Thecamoebians (Testate Amoebae) Straddling the Permian-Triassic Boundary in the Guryul Ravine Section, India: Evolutionary and Palaeoecological Implications

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Abstract

Exceptionally well-preserved organic remains of thecamoebians (testate amoebae) were preserved in marine sediments that straddle the greatest extinction event in the Phanerozoic: the Permian-Triassic Boundary. Outcrops from the Late Permian Zewan Formation and the Early Triassic Khunamuh Formation are represented by a complete sedimentary sequence at the Guryul Ravine Section in Kashmir, India, which is an archetypal Permian-Triassic boundary sequence [1]. Previous biostratigraphic analysis provides chronological control for the section, and a perspective of faunal turnover in the brachiopods, ammonoids, bivalves, conodonts, gastropods and foraminifera. Thecamoebians were concentrated from bulk sediments using palynological procedures, which isolated the organic constituents of preserved thecamoebian tests. The recovered individuals demonstrate exceptional similarity to the modern thecamoebian families Centropyxidae, Arcellidae, Hyalospheniidae and Trigonopyxidae, however, the vast majority belong to the Centropyxidae. This study further confirms the morphologic stability of the thecamoebian lineages through the Phanerozoic, and most importantly, their apparent little response to an infamous biological crisis in Earth’s history.

Introduction

The Permian-Triassic Boundary (PTB) extinction was a catastrophic event in Earth’s history, where more than 90% of marine and 70% terrestrial life went extinct [2, 3]. Multiple studies have examined the timing, nature and biogeographic extent of this extinction event, including the low to middle palaeolatitude sites in the Palaeotethys [4–13], part of Panthalassa around Japan [14], and in the northern high latitudes [15–20]. However, the high southern palaeolatitude PTB
successions have become a cynosure to study the extinction patterns of marine and non-marine fauna [19, 21–27]. The Guryul Ravine PTB succession in the Kashmir Northwest Himalaya belonged to the peri-Gondwanan region that covered the northern margin of Gondwana and the southern margin of Palaeotethys/Neo-Tethys (Fig 1) (S1 Fig). Well-preserved marine [28–35] elements have been recovered from this section, as well as some terrestrial [36] remains, which provide an important biologic perspective of the PTB event (Fig 2).

Thecamoebians (testate amoebae) are eukaryotic heterotrophic protists that are polyphyletic in origin, based on molecular RNA analysis [37]. In modern environments, they colonize fresh to slightly brackish water aquatic environments (<4 psu) [38] and they form a simple secreted (autogenous) or agglutinated (xenogenous) test (or shell) that can be preserved in the sedimentary record following their death. Owing to their tight ecological zonation with respect to salinity, pH, and moisture content, subfossil thecamoebian assemblages preserved in late Holocene successions are used to reconstruct salinity [39, 40] and sea-level variations [41,42], precipitation variability [43] and anthropogenic impacts on coastal and lacustrine environments [44,45]. However, their pre-Quaternary fossil record is sparse, promoting some uncertainty in our understanding on the evolution of important taxonomic lineages, and the group’s response to critical environmental perturbations in Earth’s history.

The thecamoebian fossil record is currently dominated by Mesozoic observations [46–54], with few in the Paleozoic and Tertiary [55–64] (Fig 3) (S2 Fig). The preservation of the thecamoebians is like other organic-based microfossil groups, where agglutinated test have a better preservation potential than more fragile autogenous test [46]. Some of the better-preserved fossil thecamoebian assemblages have been recovered from both lacustrine and eustuarine successions that are nearly identical to modern forms [46,55,65,66], which suggests little morphologic variability in the group over the Phanerozoic [47–49,50,56,57, 65–69] (S2 Fig). The oldest fossil record of the thecamoebians is from the Neoproterozoic [65,70] with accounts...
Fig 2. Permian Triassic Boundary (PTB) study section at Guryul Ravine, Kashmir (after Kapoor 1996) Red Triangles pointing to the levels of reported occurrence of thecamoebians along with previously studied faunal elements. Conodont biozones after Algeo et al., 2007. PTB- Permian-Triassic boundary; LPME- Late Permian Mass Extinction. Occurrence of thecamoebians.

doi:10.1371/journal.pone.0135593.g002
also available from the Carboniferous [71]. Early Permian thecamoebians from the Tethys Himalaya are presented by Kumar et al. [66], and Late Permian thecamoebians have recently been recorded from the Raniganj Formation of the Godavari Graben [68]. Thus far, the thecamoebian fossil record is represented by eleven modern families: Arcellidae, Centropyxidae, Plagiopyxidae, Difflugidae, Hyalophenidae, Phyrganellidae, Euglyphidae, Cyphoderiidae, Amphitremidae, Trigonopyxidae and Trinematidae [46, 66, 69].

This paper presents the first account of the thecamoebians straddling the PT Boundary at the Guryul Ravine PTB Section in India, and the only one record of Late Permian thecamoebians from the Northwest Himalayan region of Jammu and Kashmir. These results provide direct evidence for the successful crossing of the thecamoebian (testate amoebae) group across the PT Boundary extinction event.

**Geological Setting**

The Guryul Ravine Section lies in the northernmost Indian state of Kashmir [72] (Fig 4), the geology of which has been extensively reviewed by Nakazawa et al. [27], Kapoor [1] and Tewari et al [36]. During the Late Permian and Early Triassic, the Kashmir region of the Indian sub-continent was located in northern Gondwana, at 35°S palaeolatitude along the southern margin of the Tethys Sea [73,74]. The depositional setting of the Late Permian Zewan Formation was a shallow marine environment with relatively high terrigenous sediment supply, whereas the Early Triassic Khunamuh Formation was deposited during a transgressive episode [74]. Marine sediments of the Guryul Ravine accumulated above pre-existing volcanic rocks [1]. Isotopic evidence of Proemse et al., 2013 [75] indicates relatively oxic conditions in the shallow marine regions of the Northwest margin of Pangea throughout the Late Permian Mass Extinction (LPME). However, the organic carbon flux study of Algeo et al., 2013 [76], and others [74,77] on the PTB sections have suggested that the well-oxygenated conditions were briefly interrupted by periods of anoxia in the Late Permian-Early Triassic shallow marine environments. The Guryul Ravine Section represents a continuous gradational sequence across the PT Boundary, whereas depositional hiatuses present in other Kumaon and Spiti Himalayas sections preclude a continuous record of paleoenvironmental changes during the PT Boundary Event. Our study of organic matter at the Guryul Section [36], reveals the prevalence of amorphous organic matter (AOM), which perhaps suggests a regional prevalence of anoxic conditions.

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**THECAMOEBIAN FOSSIL RECORD**

| THECAMOEBIAN FAMILIES | THECAMOEBIAN FOSSIL RECORD |
|------------------------|-----------------------------|
|                        | Cenozoic | Mesozoic | Paleozoic |
|                        | Holoc. | Pleist. | Plioc. | Mioc. | Oligoc.| Eoc. | Paleoc. | Creto. | Jur. | Tri. | Perm. | Carb. | Dev. | Sil. | Ord. | Camb. | Neoprot. |
| Arcellidae             |         |         |         |         |       |       |       | a| b| c|       |       |       |       |       |       |
| Centropyxidae          |         |         |         |         |       |       |       | e| h| i|       |       |       |       |       |       |
| Hyalospheniida         |         |         |         |         |       |       |       | f| g|       |       |       |       |       |       |       |
| Trigonopyxidae         |         |         |         |         |       |       |       | e| i|       |       |       |       |       |       |       |
|                        |         |         | FRESHWATER / BRACKISH | MARINE |         |       |       |       |       |       |       |       |       |       |       |

Fig 3. Thecamoebian fossil record of the families Arcellidae and Centropyxidae. Thecamoebians preserved in sediments noted by a circle, whereas thecamoebians preserved in amber are noted by a triangle. The basal part of the figure depicting ecology of the genera Centropyxis and Arcella through time has been modified in the light of this study and other published data. (a) Wolf, 1995; (b) Kumar et al., 2011; (c) Farooqui et al., 2014; (d) Wightmann et al., 1994; (e) Medioli et al., 1990a; (f) Schönborn et al., 1999; (g) Poinar et al., 1993; (h) Schmidt et al., 2004; (j) Waggoner, 1996b; (k) Porter and Knoll, 2000 and (*) denotes this study. The geological time axis is not to scale. The figure has been modified after van Hengstum et al. 2007 (with written permission from the original author van Hengstum).

doi:10.1371/journal.pone.0135593.g003
Stratigraphically, both the Zewan and Khunmuh Formations have been further sub-divided into members and units, respectively, based on lithological and paleontological characteristics. The Zewan Formation is divided into four Members (A-D) (Fig 2). Carbonate rocks and sandy shale comprise Member A, Member B is shale with low carbonate content, Member C is thick bedded sandy limestone, sandy shale and muddy sandstone, and Member D is calcareous muddy sandstone. Only Members A, C and D are rich in marine fossils. An abrupt change in sedimentation to intercalated grey to black limestone and black shale demarcates the onset of the Khunamuh Formation. This Formation is divided in to six members E-J (Fig 2), with the lower units in Member E marking the PT Boundary Event. Member E is sub-divided into Units E1, E2 and E3. The Unit E1 contains mixed faunal elements of Late Permian and Early Triassic age. The PT Boundary has been placed at the base of the conodont *Hindeodus parvus* zone at the contact of E1 and E2 (Fig 2).

Pioneering faunal work at the Guryul Ravine PTB Section was carried out by [28], who identified four faunal divisions: I to III in the Zewan Formation (Late Permian) and IV in the Unit E1 of the Khunamuh Formation (Early Triassic) (Fig 2). The faunal divisions I and II correspond to the units A and B, respectively, and contain bryozoans, brachiopods and foraminifers. The faunal diversity of division II is less than that of division I. The faunal division III is

![Image](https://example.com/image.png)
displayed by the litho units C and D and shows the dominance of gastropods and bivalves over brachiopods. The faunal division IV is displayed by bivalves and ammonoids. Brachiopods, bivalves and conodonts have also been recovered from this faunal division, which provide chronological control for the section (Fig 2).

Material and Methods

This study is a part of Birbal Sahni Institute of Palaeobotany (BSIP) Project Number 2.3 entitled "Mega- and microfloristics of the Permo-Carboniferous sediments of Kashmir region: Evolutionary, biostratigraphical, palaeoecological and palaeophytogeographical implications" under Thrust Area 2—"Phanerozoic Terrestrial and Coastal Ecosystems: Biostratigraphical, Palaeoenvironmental, Palaeoecological And Palaeobiogeographical Aspects". All necessary permits were obtained from the Director, BSIP for the field visit and the described study, which comply with all relevant regulations.

A total of nine bulk sediment samples (GR1 to GR9) were collected from C and D members of Zewan Formation and E Member of Khunamuh Formation (Fig 2), which were processed-following the palynological procedure used by Kumar et al, [66]. Samples were first treated with 30% hydrochloric acid followed by wet sieving on a 20 μm-mesh to concentrate microfossils, with the recovered residue mounted on slides with canada balsam. Prepared slides were then studied under a high power light Microscope Leitz Laborlux D to study morphological features of the recovered thecamoebian tests.

The absolute abundance of the number of recovered forms of different species has also been studied (Fig 5). Morphological data of all the examined individuals has been given in tabular form. (Table 1). The slides are deposited in the repository of the Birbal Sahni Institute of Palaeobotany, Lucknow (www.bsip.res.in/Museum.html) vide museum statement no. 1354. The museum accession numbers of the slides are 14869, 14971–14976 and 14881. Existing
taxonomic guides from Medioli et al. [78–80], Smirnov et al. [81] and Ogden and Hedley [82] were followed for thecamoebian identification.

### Results and Systematics

A total of 24 thecamoebians were recovered from the Guryul Ravine Section, most of which can be confidently assigned to the modern genera *Centropyxis*, *Arcella*, *Cucurbitella*, and *Cyclopyxis*. From the Zewan Formation in the Late Permian (C Member, Sample GR-2 on Fig 2), *Centropyxis aculeata*, *C. aculeata var. spinosa* and *Centropyxis aculeata var. discoides* were recovered. The *Centropyxis aculeata* tests preserved in the Member C show very less Brown Degraded Organic Matter (BDOM). In the Early Triassic Khunamuh Formation, thecamoebians were recovered from Member E in the Units E2 (Sample GR-8) and E3 (Sample GR-9). In E2, *Centropyxis aculeata*, *Centropyxis aculeata var. spinosa*, *Centropyxis aculeata var. discoides*, forms belonging to *Centropyxis constricta*-complex, *Centropyxis Stein 1857*, *Centropyxis platystoma*, *Cucurbitella tricuspis*, *Cyclopyxis eurystoma* and an unidentified individual from Unit E2. *Arcella* and centropyxids were recovered from the Unit E3 Unit of the Khunamuh Formation. The thecamoebian forms preserved in the Unit E2 and E3 show fairly large amount of BDOM. Similarly, our sedimentary dispersed organic matter study of the GR section shows very low BDOM content in the Member C as compared to the Units E2 and E3 having

### Table 1. A list of examined thecamoebian forms and their morphological details. The morphological features (hypostome shape and dimensions, number of visible spines) have been subjected to post-depositional compression and compaction and are thus incomparable to the recent forms. All the morphometric measurements are in μm.

| Examined Specimen (Position in the Figs) | Shell Length | Maximum Shell width | Pseudostome length of long axis, short axis | Spines |
|----------------------------------------|--------------|---------------------|-------------------------------------------|--------|
| 1. *Centropyxis aculeata var. spinosa* (7 A) | 90           | 90                  | 33                                        | 4 visible |
| 2. *C. aculeata var. discoides* (7 J,K,L) | 104          | 100                 | 44,33                                     | 3 visible: 1 complete, 2 broken |
| 3. *C. aculeata var. spinosa* (7 E) | 120          | 102                 | 37                                        | 4 visible: 1 complete, 1 broken |
| 4. *C. aculeata var. spinosa* (8 A,B) | 117          | 120                 | 50,29                                     | 3 visible: 1 not clear |
| 5. *C. aculeata var. spinosa* (7 B,C) | 90           | 85                  | 36,30                                     | 3 visible |
| 6. *C. aculeata var. Spinosa* (7 D) | 140          | 147                 | 64,50                                     | 9–10 visible |
| 7. *C. aculeata var. Spinosa* (7 F) | 130          | 120                 | 45,32                                     | 4 visible |
| 8. *Cucurbitella tricuspis* (6 C) | 56           | 56                  | 19                                        | Absent |
| 9. *C. aerophila* (6 E,F) | 60           | 60                  | 25,20                                     | Absent |
| 10. *C. aerophila* (6 G) | 55           | 50                  | 22,13                                     | Absent |
| 11. *Centropyxis platystoma* (6 A,B) | 87           | 45                  | 30                                        | Absent |
| 12. *Centropyxis aculeata* (8 C,D) | 114          | 114                 | 53,21                                     | 3 broken |
| 13. *C. aculeata* (8 G,H) | 85           | 85                  | 26,19                                     | 4–5: Not clearly visible |
| 14. *C. aculeata* (8 E,F) | 120          | 109                 | 40,30                                     | 4–5: |
| 15. *C. aculeata* (8 I,J) | 96           | 90                  | 38,23                                     | 5 |
| 16. *C. aculeata* (8 K,L) | 138          | 98                  | 47,50                                     | 4 |
| 17. *C. aculeata var. discoides* (7 G,H) | 112          | 109                 | 40                                        | 1 visible |
| 18. *C. aculeata var. discoides* (7 I) | 111          | 120                 | 46                                        | 1 broken |
| 20. *Cyclopyxis eurystoma* (6 H,I) | 37           | 37                  | 19                                        | Not clearly visible |
| 21. *Centropyxis Stein, 1857* (6 D) | 61           | 53                  | 27,21                                     | 1 broken |
| 22. *Centropyxis sp.* | 54           | 54                  | 20,14                                     | Absent |
| 23. *Arcella* (6 J) | 80           | 80                  | 16                                        | Pores are visible around the aperture |
| 24. Unidentified | 37           | 37                  | 2 apertures diameter 15, 20 |

doi:10.1371/journal.pone.0135593.t001
relatively high BDOM [36]. In the Early Triassic Khunamuh Formation, occurrence of thecamoebians in the Unit E3 is relatively low in comparison to the Member C and Unit E2. One form that appears to have two apertures remains unidentified (incertae sedis) (Fig 6K and 6L), which may or may not be an artifact of taphonomic processes. The recovered thecamoebians can be organized into the following systematics:

- **Phylum Amoebozoa** [83]
- **Subphylum Lobosa** [84,85]
- **Class Tubulinea** [86,87]
- **Order Arcellinida** [88]

**Family Arcellidae** [89]
- **Genus Arcella** [89] (Fig 6J)

**Family Centropyxidae** [90]
- **Genus Centropyxis** [91]
  - **Centropyxis** [91] (Fig 6D)
  - **Centropyxis aculeata** [92] (Fig 7C–7L)
  - **Centropyxis aerophila-complex** [93] (Fig 6E–6G)
  - **Centropyxis aculeata var. discoides** [94] (Fig 8G–8L)
  - **Centropyxis aculeata var. spinosa** (Fig 8A–8F; Fig 7A and 7B)

**Family Hyalospheniidae** [95]
- **Genus Cucurbitella**, [96]
  - **Cucurbitella tricuspis** [97] (Fig 6C)

**Family Trigonopyxidae** [98]
- **Genus Cyclopyxis**
  - **Cyclopyxis eurystoma** [98] (Fig 6H and 6I)

**Discussion**

Despite the overall low recovery of fossil thecamoebians from the Guryul Ravine Section, their recovery at such a critical environmental transition has significant taxonomic and ecological implications. Many of the preserved individuals are intact organic linings as a result of the palynological preparation procedures, and like individuals preserved in Mesozoic amber, allows for an examination of the autogenous (or secreted) mucopolysaccharide test structure. In contrast, other fossil thecamoebians that are typically sieved from bulk sediments, preferentially congregate individuals with agglutinated (or xenogenous) test and damaging many of the organic structures. Structures like inner shell lining, apertural bridges, and also test ornamentation (i.e., spines on the fundus) are all evidenced in the collection from the Guryul Ravine Section (Figs 6–8). In addition, pores around the periphery of the aperture in the autogenous test of Arcella are not commonly preserved in fossil Paleozoic thecamoebians. However, they have been documented in Permian examples by Kumar et al. [66] and Farooqui et al. [68] (Fig 6I). Such test characteristics are easily observed in the modern thecamoebian lineages and yet rarely observed in fossil examples.

The most significant result of this study is providing direct evidence that very common thecamoebian genera successfully crossed the PT Boundary (e.g., Centropyxis and Arcella). Previously, this could be inferred based on their preservation in both Late Paleozoic and Mesozoic amber deposits, but the Guryul Ravine Section provides individuals on other side of the
Fig 6. A,B. *Centropyxis platystoma* (Penard, 1890) Elongated shell, apertural view, 3- shows inner lining of the test, slide no. 14974. C. *Cucurbitella tricuspis* (Y53/4), slide no.14974. D. *Centropyxis* Stein, 1857, (Q40/3), test agglutinated and small in size, slide no.14881. E-G. *Centropyxis aerophila*-complex Foissner and Korganova, 2000 (E,F: S11/4; 7: E35/4), E,F- apertural and dorsal view, respectively, G- apertural view, slide nos. (E,F) 14976, (G) 14973. H,I. *Cyclopyxis eurystoma* (Deflandre, 1929) (R15/3) H-Ventral view and I-dorsal view, test is small in size, slide no. 14976. J. *Arcella* Ehrenberg, 1832 (T63/4), slide no.14971. K,L. Incertae sedis (U18/2), test shows two apertures, K-aperture one, L- aperture two, test small in size, slide no. 14976.

doi:10.1371/journal.pone.0135593.g006
boundary at the same paleogeographic locale. These observations attest to the resiliency of the thecamoebian group to global climatic events through the Phanerozoic.

An important omission in this collection is the lack of *Difflugia* preserved in the Guryul Ravine Section. Many specimens comprise the genus *Difflugia*, which are abundant in late Holocene freshwater environments. It is possible that taphonomic issues prevented their preservation, but this seems unlikely given the preservation of more fragile autogenous *Arcella* tests. In other fossil thecamoebian collections that have been sieved out of bulk sedimentary samples, individuals of *Difflugia* have been more common than *Centropyxis* [46]. It is possible that this generic bias is related to sample processing techniques (sieving vs. chemical palynological processing).

In general, there are very few studies on thecamoebians from deep-time sequences. The earliest record of thecamoebians is likely from Neoproterozoic marine sediments of Chuar group, Grand Canyon, which were originally described as Vase Shaped Microfossils (VSM’s) [65]. Since modern thecamoebians are not found in marine settings, this perhaps suggests a marine origin for the group with their ecological shift to lacustrine or brackish environments in the Early to Middle Paleozoic. During the Carboniferous when land plants greatly diversified and formed widespread swamp depositional environments, thecamoebians were preserved in the resultant organic-rich coal deposits now presently located in Nova Scotia, Canada [99, 69, 56]. The recovered fossil thecamoebians from the PT Boundary at the Guryul Ravine Section can be interpreted in one of two ways. The thecamoebians were transported to the locality along with other terrigenous material from the adjacent coastal zone, or perhaps they represent an in situ or primary assemblage. The implications of the later interpretation would be that some members of the thecamoebian group also occupied marine habitats in some capacity through the entirety of the Paleozoic. For example, the two Late Permian occurrences of *Centropyxis*, one from the fresh water sediments of the Raniganj Formation, Godavari Graben [68] and the other from the marine sediments of Zewan Formation (this study) suggest that the genus occupied both fresh water as well as marine environments during this time. Similarly, the genus *Arcella* has been reported from Carboniferous freshwater coals [56] and from the Late Permian sediments of Raniganj Formation at Lingala-Koyagudam coal belt, Godavari graben [68], whereas this study presents the occurrence of *Arcella* from the marine Early Triassic Unit E3. If indeed thecamoebians occupied marine environments throughout the Paleozoic, however, it remains puzzling why more occurrences of marine thecamoebians have not been reported in the global palynological surveys of Paleozoic marine sediments. Therefore, it remains important to continue documenting fossil thecamoebians to accurately resolve their Paleozoic paleoecological tolerance to salinity and evolutionary history.

Another important observation based on this PT Boundary collection is the variability in the absolute number of spines ornamented onto the tests in the species *Centropyxis*. The taxonomy of these species remains complex, in part because of the intragradational character in the external morphology of many thecamoebian species [100,101]. Some authors consider dividing this genus into species based on the absolute number of spines ornamenting the test or their geometric orientation [102,103]. Most thecamoebian workers agree with the notion of considerable phentotypic plasticity in the *Centropyxis* genus, and recognize that the most important variability for paleoecologic work is taxonomic consistency. Here, the recovered centropyxids...
are also phenotypically diverse, with multiple numbers of spines that we divide into morphotypes, or variants, based on the absolute number of spines. For example, the diagnosis of *Centropyxis aculeata var. spinosa* Ehrenberg, 1832 (Q31/4), apertural view, slide no. 14974. B. *Centropyxis aculeata var. spinosa* Ehrenberg, 1832 (E41/3), B-dorsal view showing spines, xenosomes on the test, C. ventral/apertural view, slide no. 14869. D. *Centropyxis aculeata var. spinosa* Ehrenberg, 1832 (T40/3), apertural view showing 9–10 spines at the margin, degraded brown organic matter and detrital grains on the agglutinated test, slide no. 14975. E. *Centropyxis aculeata var. spinosa* Ehrenberg, 1832 (U21/3), apertural view, dark coloured test with three spines, slide no. 14976. F. *Centropyxis aculeata var. spinosa* Ehrenberg, 1832 (H18/4), apertural view, test light coloured agglutinated formed by material from the surrounding, slide no. 14973. G. H. *Centropyxis aculeata var. discoides* Penard, 1902 (P29/2), test constituted of both autosomes and xenosomes, slide no. 14974. I. *Centropyxis aculeata var. discoides* Penard, 1902 (K34/1), slide no. 14976. J-L *Centropyxis aculeata var. discoides* Ehrenberg, 1832 (H30/4), apertural view, J, image is focussed on the margin of the test showing two broken spines, K- aperture focused, L- Margin focused showing a complete spine, slide no. 14976.

doi:10.1371/journal.pone.0135593.g008

The conclusions

Conclusions

This study documents exceptionally well-preserved thecamoebians across the PT Boundary event from the Guryul Ravine Section in Kashmir, India. The site was paleogeographically situated at the northern margin of Gondwana, and the recovered thecamoebians are from the Late Permian Zewan and the Early Triassic Khunamuh Formations. The Guryul Ravine Section is an archetypal PT Boundary sequence, and the thecamoebians provide an additional faunal signature to the previously documented foraminifera, brachiopods, bivalves, ammonoids and conodonts. The recovery and preservation of the thecamoebians from the Guryul Ravine Section is not only new to this section but for any PTB section worldwide. The preservation of these fragile microfossils was likely enhanced by punctuated local or regional anoxic/dysoxic conditions, which are evinced by the presence of amorphous organic matter in this section [36]. Even the intraspecific variability within the *Centropyxis* genera could be observed in the recovered individuals. Thecamoebians have a poorly resolved fossil record, but the results presented here confidently indicate that some of the most common modern thecamoebian genera successfully transitioned across the PT Boundary extinction event with apparently little ecological challenge.

Supporting Information

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Acknowledgments

We thank Professor Sunil Bajpai, Director of the Birbal Sahni Institute of Palaeobotany in Lucknow for providing necessary facilities to carry out the research, discussions with Alexey Smirnov on taxonomy, and to the anonymous reviewers for providing constructive suggestions. This is BSIP contribution no. 66/2013-14.
Author Contributions
Conceived and designed the experiments: VS RT. Performed the experiments: VS. Analyzed the data: VS RT PJVH. Contributed reagents/materials/analysis tools: RT VS SKP SSKP DA KK GDB. Wrote the paper: VS RT PJVH SKP.

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