranging in size from granular to medium pebble, clasts include quartzite, shale and carbonate	157
10–6		Non-pebbly Unit NP-2	Black, greyish-black, non-calcareous bleached and limonitized pyritiferous shale/slate and siltstone with minor pockets of dolomite/dolomitic limestone	356
		Pebbly Unit P-2	Grey, bluish-grey, calcareous, matrix-supported phyllite/slate and greenish quartzite, medium and small pebble clasts of quartzite, shale and dolomite/dolomitic limestone, stretched clasts conspicuous	315
5–1		Non-pebbly Zone NP-1	Grey, bluish-grey, non-calcareous, slate and phyllite with subordinate siltstone and black shale with occasional limonization	417
		Pebbly Unit P-1	Foliated calcareous, matrix-supported pebbly slate/phyllite and quartzite with sparsely distributed translucent quartz vein granules in lower part	715
	Chamba		Fine-grained, greyish-green quartzite and phyllite	Not measured

Table 1. Lithostratigraphy of the Manjir Formation along the Khundi–Maral–Raula section (Siul River) in Chamba District, Himachal Pradesh, India.

The detailed regional lithostratigraphy and thicknesses of four pebbly and three non-pebbly horizons are given in Table 1.

MATERIAL AND METHODS

A total of 12 samples, five each from NP-1 and NP-2, and two from NP-3 were studied (Fig. 1). Testate amoebae were isolated from the shale/slate samples after treatment with hydrochloric acid (HCl), generally used for isolating palynomorphs from hard calcareous sediments. After washing out the acid, the samples were sieved through 600 mesh ($> 15 \mu\text{m}$) and the residue of the larger fraction was mounted on glass slides in glycerol. The slides were scanned for thecamoebians under a high-power light microscope (Olympus BX-52). The identifications are based on Medioli & Scott (1983), Kumar & Dalby (1998) and Beyens & Meisterfeld (2002).

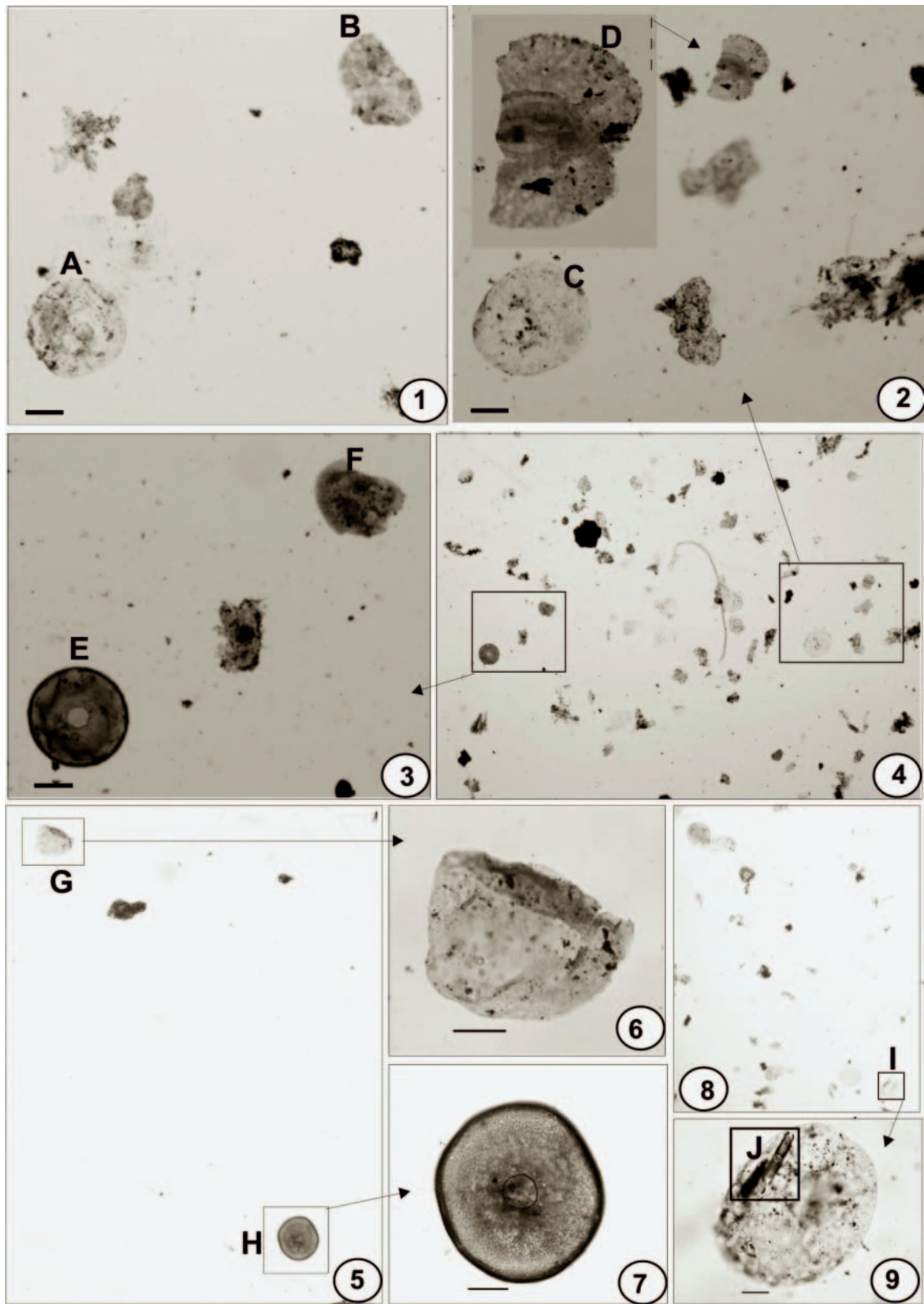
For the purposes of identification of Manjir Formation thecamoebians, and to compare their morphological affinities with extant thecamoebians, several modern lake/pond sediments were also studied from various parts of India. Sediment–water interface samples were collected mainly from the periphery of the lakes/ponds. Some 10g of air-dried sediment was warmed in 5% potassium hydroxide (KOH) to remove organic matter coagulation. After sieving through a 150 mesh ($\sim 105 \mu\text{m}$), the filtrate was kept overnight and the supernatant was decanted. The residue was acetolysed (Erdtman, 1943) in order to study the slides under a high-power light microscope.

RESULTS

The three non-pebbly units NP-1, NP-2 and NP-3 yielded fairly good assemblages of thecamoebian tests (Pls 1–6) as well as characteristic Early Permian palynomorphs (Pl. 7). Plates 1 and 2 show co-occurrences of various age-diagnostic Early Permian palynomorphs and thecamoebians in the same field-of-view, thus authenticating the presence and age of thecamoebians in the Manjir Formation. The total counts of the thecamoebians recovered in 10 g samples are given for all the 12 samples in Figure 2. The preservation of these tests is good enough to study their basic morphology and identification. Although the Manjir Formation thecamoebian assemblages are of Early Permian age, most of them demonstrate very close morphological similarity with extant forms even at the strain level (Reinhardt *et al.*, 1998). Several of them look almost identical to the forms recovered from modern lakes in India. We have demonstrated this fact by placing several fossil forms beside extant ones in Plates 4–6. We faced a dilemma about naming them, whether to propose new names for these microfossils or assign them names of Holocene thecamoebians. Since it was possible to identify ~ 300 Ma old forms with extant ones we decided to use current nomenclature rather than giving them new names. We believe giving new names would have created nomenclatural confusion for almost identical forms. The characteristics of the assemblages are as follows.

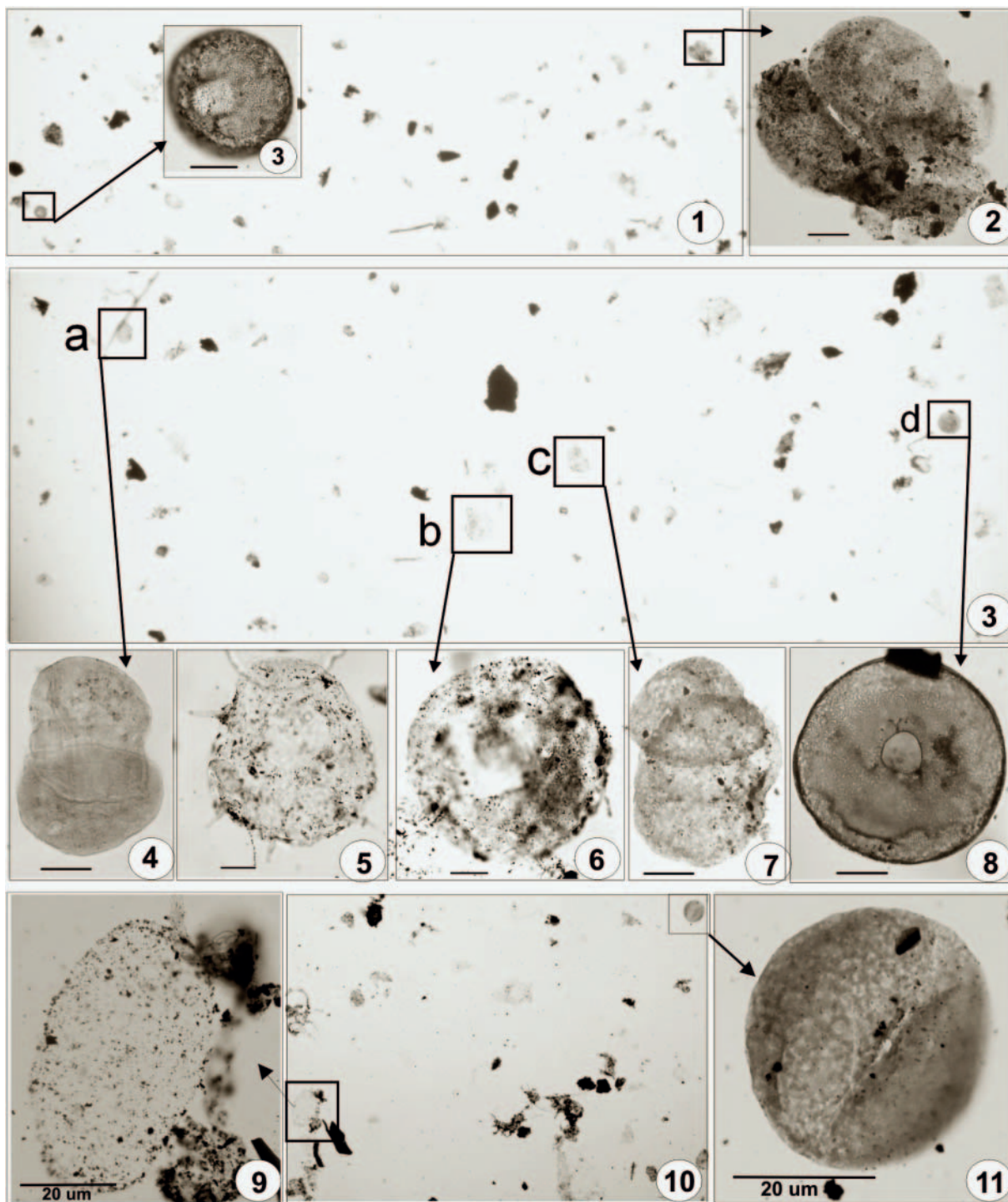
NP-1

This lithological unit overlies the pebbly unit P-1 and is characterized by grey to bluish-grey, non-calcareous, slate and phyllite



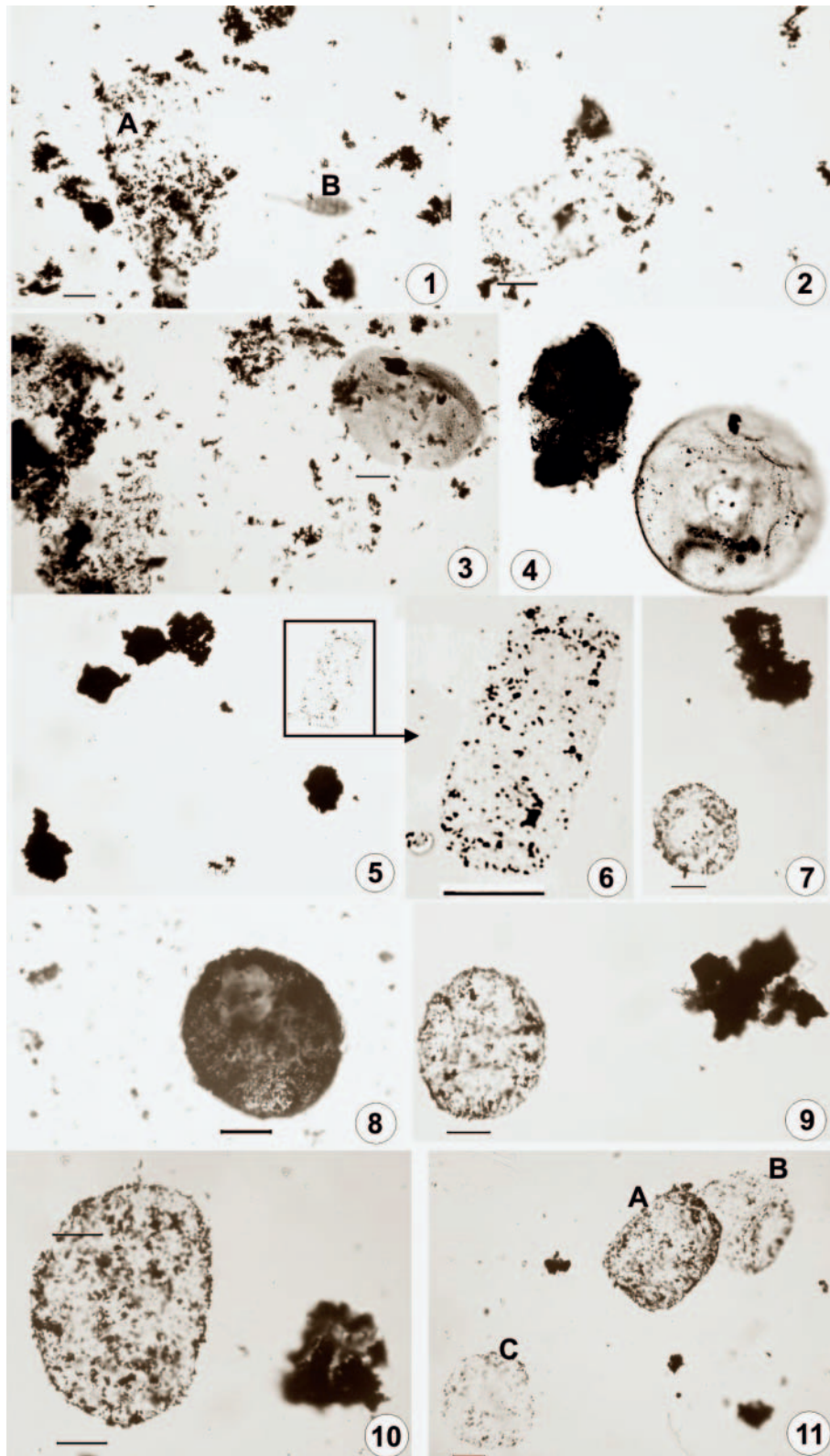
Explanation of Plate 1.

fig. 1. cf. *Trigonopyxis* sp. (A) and *Scheuringipollenites maximus* (J45/4) (B), slide no. 12865A. **fig. 2.** *Centropyxis arcelloides* (C) and *Primuspollenites* sp. (D), slide no. 12865A. **fig. 3.** *Arcella artocrea* (G25/3) (E) and *Scheuringipollinites* sp. (F). **fig. 4.** A view showing both pollen and thecamoebians together in a slide. **fig. 5.** Pollen (G) and thecamoebian (H), slide no. 12865. **fig. 6.** *Faunipollenites* sp. **fig. 7.** *Arcella artocrea* (G29/3). **figs 8, 9.** *Centropyxis aculeata* 'aculeata': (I) and showing diatom frustules (J) (G25/3), slide no. 13964. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale 20 μ m.



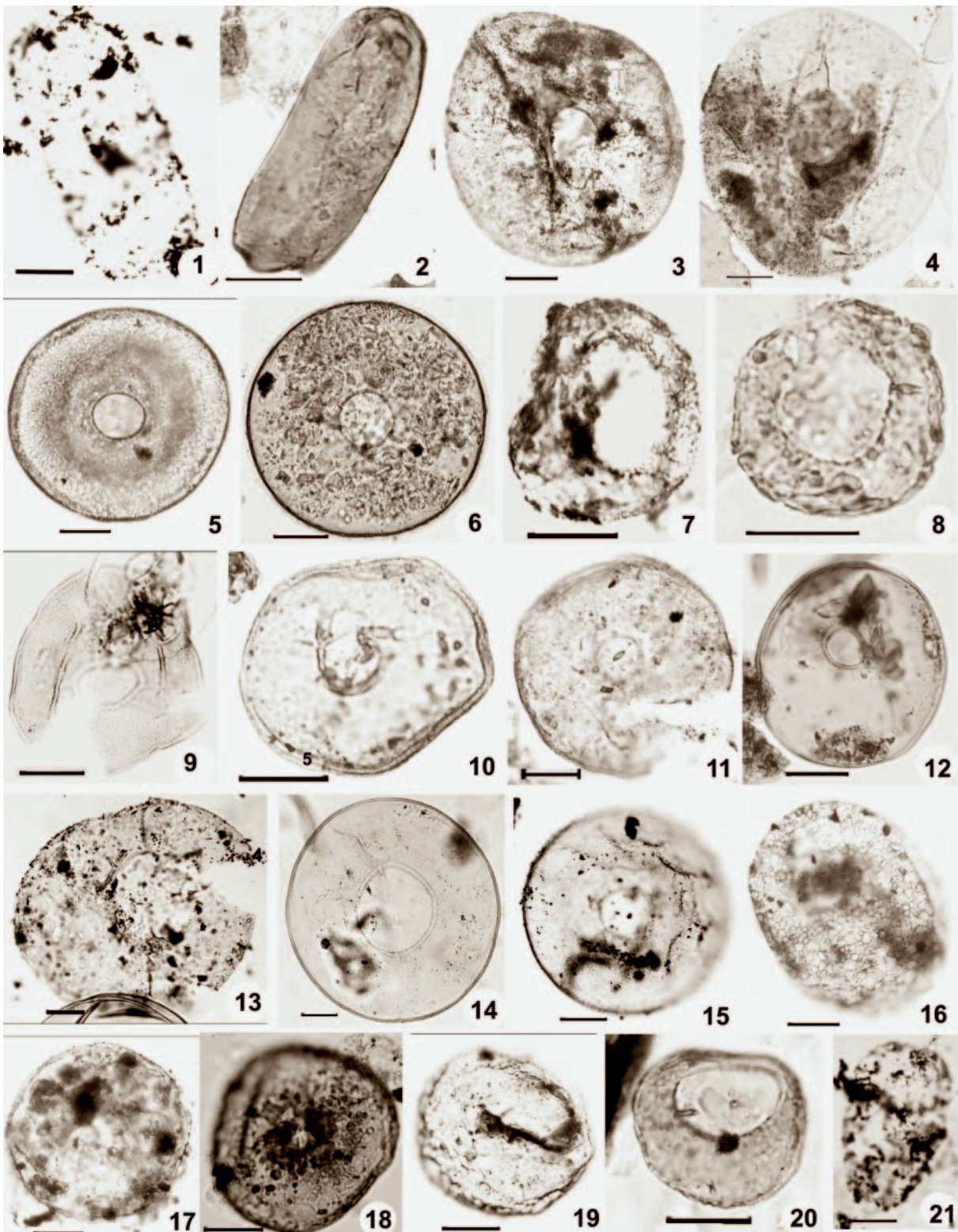
Explanation of Plate 2.

fig. 1. Pollen and thecamoebian (*Arcella* 3) in slide no. 12865A. **figs 2, 7, 11.** *Scheuringipollenites* sp.: 2, (M22/5); 7, (L43/3). **fig. 3.** Pollen and thecamoebians in slide no. 12865A. **fig. 4.** *Faunipollenites* (L33/3), slide no. 12865A. **fig. 5.** *Centropyxis aculeata* 'aculeata' (F26/4), no. slide 12865A (not in view of fig. 3). **fig. 6.** *Centropyxis* sp. (L42/4). **fig. 8.** *Arcella artocrea* (M43/1). **fig. 9.** *Amphitrema flavum* (N22/5), slide no. 13956. **fig. 10.** *Amphitrema* sp. and *Scheuringipollenites* sp. in low power. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale 20 μ m.



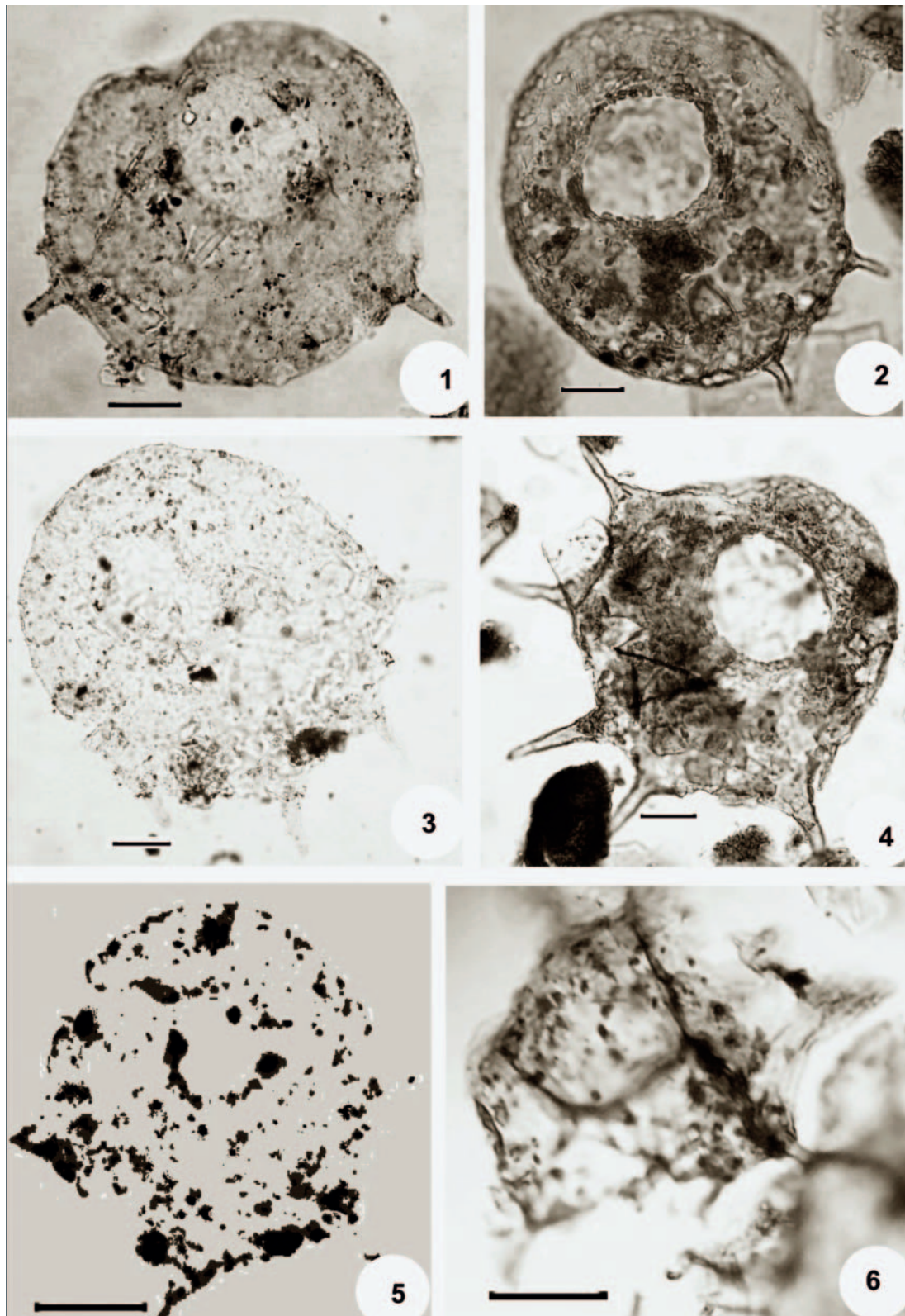
Explanation of Plate 3.

fig. 1. Dispersed organic matter in slide no. 13956: *Amphitrema flavum* (A) and fungal spore (B). **figs 2, 5, 6.** *Amphitrema flavum*: 2 (G34/2); 5, 6 (J35/2), slide no. 13966. **fig. 3.** *Arcella* sp. (N21/2), slide no. 13965. **fig. 4.** *Arcella gibbosa* (P21/2), slide no. 12861. **fig. 7.** *Arcella megastoma* (K33/1), slide no. 13966. **fig. 8.** *Diffflugia gramen* (F35/2), slide no. 13959. **fig. 9.** *Centropyxis* sp. (L42/2), slide no. 13962. **fig. 10.** *Centropyxis aerophila* (G21/1), slide no. 13965. **fig. 11.** *Diffflugia penardi* (A), cf. *Cyclopyxis kahlui* (B) and *Arcella megastoma* (F32/1) (C), slide no. 13960. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale is 20 μ m.



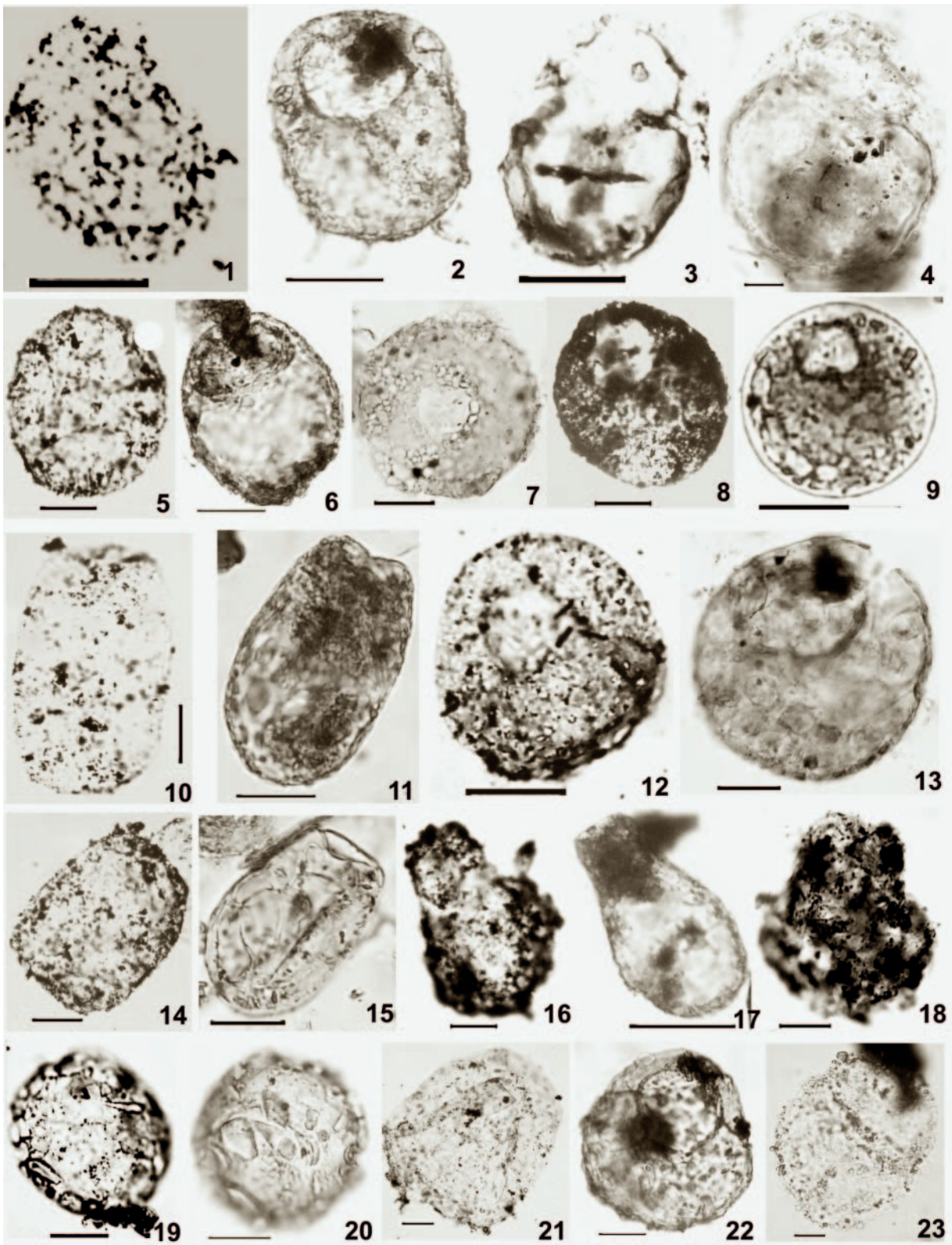
Explanation of Plate 4.

figs 1, 2. *Amphitrema flavum*: **1**, fossil (G34/2), slide no. 13956; **2**, Recent, source – fresh water, Sadatal lake, India. **figs 3, 4.** *Arcella arenaria*: **3**, fossil (U30/1), slide no. 12865A; **4**, Recent, source – mouth Godavari River, Andhra Pradesh, India. **figs 5, 6.** *A. artoceca*: **5**, fossil (Q35 & Q35/1), slide no. 12865A; **6**, Recent, source – coastal wetland, Pichavaram, Tamil Nadu, India. **figs 7, 8.** *A. megastoma*: **7**, fossil (T30/3), slide no. 12865; **8**, Recent, sources – fresh-water lakes, coastal wetlands, mouth of the rivers, sewage drainage system, India. **figs 9–12.** *A. discoides*: **9**, fossil (W38/2), slide no. 12861; **10**, Recent, source – Bet Dwarka, archaeological site, Gujarat, India; **11**, fossil (V22/1), slide no. 13963; **12**, Recent, source – Nilarevu mouth, Godavari River, India. **figs 13, 14.** *A. vulgaris*: **13**, fossil (W20/3), slide no. 13964; **14**, Recent, source – Sadatal lake, India. **fig. 15.** cf. *A. gibbosa* (fossil) (P21/2), slide no. 12861. **fig. 16.** cf. *Centropyxis hirsuta* (fossil) (U22/1), slide no. 13960. **figs 17, 18.** cf. *Trigonopyxis arcuata*: **17**, fossil (S12/3), slide no. 13958B; **18**, Recent, sources – coastal wetland, river mouths, east coast, India. **figs 19, 20.** *Cyclopyxis* sp.: **19**, fossil (P36/4), slide no. 13957; **20**, Recent, source – Nilarevu mouth, Godavari River, India. **fig. 21.** *Trinema* sp. (fossil) (Q38/1), slide no. 13960. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale 20 μ m.



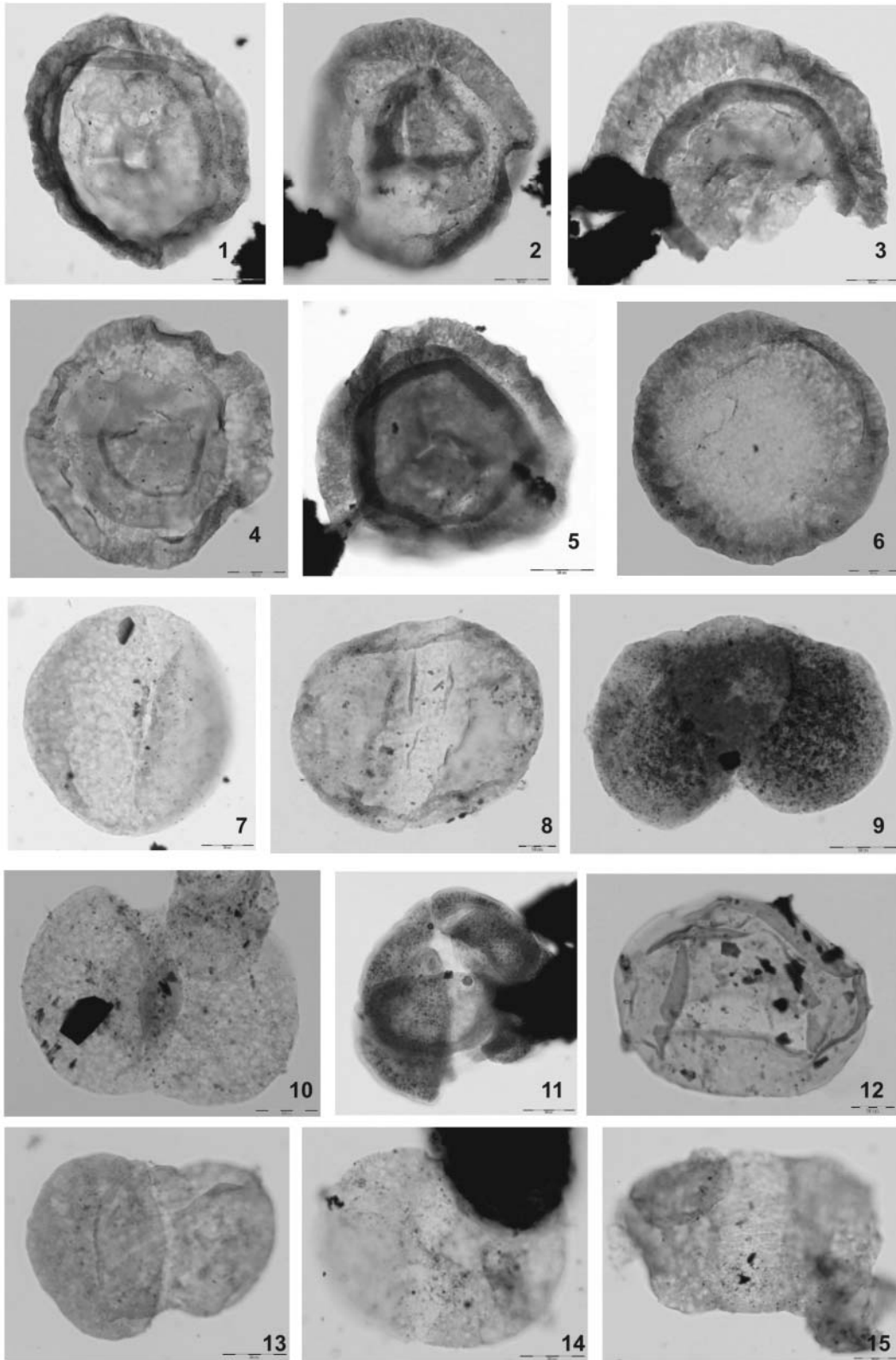
Explanation of Plate 5.

figs 1, 2. *Centropyxis aculeata* 'aculeata': **1**, fossil (U38/3), slide no. 12865A; **2**, Recent, source – Sadatal lake, India. **figs 3, 4.** *C. constricta* 'spinosa': **3**, fossil (W39), slide no. 12865B; **4**, Recent, source – Sadatal lake, India. **figs 5, 6.** *C. constricta* 'spinosa': **5**, fossil (P37/3), slide no. 13964; **6**, Recent, source – Wadhawana palaeolake (~5000 years BP), Gujarat, India. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale is 20 µm.



Explanation of Plate 6.

figs 1, 2. cf. *Centropyxis constricta* 'spinosa': 1, fossil (V34), slide no. 13964; 2, Recent, source – sewage disposal ponds (flowing water), India. figs 3, 4. cf. *C. aerophila* 'aerophila': 3, fossil (G33/2), slide no. 13961; 4, Recent, source – in association with bryophytes and lichens growing on Mango tree bark, Malihabad, Lucknow, India. figs 5, 6. *C. aerophila* 'aerophila': 5, fossil (H12/1), slide no. 13957; 6, Recent, source – with bryophytes, lichen (as above). fig. 7. *Centropyxis arcelloides* (fossil) (J11/4), slide no. 13960. figs 8, 9. *Diffugia gramen*: 8, fossil (J35/2), slide no. 13966; 9, Recent, source – stream polluted with sewage (flowing throughout the year), Lucknow. figs 10, 11. *D. oblonga*: 10, fossil (P13/4), slide no. 13959; 11, Recent, source – Sadatal Lake, India. figs 12, 13. *D. oviformis*: 12, fossil (S23/1), slide no. 13957; 13, Recent, source – Sadatal Lake, India. figs 14, 15. *D. penardi*: 14, fossil (F32/1), slide no. 13960; 15, Recent, source – Sadatal Lake, India. figs 16, 17. *D. pyriformis*: 16, fossil (G42 & G43), slide no. 13962; 17, Recent, source – Sadatal Lake, India. fig. 18. *Lagenodiffugia* (fossil) (F33/1), slide no. 13957. figs 19, 20. Incerta sp., agglutinated sphere of unknown affinity: 19, fossil (J10/1 & 10/2), slide no. 13958; 20, Recent, source – sewage drainage system, Lucknow, India. figs 21, 22. cf. *Cucurbitella tricuspis*: 21, fossil (H45/2), slide no. 13961; 22, Recent, source – Sadatal Lake, India. fig. 23. *D. urceolata* type (fossil) (V40/1), slide no. 12861b. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale 20 μ m.



Explanation of Plate 7.

figs 1, 3, 5. *Plicatipollenites*: **1**, (J42), slide no. 12861; **3**, (Q42/1), slide no. 12861; **5**, (Q40/2), slide no. 12866. **figs 2, 4.** *Barakarites*: **2**, (K45), slide no. 12861; **4**, (Y48/1), slide no. 12862. **fig. 6.** *Parasaccites* (K31/1), slide no. 12859. **fig. 7.** *Scheuringipollenites* (M43/3), slide no. 12865. **fig. 8.** *Faunipollenites* (Q41/3), slide no. 12869. **fig. 9.** *Platysaccus* (H35/1), slide no. KR-11-5. **fig. 10.** *Pinuspollenites* (E53), slide no. 12869. **fig. 11.** *Corisaccites* (F68), slide no. KR 63-A9. **fig. 12.** *Latosporites* (G30/2), slide no. 12859. **figs 13, 15.** *Striatopodocarpites*: **13**, (F36/2), slide no. 12865 A; **15**, (S65), slide no. KR-11-Z. **fig. 14.** *Faunipollenites* (M40/1), slide no. 12865. All slides are housed in the Birbal Sahni Institute of Palaeobotany, Lucknow. England Finder coordinates in brackets. Scale 20 μ m.

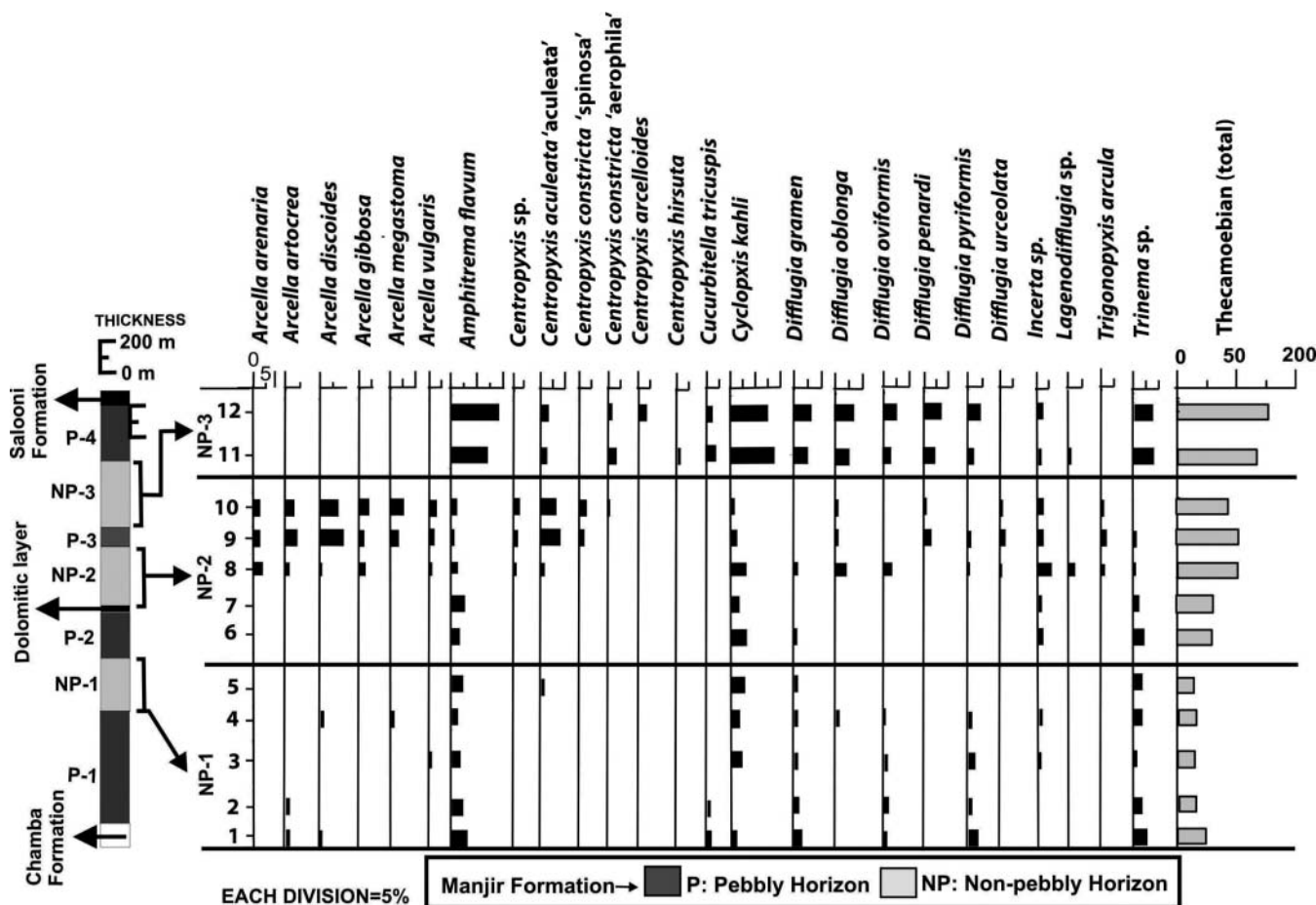


Fig. 2. Thecamoebian spectrum in Non-pebbly Units of the Manjir Formation, Himachal Pradesh, India. Some rare taxa omitted.

with subordinate siltstone and black shale. The thecamoebians show low counts but are dominated by *Amphitrema flavum*, *Trinema* sp. (~25%) followed by *Diffugia oviformis*, *D. gramen*, *D. pyriformis*, *Cyclopyxis kahli* (6–12%). The lowest count was of *Arcella artocrea* and *A. discoides*.

NP-2

Separated by pebbly unit P-2, this non-pebbly unit is a black to greyish-black, non-calcareous shale/slate and siltstone with minor pockets of dolomite/dolomitic limestone. The overall thecamoebian count and taxonomic diversity are higher in this non-pebbly unit. The highest percentage occurrence was of *Centropyxis aculeata* 'aculeata', *Arcella artocrea*, *A. discoides* and *Cyclopyxis kahli*, each ranging from < 5–10%. Other species of *Diffugia* and *Arcella*, as shown in Figure 2, constitute < 5%.

NP-3

This unit is again separated by a pebbly unit (P-3) and is similar to NP-1 with a similar thecamoebian community. The sediment is non-pebbly, non-calcareous, greyish-black slate with occasional siltstone bands. The highest percentage of *Cyclopyxis kahli* and *Amphitrema flavum* ranged between 15% and 19% in this unit. Other forms, such as centropxyids, *Cucurbitella* and *Diffugia* species range between 3% and 8%. The following thecamoebian taxa were observed and the taxonomic and

nomenclatural details are primarily from Medioli *et al.* (1987; 1999; 2003).

Phylum **Protozoa** Goldfuss, 1818

Subphylum **Sarcodina** Schmarda, 1871

Class **Rhizopoda** von Siebold, 1845

Subclass **Lobosa** Carpenter, 1861

Order **Arcellinida** Kent, 1880

Family **Amphitremidae** Poche, 1913

Genus *Amphitrema* Archer, 1869

Amphitrema flavum Archer, 1869 (Pl. 3, figs 2, 5, 6; Pl. 4, figs 1, 2)

Family **Arcellidae** Ehrenberg, 1832

Genus *Arcella* Ehrenberg, 1832

Arcella arenaria Greeff, 1866 (Pl. 4, figs 3, 4)

A. artocrea Leidy, 1876 (Pl. 4, figs 5, 6)

A. discoides Ehrenberg, 1843 (Pl. 4, figs 9–12)

A. gibbosa Penard, 1890 (cf. Pl. 4, fig. 15)

A. megastoma Penard, 1923 (Pl. 4, figs 7, 8)

A. vulgaris Ehrenberg, 1832 (Pl. 4, figs 13, 14)

Family **Centropxyidae** Jung, 1942

Genus *Centropyxis* Stein, 1857

- Centropxyxis aculeata* 'aculeata' Reinhardt *et al.*, 1998 (Pl. 5, figs 1, 2)
 ?*C. constricta* 'spinosa' (Pl. 5, figs 5, 6)
C. arcelloides Penard, 1902 (Pl. 6, fig. 7)
 cf. *Centropxyxis constricta* 'spinosa' Reinhardt *et al.*, 1997 (Pl. 6, figs 1, 2)
C. constricta 'aerophila' Deflandre, 1929 (Pl. 6, figs 4–6)
 ?*C. constricta* 'aerophila' Deflandre, 1929 (Pl. 6, fig. 3)
C. constricta 'spinosa' Ehrenberg, 1843 (Pl. 5, figs 3, 4)
C. hirsuta Deflandre, 1929 (Pl. 4, fig. 16)

Family **Difflogiidae** Stein, 1859

Genus *Difflogia* LeClerc, 1815

- Difflogia gramen* Penard, 1923 (Pl. 6, figs 8, 9)
D. oblonga Ehrenberg, 1838 (Pl. 6, figs 10, 11)
D. oviformis Cash, 1909 (Pl. 6, figs 12, 13)
D. penardi Hopkinson, 1909 (Pl. 6, figs 14, 15)
D. pyriformis Ehrenberg, 1838 (Pl. 6, figs 16, 17)
D. urceolata Carter, 1864 (Pl. 6, fig. 23)

Genus *Lagenodifflogia* Leidy, 1874

Lagenodifflogia sp. (Pl. 6, fig. 18)

Family **Hyalospheniidae** Schultze, 1877

Genus *Cucurbitella* Penard, 1902

- Cucurbitella tricuspid* (Carter) Reinhardt *et al.*, 1998 (Pl. 6, figs 21, 22)

Family **Trigonopyxidae** Loeblich & Tappan, 1964

Genus *Cyclopyxis* Deflandre, 1929

- Cyclopyxis kahlii* (Deflandre, 1929) Bonnet, 1953 (Pl. 4, figs 19, 20)

Genus *Trigonopyxis* Leidy, 1879

- Trigonopyxis arcuata* Leidy, 1879 (Pl. 4, figs 17, 18)

Family **Trinematidae** Hoogenraad & Groot, 1940

Genus *Trinema* Dujardin, 1841

Trinema sp. (Pl. 4, fig. 21)

Incertae sedis

- Incerta sp. – agglutinated sphere of unknown affinity (cf. Dalby *et al.*, 2000).

DISCUSSION

Palaeoecology and depositional environment

Draganits *et al.* (2008, pp. 128–129) consider the Manjir Formation 'probably represents glaciomarine debris flow deposits that accumulated during glacial lowstand' and correlated it with other glaciomarine deposits in the Lesser Himalaya described by Frank *et al.* (1995) and Dipietro & Pogue (2004). Stephenson *et al.* (2007) reviewed Early Permian palaeontological data from Gondwana and concluded that diversity increased from glacial conditions to post-glacial conditions. A similar review of palynological data indicates that a change from monosaccate pollen assemblages associated with fern spores, to more diverse assemblages with common non-taeniate pollen occurs through the deglaciation period in Gondwana (Stephenson, 2008).

During the Early Permian the uplands in Oman witnessed changes from a glacial monosaccate pollen-producing flora to a warmer climate bisaccate pollen-producing flora. A similar trend was also observed in Early Permian Manjir Formation palynomorph assemblages dominated by monosaccate pollen, such as *Parasaccites*, *Plicatipollenites* and *Barakarites* (Pande *et al.*, 2004). Monosaccate pollen dominated the Early Permian Talchir Formation of Peninsular India, which is a well-known glacial deposit (Tiwari & Tripathi, 1992). Several Early Permian age marine successions of various parts of the Himalayas are dominated by monosaccate pollen assemblages (Srivastava *et al.*, 1987; Upadhyay *et al.*, 1999a, b; Sinha *et al.*, 2004). The dominance of monosaccate pollen flora in the Early Permian has also been observed on other continents and countries of Gondwana, for example: Africa (Falcon, 1975; Anderson, 1977; Utting, 1978); Antarctica (Barret & Kyle, 1975; Kemp *et al.*, 1977; Kyle & Schopf, 1982; Masood *et al.*, 1994); Australia (Truswell, 1980); Brazil (Bhardwaj *et al.*, 1976) and India (Lele & Chandra, 1973; Bhardwaj, 1975; Lele, 1975). Palynomorph assemblages are well known from the Early Permian marine and inter-trappean volcanic sediments across the Himalayan region (Srivastava *et al.*, 1987; Prasad *et al.*, 1989; Singh *et al.*, 1995; Upadhyay *et al.*, 1999a, b; Srivastava & Bhattacharya, 2000; Sinha *et al.*, 2004). A more or less similar trend is observed in all these palynomorph assemblages.

Late Carboniferous–Early Permian glaciation was widespread over Gondwana and sequences of marine and non-marine sediments are common in Permo-Carboniferous deposits. Widespread distribution of glacial sediments occurs in South America, Africa, Madagascar, Arabia, India, Antarctica and Australia. During the Early Permian the location of the Chamba Basin would have been around 50–55°S latitude, making it a very cold region at that time (Fig. 3). The shale/slate units of the Manjir Formation represent marine tongues formed during deglaciation phases (Draganits *et al.*, 2008). Thus, it is clear that the thecamoebian assemblage reported from the Manjir Formation represent glaciomarine environments.

Transition from marine to terrestrial habitats

Extant thecamoebians inhabit a wide variety of terrestrial environments, for example, fresh-water bodies such as lakes, ponds and rivers, slightly brackish and estuarine environments, and salt- and fresh-water marshes (Scott *et al.*, 2001; Patterson & Kumar, 2002). Although there are no known truly marine occurrences of extant thecamoebians, their geological record includes marine environments. Wightman *et al.* (1994) described agglutinated foraminifera and thecamoebian assemblages from Carboniferous (late Westphalian–Stephanian) cyclothems of the Sydney coal field in Nova Scotia. They defined four foraminiferal and thecamoebian assemblages and concluded that the host sediments were deposited on an extensive coastal platform. The *Trochammmina* and thecamoebian assemblages were found within the upper part of the tidal range, and thecamoebian assemblages dominated by an agglutinated difflogiid type were interpreted to indicate fresh-water palaeoenvironments. Scott *et al.* (2001) mention a few other such reports of pre-Quaternary occurrences of thecamoebians in marginal marine environments.

As discussed earlier, the oldest thecamoebians were described as VSMs from the Neoproterozoic rocks of Grand Canyon,

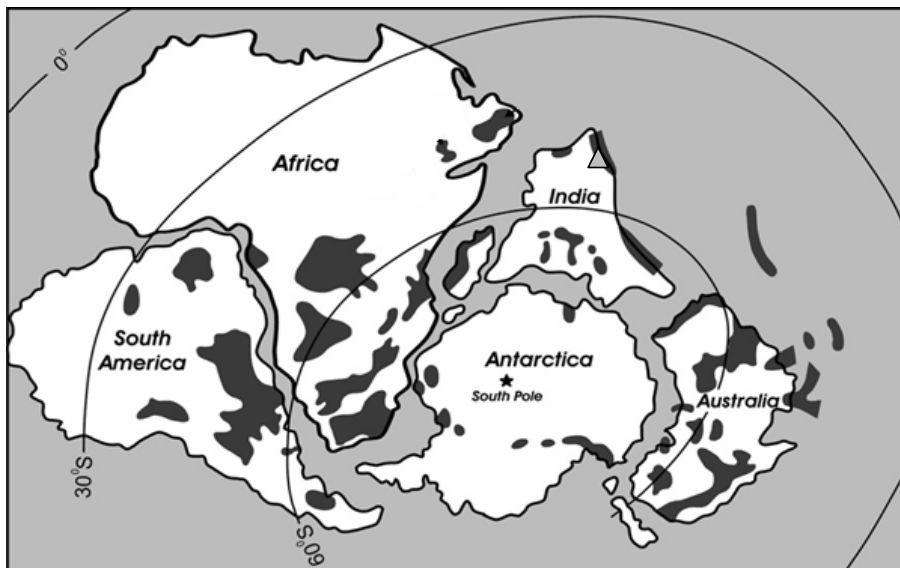


Fig. 3. Palaeogeography of Late Carboniferous–Early Permian Gondwana and distribution of glacial deposits (black shading). Location of Chamba Basin indicated by grey triangle. Modified after Bussert & Schrank (2007).

USA by Porter & Knoll (2000) and Porter *et al.* (2003). These VSMs were reported from carbonate nodules in black shales of the Walcott Member (Kwagunt Formation) of the Chuar Group in the Grand Canyon. This stratigraphic unit is a marine deposit because these VSMs occur with several acritarch taxa that are found elsewhere in marine successions. The presence of certain acritarch taxa in the Precambrian sediments does not necessarily indicate marine environments; however, based on many lines of geological evidence, Porter & Knoll (2000, p. 364) conclude that, ‘The abundant VSMs found in the upper Walcott member appear to have accumulated in a quiet subtidal marine environment characterized by high rates of organic carbon burial’. This discussion clearly demonstrates that the earliest thecamoebians inhabited marine environments. The present report of early Permian marine thecamoebians from the Himalayas supports the view that this group of protists inhabited shallow-marine environments from their origins in the Neoproterozoic until at least Early Permian times.

Although extant testate amoebae are predominantly terrestrial, they are not totally absent from marginal marine environments, and members of both Testacealobosa and Testaceafilosa inhabit tidal pools and beach sands (Sudzuki, 1979; Porter & Knoll, 2000). There are a few reports of thecamoebians from deep sediments of fjords of British Columbia (Patterson *et al.*, 2000; Kumar & Patterson, 2002) but they are mostly allochthonous, transported from land by streams and rivers. Thus, it is concluded from the above discussion that thecamoebians did inhabit subtidal marine environments during their early history (Neoproterozoic to at least Early Permian) but subsequently their habitat moved primarily to terrestrial environments and the closest they now inhabit to a marine environment is coastal marshes and other marginally brackish environments.

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