



PALEONTOLOGY

Faunipollenites Bharadwaj 1962 and Protohaploxylinus Samoiloich 1953 emend. Morbey 1975: morphologic comparison of oxidized and non-oxidized specimens from India and Brazil, and its taxonomic importance

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Abstract: *Faunipollenites* Bharadwaj is considered a junior synonym of *Protohaploxylinus* Samoiloich emend. Morbey. However, Indian workers claim it is a valid genus due to a poorly defined corpus and absence of folds in distal attachment. In India, a standard method is applied including the oxidization with HNO_3 more than 48 hours (+10' of KOH). We analyze the effects of that treatment on the morphology of pollen grains of both genera in samples from the Permian of India and Brazil. The same samples are also processed with HCl, HF, two hours of HNO_3 and 2' of KOH and slides are mounted after each step. Our analysis reveals that distinct or indistinct central body and presence/absence of folds in distal attachment do not change in contrast to the indistinct central body and mostly absence of folds from samples that underwent a longer period of oxidization (24-48 hours and KOH 10'). The synonymization of *Faunipollenites* to *Protohaploxylinus* is confirmed. Species of *Faunipollenites* are reassigned to the revised species of *Protohaploxylinus*. The usage of the latter genus and its species in Permian biostratigraphic studies of India will improve Gondwanan correlations and paleobiogeographic reconstructions in future studies.

Key words: *Faunipollenites*, India, morphology, Permian, *Protohaploxylinus*, taxonomy.

INTRODUCTION

Faunipollenites was erected by Bharadwaj (1962) to include haploxylinoid striate bisaccate pollen grains bearing a central body with an ill defined outline and infrareticulate cappa, recovered from the sediments of the Permian Raniganj Formation of the East Raniganj Coalfield, Damodar Basin India (Fig. 1a). Its usage was questioned or rejected by many researchers (e.g. Hart 1964, Balme 1970, Foster 1979), except for Indian workers that are still using it. On the other hand, *Protohaploxylinus* defined by Samoiloich 1953 was widely discussed by several authors

especially Hart (1964), who formally emended it to exclude non taeniate pollen grains. Balme (1970) proposed the combination of the type species *Faunipollenites varius* Bharadwaj 1962 to *Protohaploxylinus* and discarded Hart's (1964) taxonomic proposal because of the morphological overlapping mainly created with *Lunatisporites* Leschik emend. Mädlar that also displayed a haploxylinoid to slightly diploxylinoid with three-five taeniae. Hence, Morbey (1975) proposed a new emendation of *Protohaploxylinus* to exclude beyond the non taeniate, the taeniate pollen grains with less

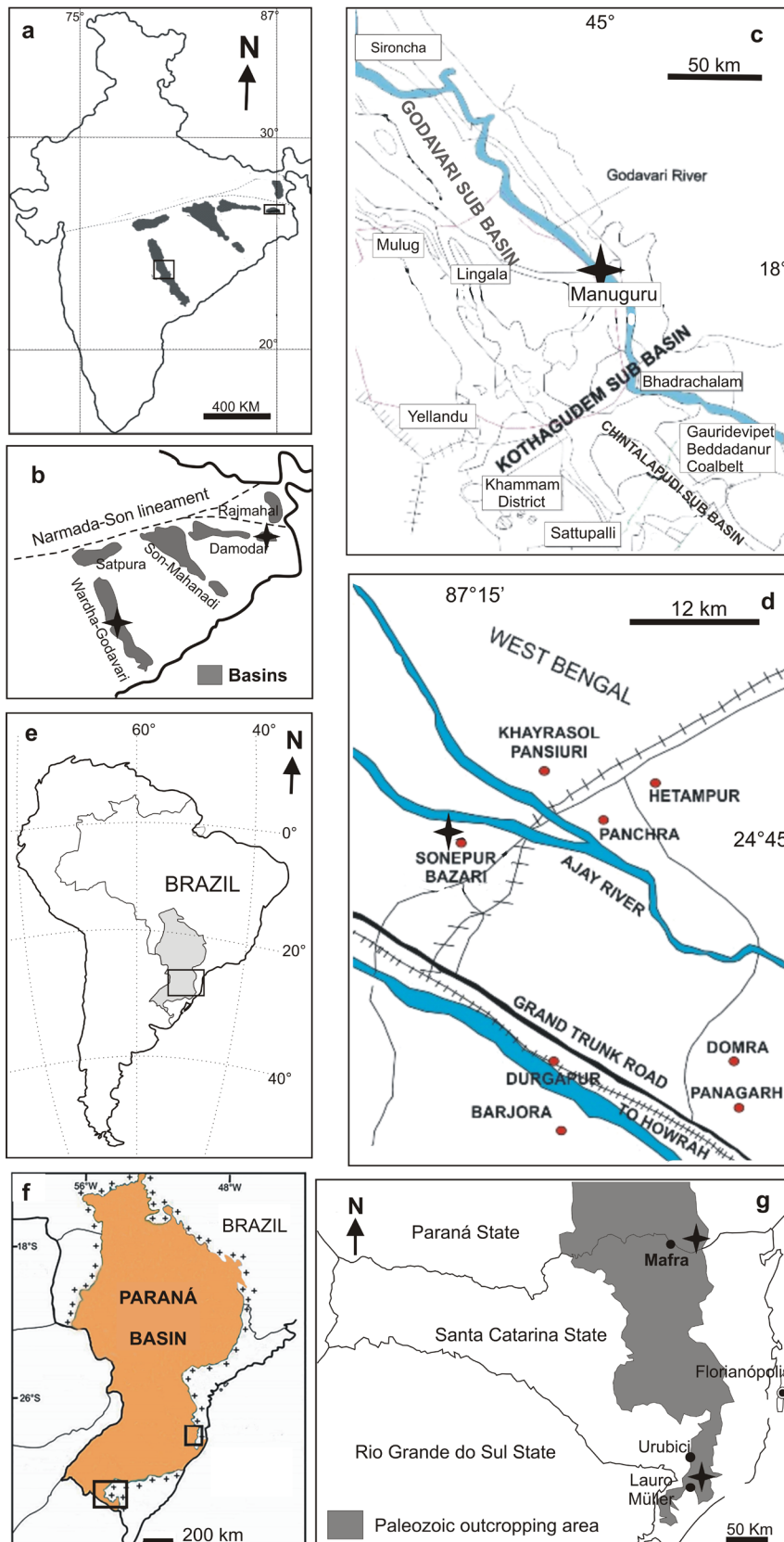


Figure 1. a. Map showing the geographic position of Permian basins in India. b. Precedence of the samples from the Barakar Formation (Damodar) and the Raniganj Formation (Godavari). c-d. Detailed maps of the Manuguru (Kavali & Jha 2014) and Sonepur areas (Jasper et al. 2012). e. Geographic distribution of the Paraná Basin in South America. f-g. Precedence of the samples from the early Permian of Río Bonito Formation (unpublished work) close to Mafra city in southern Paraná State, and from the Guadalupian Serra Alta and lower Río de Rastro formations at Lauro Müller and Urucibi areas of Santa Catarina State (di Pasquo et al. 2018).

than three taeniae in the cappa (*Lunatisporites*, *Lueckisporites*). He provided synonymy lists for the genus and several of its species. This amendment was followed by many researchers (e.g. Foster 1975, 1979, MacRae 1988, Utting 1994, Stephenson 2015) and among them, Foster (1979) discussed the status of many species and provided long lists of synonyms. He discussed the morphological status of the type species *Protohaploxypinus latissimus* (Luber in Luber & Waltz) Samoilovich 1953 although he did not find it in Australia. Instead, this species was described and illustrated by MacRae (1988, Pl. 25, figs. 13, 14) and Utting (1994, Pl. 6, figs. 27-29), based on its original description (i.e. haploxytonoid to weakly diploxytonoid amb, general oval shape in polar view, central body circular to slightly

oval in transverse section, large saccus overlap resulting in a narrow cappula of less than 1/3 than the body width, ten taeniae entire and wedge shape). Foster (1979) also discussed the taxonomic status of *Faunipollenites* and tentatively assigned it as a junior synonym of *Protohaploxypinus* Samoilovich 1953 emend. Morbey 1975. Indian workers (Venkatachala & Kar 1968, Sinha 1972, Tiwari 1974), and especially Tiwari et al. (1989), who treated *Faunipollenites* in detail, strongly rejected the taxonomic changes proposed for this genus and its type species, on the grounds of an ill defined central body outline. As this taxonomic controversy still requires a clarification, specimens attributed to *Faunipollenites* in palynological material from the Permian of India (Fig. 1a-d)

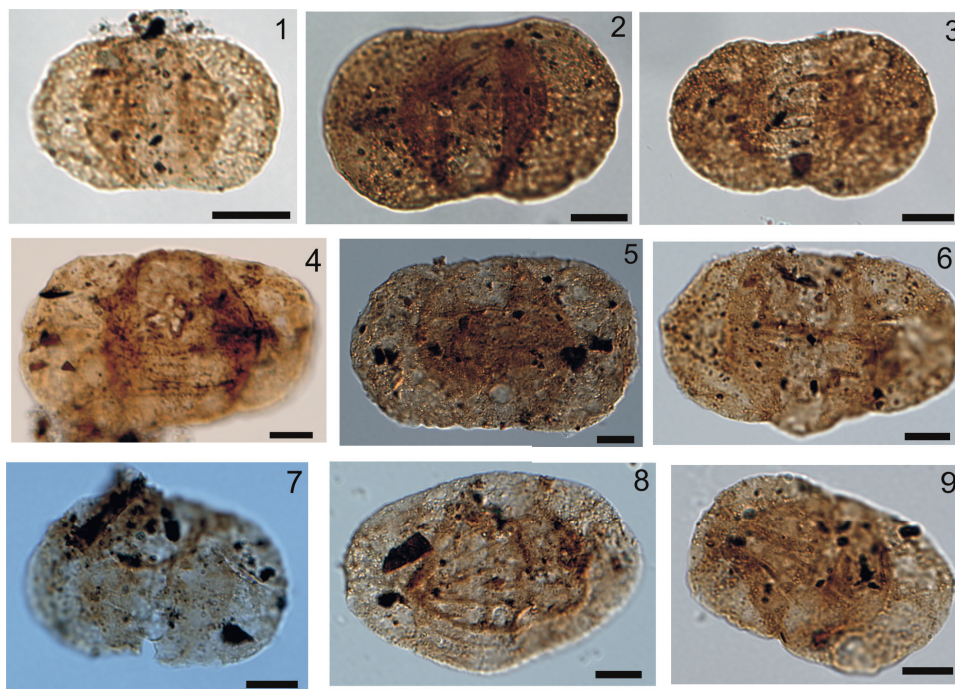


Figure 2. Species after HCl treatment. Scale bar= 20 μ m in Figs. 1-3 and in the remaining is 10 μ m.

1. *Protohaploxypinus limpidus*. UERJ No. DEPA 17122, England Finder (EF)- C.20.3.
2. *Protohaploxypinus hartii*. UERJ No. DEPA 17122, EF- R.35.
- 3, 5. *Protohaploxypinus perfectus*. 3. UERJ No. DEPA 17122, EF- C.20.3; 5. UERJ No. DEPA 17124, EF- H.22.3.
4. *Protohaploxypinus samoilovichii*. UERJ No. DEPA 17124, EF- K.42.2.
6. *Protohaploxypinus latissimus*. UERJ No. DEPA 17124, EF- O.42.1.
- 7, 9. *Protohaploxypinus pennatulus*. 7. UERJ No. DEPA17124, EF- H.20; 9. UERJ No. DEPA 17124, EF-L.34.2.
8. Specimen attributable to *Protohaploxypinus limpidus* or *Illinites unicus*. UERJ No. DEPA 17124, EF- O.22.3.

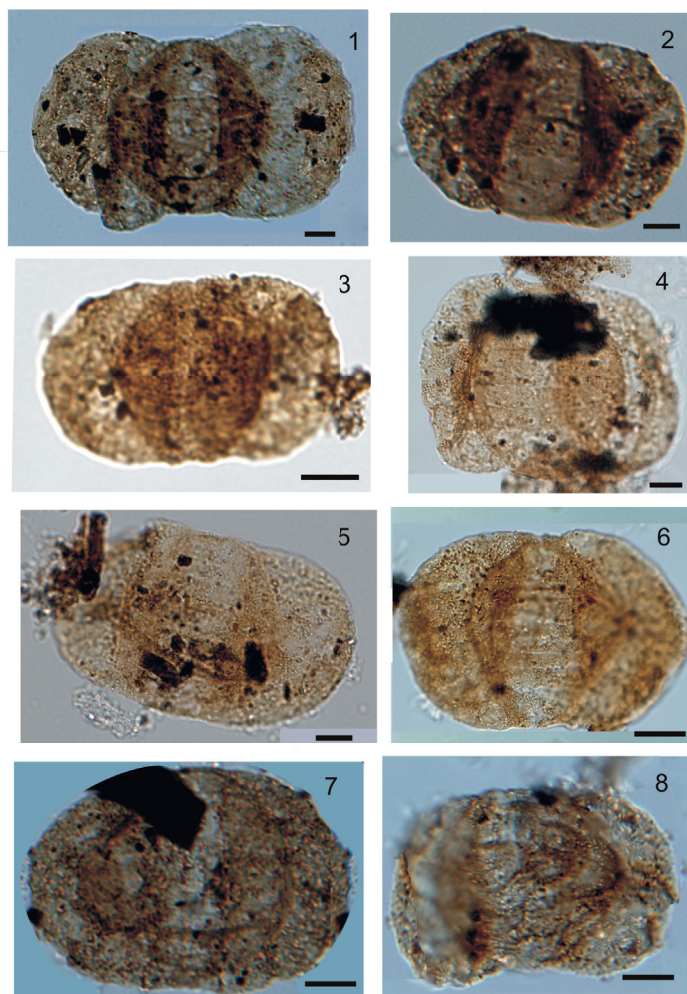


Figure 3. Specimens after HCl and HF treatment. Scale bar= 15 µm.
1. *Protohaploxyipinus samoilovichii*. UERJ No. DEPA 17126, EF- M.36.3.
2. *Protohaploxyipinus hartii*. UERJ No. DEPA 17127, EF-S.41.4.
3. *Protohaploxyipinus pennatulus*. UERJ No. DEPA 17128, EF-H.30.
4. *Protohaploxyipinus perexiguus*. IGc No. GP/4T-332, EF- D.38.1.
5. *Protohaploxyipinus limpidus*. IGc No. GP/4T-332, EF- E.17.3.
6. *Protohaploxyipinus microcorpus*. IGc No. GP/4T-332, EF- B.34.4.
7, 8. *Protohaploxyipinus perfectus*. **7.** UERJ No. DEPA 17127, EF- H.50.3; **8.** UERJ No. DEPA 17125, EF- C.20.3.

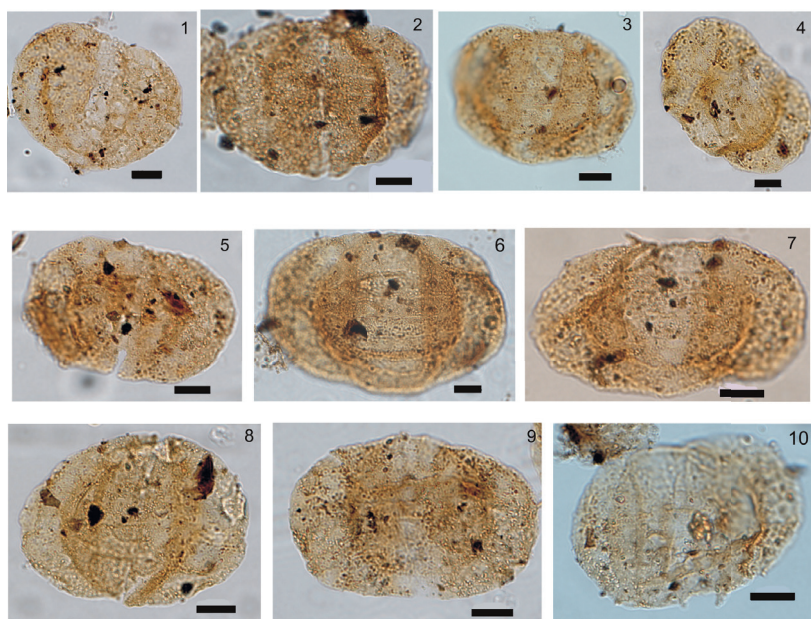


Figure 4. Specimens after the treatment with HCl and HF and HNO₃ (2 hours, KOH 2'). Scale bar= 10 µm.
1, 2. *Protohaploxyipinus pennatulus*. **1.** IGc No. GP/4T, EF- O.33.1; **2.** IGc No. GP/4T, EF-O.33.1; **5 4.** IGc No. GP/4T, EF- P.32.3.
3. *Protohaploxyipinus limpidus*. IGc No. GP/4T, EF- T.33.3.
6, 7. *Protohaploxyipinus perfectus*. **6.** IGc No. GP/4T, EF- M.26.1; **7.** IGc No. GP/4T, EF-M.26.1.
4. *Protohaploxyipinus hartii*. IGc No. GP/4T, EF- K.32.4.
8. *Protohaploxyipinus perexiguus*. IGc No. GP/4T, EF- M.35.
9, 10. *Protohaploxyipinus latissimus*. **9.** IGc No. GP/4T, EF- N.35; **10.** IGc No. GP/4T, EF-Q.31.4.

and *Protohaploxylinus* in Brazil (Fig. 1e-g) are examined and compared using optical light microscope (Figs. 2-6), confocal laser scanning (Fig. 7) and Scanning electron (Fig. 8). This analysis aims to assess the taxonomic status of *Faunipollenites* to confirm its synonymization with *Protohaploxylinus*. Their presence in Permian assemblages of Gondwana and elsewhere will enhance future biostratigraphic correlations and paleobiogeographic reconstructions.

MATERIALS AND METHODS

Procedence of samples

The studied specimens were recorded from the Damodar and Godavari basins in India (Fig. 1a-d) and compared to the material from the Permian of Paraná Basin in Brazil (Fig. 1e-g). The former palynological materials come from the Godavari Basin, obtained from the subsurface levels of the Barakar Formation (early Permian) of Borehole 1007 in Manuguru area (Fig. 1c, further details in Kavali & Jha 2014), and from the Damodar Basin, obtained from the Lopingian shale (Raniganj Formation) above Seam VI in Sonapur Bazari area of Raniganj Coalfield, near Asansol (Fig. 1d, further information in Jasper et al. 2012). Palynological materials from Brazil were obtained from surface samples of the Paraná Basin at two locations (Fig. 1e-g), one from early Permian of Rio Bonito Formation in southern Paraná State (unpublished) and the other from the Serra Alta and lower Rio de Rastro formations (Guadalupian) in Santa Catarina State (di Pasquo et al. 2018).

Laboratory procedures and repositories

Samples were processed applying HCL (10%, 4 hours) and HF (40%, 18 hours), washed with distilled water, sieved through a 10 µm mesh and slides prepared with +10 residues using Entellan

and cellosize products. The residues were divided in two sets and each one oxidized with HNO₃ (80%), one for two hours and the other 24-48 hours, KOH (10%) applied for 2 minutes and after sieving, last set of slides were mounted. These procedures were carried out at three laboratories where the samples (residues, slides, rocks) are housed: 1- India (Birbal Sahni Institute of Palaeosciences, acronym BSIP), 2- Brazil (Institute of Geosciences of the Universidade de São Paulo, acronym IGc, Universidade do Estado do Rio de Janeiro, acronym UERJ DEPA, Universidade Federal do Rio Grande do Sul, acronym MP-P), 3- Argentina (CICYTTP-CONICET-ER-UADER, acronym CICYTTP-PI). The slides were analyzed using light microscopes Olympus BX61 microscope with DP-25 digital camera using Cell A software in India, Zeiss Scope.A1 camera and software Zen 2.3 lite in Brazil and Nikon Eclipse E200 with a videocamera Labomed (5.0 Mp) in Argentina. England Finder coordinates are used for illustrated specimens. Confocal Laser Scanning Microscope (CLSM) images were obtained at BSIP in India and the CENPES Institute of PETROBRAS in Brazil. Scanning electron microscopy (SEM) images were obtained at BSIP and the Electronic Microscopy Centre of the Institute of Geosciences, Universidade de São Paulo, Brazil.

RESULTS

Morphological comparison of *Faunipollenites* and *Protohaploxylinus*

The effect of oxidation on main diagnostic features of well- preserved (not altered and complete) specimens attributed to *Faunipollenites* from India (Figs. 2-5) and *Protohaploxylinus* from Brazil (Fig. 6) are compared using light microscope, CLSM (Fig. 7) and SEM (Fig. 8). These features are: (i) saccus condition, (ii) central body, (iii) folds, (iv) striae/

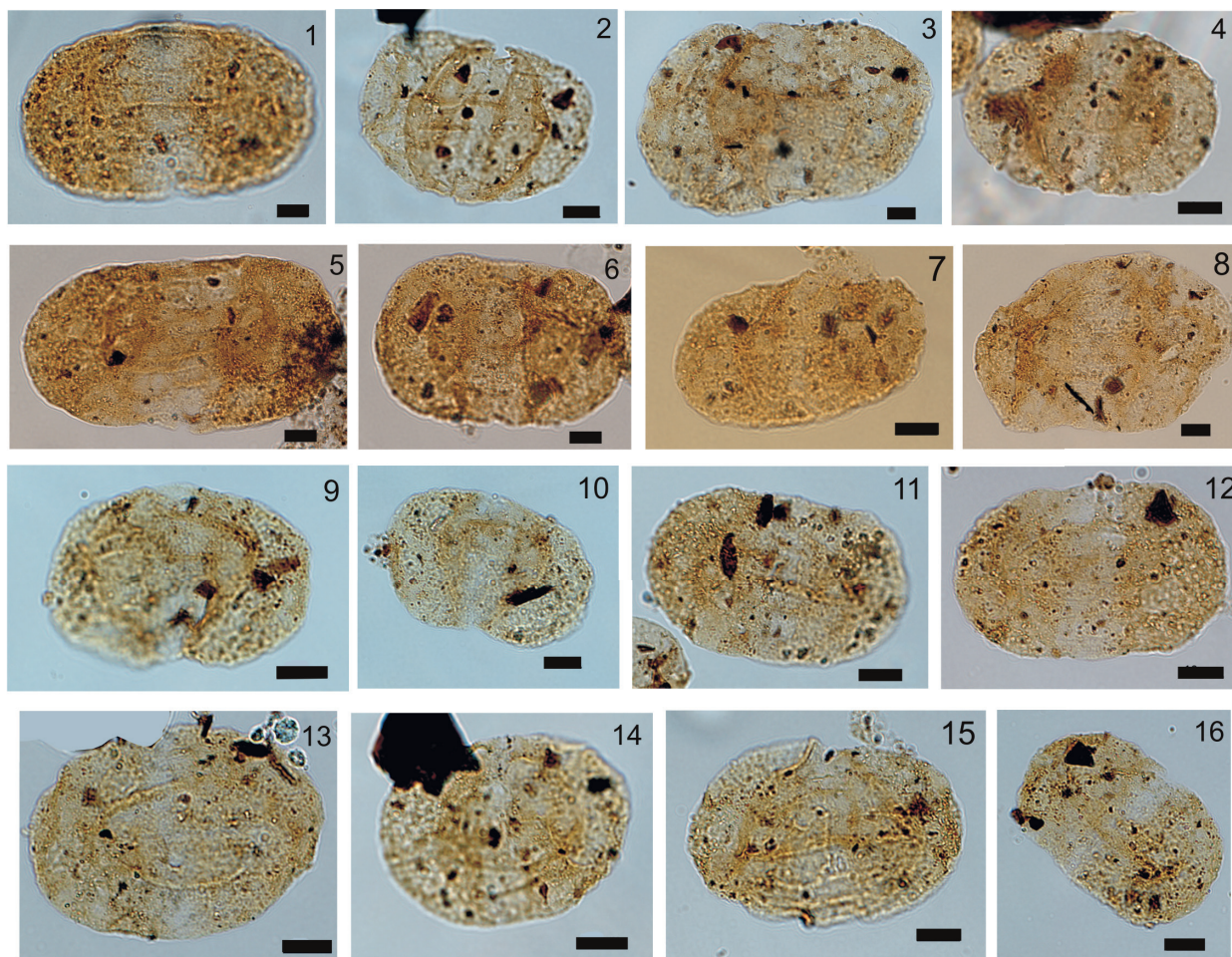


Figure 5. Specimens after the treatment with HCL and HF and HNO_3 (48 hours, KOH 15'). Scale bar= 10 μm .

- 1, 5. *Protohaploxypinus latissimus*. 1. IGc No. GP/4T-334, EF- H.28.1; 5. IGc No. EF- D.41.
 2, 4. *Protohaploxypinus hartii*. 2. IGc No. GP/4T-334, EF- B.21.1; 4. IGc No. GP/4T-334, EF- C.17.1.
 3. *Protohaploxypinus perfectus*. IGc No. GP/4T-334, EF- C.25.
 6. *Protohaploxypinus cf. hartii*. IGc No. GP/4T-334, EF- D.32.
 7, 8. *Protohaploxypinus* spp. (unable to identify the species due to disappearance of central body features). 7. IGc No. GP/4T-334, EF- D.23.2; 8. IGc No. GP/4T-334, EF- E.23.2.
 9, 10, 15. *Protohaploxypinus limpidus*. 9. IGc No. GP/4T-334, EF- E.26.2; 10. IGc. No. GP/4T-334, EF- E.26.2; 15. IGc No. GP/4T-334, EF- F.25.3.
 11, 12, 13. *Protohaploxypinus* spp. (unable to identify the species due to disappearance of central body features). 11. IGc No. GP/4T-334, EF- E.26.2; 12. IGc No. GP/4T-334, EF-E.9.3; 13. IGc No. GP/4T-334, EF- G.7.2.
 14. *Protohaploxypinus perexiguus*. IGc No. GP/4T-334, EF- E.28.
 16. *Protohaploxypinus cf. perfectus*. IGc No. GP/4T-334, EF- H.22.

taeniae, and (v) size of specimens. This analysis aims to solve taxonomic misconceptions and discrepancies between those two genera that resulted after the oxidation of samples using HNO_3 not less than 24-48 hours as a standard method in India (P. Kavali, pers. comm.).

Our results detailed below, revealed that most of the morphologic features in the specimens analyzed after each treatment with HCL and HF and after two hours of HNO_3 and 2' of KOH (Figs. 2-4) are maintained whereas morphological differences are noticed after the

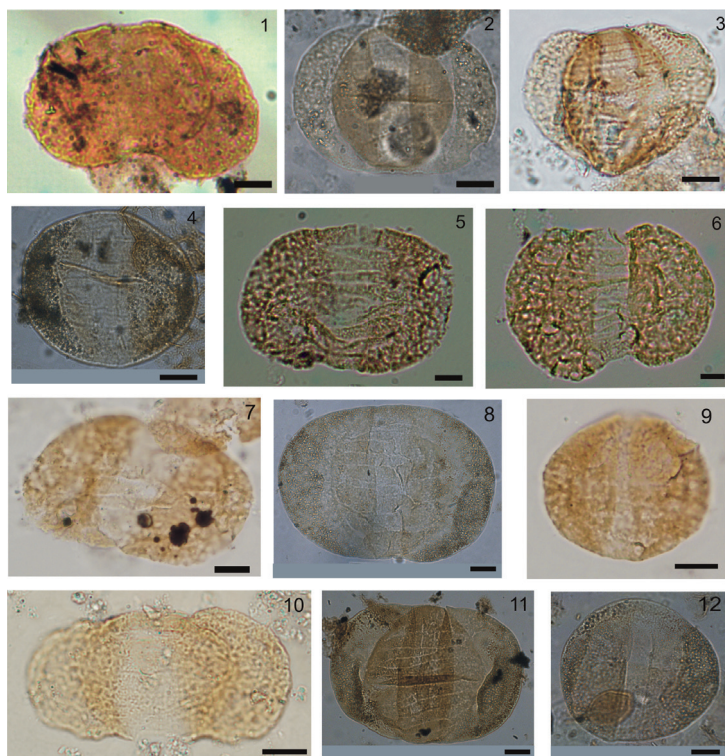


Figure 6. Specimens from Brazil after the treatment with HCl and HF. Scale bar= 15 μ m.
1, 8. *Protohaploxyipinus perfectus*. 1. CICYTTP-PI 588-8, EF- V.48; 8. DEPA 17026" EF- D.34.1.
2, 7. *Protohaploxyipinus limpidus*. 2. Slide "DEPA 17028", EF- Y.41.3. 7. CICYTTP-PI 587-4, EF- J.34.3.
3. *Protohaploxyipinus microcorpus*. CICYTTP-PI 587-4, EF- O.37.
4, 9, 12. *Protohaploxyipinus perexiguus*. 4. "DEPA 17028", EF- N.39.1; 9. CICYTTP-PI 587-4, EF- T.26.2; 12. "DEPA 17028", EF- S.45.2.
5, 6, 10. *Protohaploxyipinus latissimus*. 5. CICYTTP-PI 757-1, EF- D.27; 6. CICYTTP-PI 757-1, EF- H-25; 10. CICYTTP-PI 587-4, EF- V.37 (transitional to *P. haigii*).
11. *Protohaploxyipinus samoilovichi*. DEPA 17029", EF- G.32.3.

application of HNO_3 for 24-48 hours and 10-15' of KOH (Fig. 5).

(i). Saccus construction: Based on the original and emended diagnoses and descriptions, both *Protohaploxyipinus* (Samoilovich 1953 and Morbey 1975) and *Faunipollenites* (Bharadwaj 1962 and Tiwari et al. 1989) are characterized by haploxyylonoid to slightly diploxyylonoid saccus construction. This feature did not suffer distortions after different processes applied and confirms it is of generic importance.

(ii). Central body: In the original diagnosis of *Protohaploxyipinus* Samoilovich 1953, the different features of central body were not mentioned, whereas in the emended diagnosis stated by Morbey (1975, a distinct or not well defined circular to oval central body is described having transversal (= vertical, t-a) or longitudinal (l-a) elongation. These variations depended on the species recognized, and among them some are characterized by indistinct to diffused central

body (*P. latissimus*, *P. varius*, *P. diagonalis*), others possess a distinct central body (*P. amplus*, *P. limpidus*, *P. rugosus*, *P. samoilovichi*, *P. jacobii*, *P. harti*, *P. haigii*, *P. microcorpus*) and some others present transitional forms, from diffuse to well defined (*P. goraiensis*, *P. perexiguus*, *P. rugatus*). Thus, the nature of central body is of specific importance. In the emended diagnosis of *Faunipollenites*, Tiwari et al. (1989) distinguished *Faunipollenites* from *Protohaploxyipinus* because the central body is indistinct and the striations define the edge of the central body of the species of the Permian and Triassic of India. Contrarily, several species of *Faunipollenites* and specimens illustrated displayed distinct central bodies (e.g. Bharadwaj 1962, Pl. 17, Figs. 223, 224, 225 and Pl. 18, Figs. 230, 231, 233; Bharadwaj & Srivastava 1969, Pl. 26, Figs. 34, 35, 38; Tiwari et al. 1989, Pl. 26, Figs. 1, 2, 4, 5), including the type species of *Faunipollenites* (Bharadwaj 1962, Pl. 18, Fig. 230).

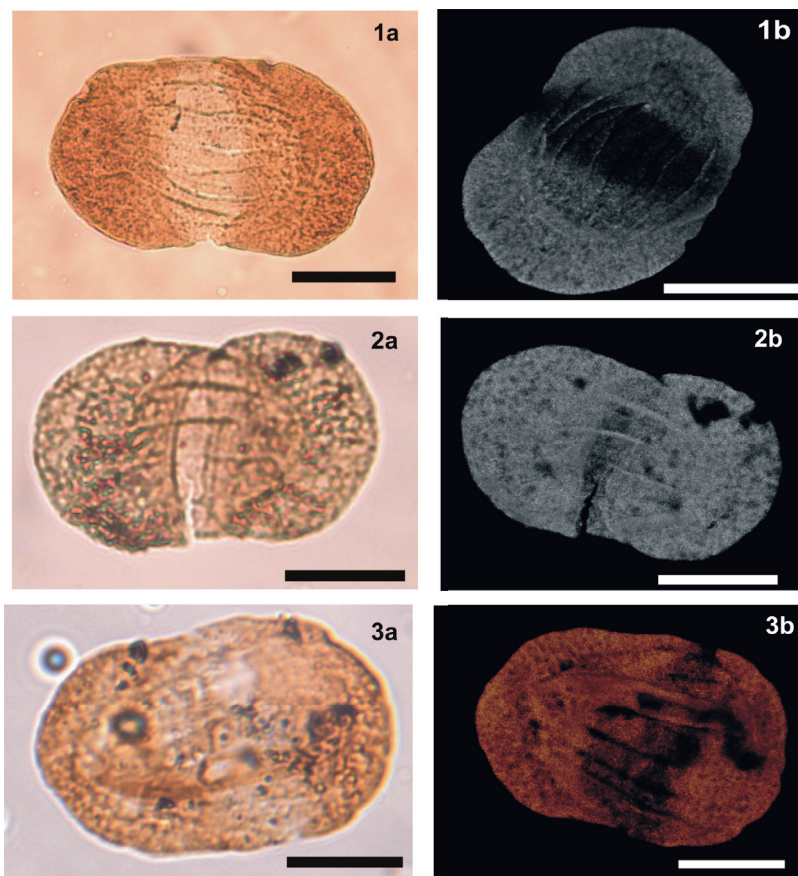


Figure 7. Specimens compared under OM and CLSM. Scale bar = 20 μm .

1a (OM) and 1b (CLSM).

Protohaploxypinus latissimus. BSIP Slide No.16354, E.58.2 showing indistinct central body after HF both under OM and CLSM.

2a and 2b. *Protohaploxypinus hartii*. BSIP Slide No. 16356, U.44 showing distinct central body under both OM and CLSM just after HNO_3 (2 hours, KOH 2').

3a and 3b. *Protohaploxypinus perfectus*. BSIP Slide No.16353, N.28 showing indistinct central body under OM after treatment with HNO_3 (48 hours, KOH 15'), and distinct central body under CLSM.

In our study almost all specimens analyzed from Brazil (*Protohaploxypinus*) and India (*Faunipollenites*) maintained their features of central body (amb, striation, cappula, folds) and sacchi (Figs. 2-4, 6-8) after each treatment with HCl, HF, and 2 hours of HNO_3 and 2' of KOH. Instead, attenuation or distortion of the features mainly concerning central body and folds occurred after a longer period of oxidation (more than 24-48 hours, Figs. 5 and 7). Therefore, we confirm that erroneous morphographic diagnoses and descriptions of species especially in India are likely due to their standard methodology. Therefore, the argument of indistinct central body and absence of folds claimed mainly by Tiwari et al. (1989) to maintain *Faunipollenites* separated from *Protohaploxypinus* is rejected herein. It is notice that specimens with transitional features between species of both

genera are observed in the studied samples irrespective the treatment applied.

(iii). Nature of cappula and folds associated to sacchi attachment on distal face:

The shape and width of the cappula are also important specific features of both genera equally developed depending on the nature and extent of saccus attachment to the central body (broad, narrow, convex, concave, straight). Folds are related to the attachment zones of sacchi and central body in the cappula. This feature is common in many striate/non-striate bisaccate and monosaccate pollen grains and it is mainly used to differentiate species except for *Cannanoropollis* and *Plicatipollenites* (see discussion in Azcuy & di Pasquo 2000 and references). The presence or absence of intexinal folds in *Protohaploxypinus* is not considered a generic feature (see Foster 1979). Some species

of *Protohaploxylinus* display very distinct zones of attachment (*P. limpidus*, *P. amplus*, *P. rugosus*, *P. hartii*, *P. hagaii*), others are devoid of distal folds (*P. varius*, *P. goraiensis*, *P. rugatus*, *P. diagonalis*), whereas some are characterized by occasional folds (*P. samoilovichi*, *P. microcorpus*, *P. jacobii*, *P. perexiguus*). In the diagnosis of *Faunipollenites*, Bharadwaj (1962) did not mention folds in the cb-sacci attachment used to maintain both genera separated (Tiwari et al. 1989).

As discussed above, specimens of both taxa bearing folds before the stronger oxidation process reveal poorly defined folds or their absence. Therefore, the variability of this feature at the generic level is prevented and must be maintained as part of the specific characters.

(iv). Striations: Striations in the original definition of *Protohaploxylinus* and *Faunipollenites* show overlapping in number and disposition (simple, forked, cuneiform). Morbey (1975) in his emended diagnosis of *Protohaploxylinus* stated a minimum number of five longitudinal taeniae or six striae to avoid the overlapping with the haploxylinoid *Lunatisporites* (3-4 taeniae separated by slightly wide striae) and the haplo-diploxylinoid *Lueckisporites* (two taeniae separated in the middle by a wider striae called *platea* by Vijaya 1992). The original diagnosis of *Faunipollenites* states 8-12 horizontal striations (Bharadwaj 1962) and the emended diagnosis states 6-20 (Tiwari et al. 1989). We observed that striations are slightly distorted after a longer period of oxidation, so this feature is not reliable to differentiate both genera. Hence, it is necessary to be careful to distinguished species when long oxidation processes are applied.

(v). Size: The size is an irrelevant feature to differentiate both genera (e.g. Lindström et al. 1997) because their type species *Protohaploxylinus latissimus* (major diameter of 83 µm) and *Faunipollenites varius* (MD 106

µm) are overlapped in their size ranges (i.e. 64 µm – 180 µm and 78-92 µm respectively). The size of specimens in general is increased in oxidized samples (see Smith & Butterworth 1967).

Systematic palaeontology

A critical morphological analysis of specimens from Permian assemblages of India and Brazil was carried out. Their comparison with species of *Protohaploxylinus* and *Faunipollenites* described and illustrated in selected literature of India and elsewhere allowed us to support that *Protohaploxylinus* is the senior genus of *Faunipollenites*. The species of *Faunipollenites* as well as some of *Protohaploxylinus* are synonymized with the convalidated species of *Protohaploxylinus* revised herein (Fig. 9, Table I). Species addressed in this section are listed in alphabetical order.

Faunipollenites

- F. bharadwajii* Maheshwari, 1967
- F. circumstriatus* Maheshwari, 1969
- F. congoensis* (Bose & Kar) Tiwari, Srivastava, Tripathi & Vijaya, 1989
- F. copiosus* Bharadwaj & Salujha, 1965
- F. enigmatus* Maheshwari, 1969
- F. gopadensis* Bharadwaj & Srivastava, 1969
- F. magnus* (Bose & Kar) Tiwari, Srivastava, Tripathi & Vijaya, 1989
- F. minor* Salujha, 1965
- F. multistriatus* Srivastava, 1979
- F. parvus* Tiwari, 1965
- F. singrauliensis* Sinha, 1972

Protohaploxylinus

- P. amplus* (Balme & Hennelly) Hart, 1964
- P. bhardwajii* Foster, 1979
- P. chaloneriei* Clarke, 1965
- P. goraiensis* (Potonié & Lele) Hart, 1964
- P. hartii* Foster, 1979

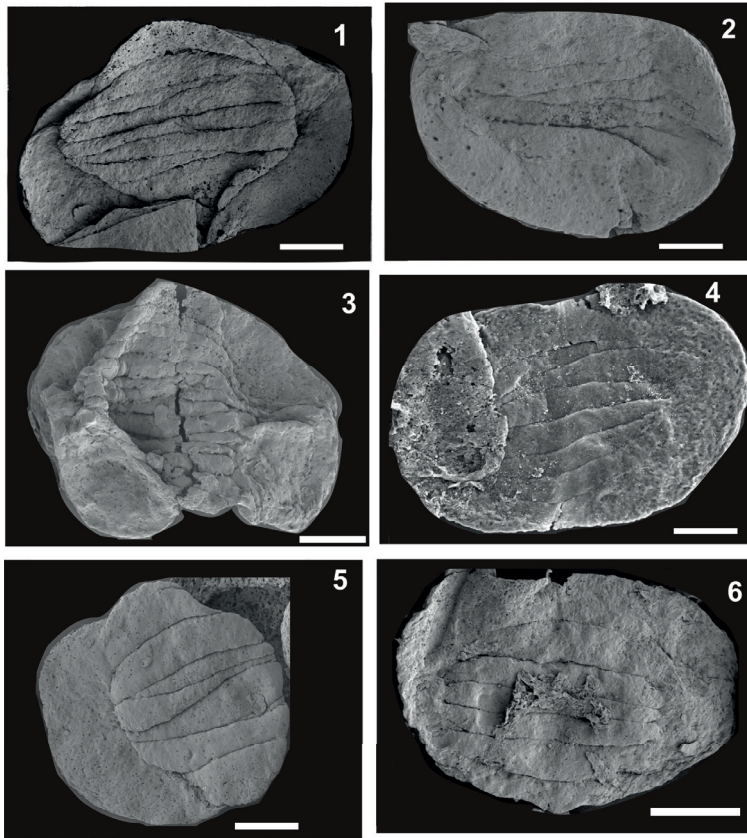


Figure 8. SEM images of *Protohaploxypinus* species with distinct central body (1-3) and indistinct central body (4-6) after HCl and HF and two hours of HNO₃ (+ KOH 2').

1. *Protohaploxypinus perfectus*.
2. *Protohaploxypinus microcorpus*.
3. *Protohaploxypinus samoilovichii*.
- 4, 5. *Protohaploxypinus latissimus*.
6. *Protohaploxypinus cf. limpidus*

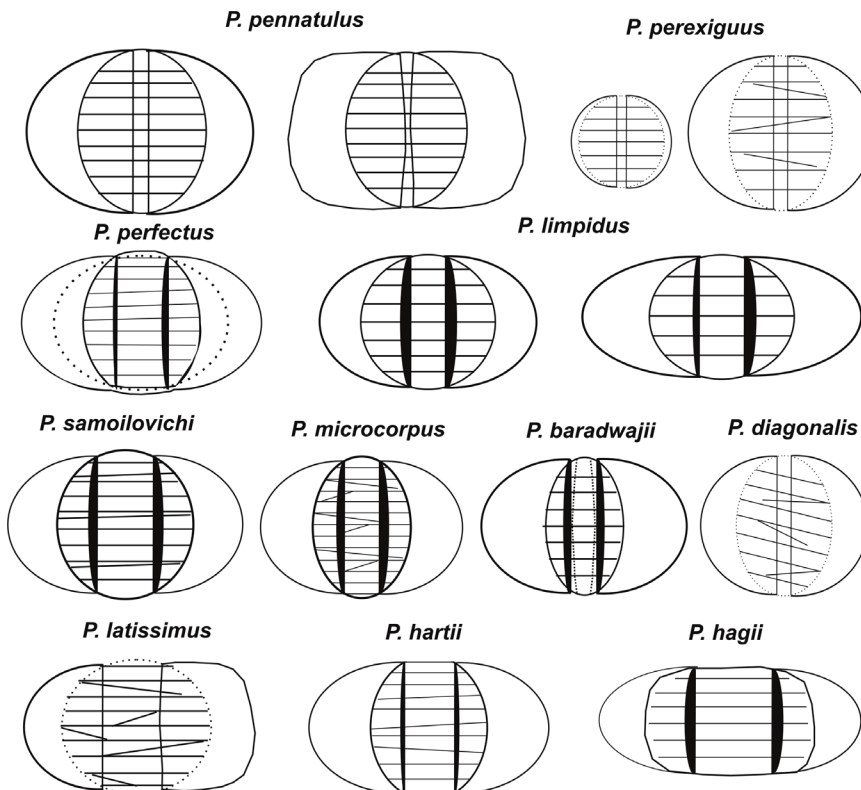


Figure 9. Morphographic features sketched to characterize the species of *Protohaploxypinus* revised and accepted in this contribution.

P. jacobii (Jansonius) Hart, 1964
P. kumaonensis (Lankhapal, Sah & Dube) Hart, 1964
P. limpidus (Balme & Hennelly) Balme & Playford, 1967
P. microcorpus (Schaarschmidt) Clarke, 1965
P. micros Hart, 1964
P. panaki Utting, 1994
P. perfectus (Naumova) Samoilovich, 1953
P. rugosus (Jansonius) Foster, 1979
P. samoilovichii (Jansonius) Hart, 1964
P. seawardii (Virkki) Hart, 1964
P. varius (Bharadwaj) Balme, 1970

Infraturma STRIATITI Pant, 1954

Genus *PROTOHAPLOXYLINUS* Samoilovich emend. Morbey, 1975

TYPE SPECIES. *Protohaploxylinus latissimus* (Luber in Luber & Waltz) Samoilovich, 1953 [SD].

REMARKS. We agree with Foster (1979, see also Foster & Gomankov 1994) in the constraintment of *Protohaploxylinus* versus *Striatoabieites* (most common *Striatoabieites multistriatus* (Balme & Hennelly) Hart 1964) and *Striatopodocarpites*. Detailed descriptions and synonymy of genus and species treated in this contribution are mainly addressed by Balme (1970), Morbey (1975), Foster (1979), McRae (1988) and Utting (1994).

Protohaploxylinus bharadwajii Foster, 1979
 HOLOTYPE. Foster (1979), Pl. 29, fig. 10.

1965 *P. microcorpus* (Schaarschmidt) Clarke, p. 338, Pl. 41, Fig. 3.

DIAGNOSTIC CHARACTERS. Haplo- slight diploxyloid subcircular to longitudinally oval amb, narrow lateral ridges somewhat present, well- defined vertical narrow corpus, cappa with parallel to wedge -shape striae in number of ca. 5 to 11, cappula lensoid to rectangular relatively broad, around 1/3 of the central body radius and folds associated to the distal roots. Total diameter 55-105 µm (from the diagnosis).

COMPARISON. We accept the combination of *P. microcorpus* proposed by Clarke based on his description. Clarke's specimen illustrated in the plate 41.3 is transferred to *P. bharadwajii* Foster based on narrower t-a central body and striae lesser than 10-11. Although, both species are herein considered morphologically transitional and possibly extremes of a morpho-group (see Fig. 9, Table I).

Protohaploxylinus diagonalis Balme, 1970

For description see Balme (p. 364-365, Pl. 10, figs. 6-8).

Protohaploxylinus haigii Foster, 1979

REMARKS. This species is distinguished from others of the genus mostly due to its broad central body and cappula in horizontal direction (see description and comparisons in Foster 1979).

Protohaploxylinus hartii Foster, 1979

Figures 2.2, 3.2, 4.4, 5.2, 5.4, 5.6, 7.2

HOLOTYPE. Foster 1979, Pl. 30, fig. 2.

1965 *P. chaloneri* Clarke, Pl. 42, Figs. 3 and 5.

REMARKS. This species bears a barely rectangular, haplo to slightly diploxyloid amb, corpus vertically oval in shape, cappula broad rectangular and cappa with 5-8 striae, parallel to wedge- shape.

COMPARISON. This species is distinguished from *P. limpidus* due to the corpus shape and frequent wedge striae beyond parallel ones, although we consider both taxa as transitional and possibly part of a morpho-group addressed below. Main features of specimens illustrated as *P. chalonerii* Clarke agree with the morphology of *P. hartii* (see above) and they are junior synonyms.

Protohaploxylinus latissimus (Luber in Luber & Waltz) Samoilovich, 1953

Figures 2.6, 3.2, 4.9-10, 5.1, 5.5, 6.5, 6.6, 6.10, 7.2, 8.4, 8.5

BASIONYM. *Pemphygaletes latissimus* Luber in Luber & Waltz, 1941, Pl. 13, fig. 221 (see Samoilovich 1953, Pl. 4, fig. 4).

1965 *Protohaploxylinus chaloneri* Clarke, p. 337, Pl. 42, Fig. 4 (holotype).

1967 *Faunipollenites varius* Bharadwaj (auct. non); Maheshwari, p. 275, Pl. 8, Fig. 62.

1970 *Protohaploxylinus varius* (Bharadwaj) Balme, p. 365, Pl. 10, figs. 4, 5.

2010 *F. varius*; Murthy et al., p. 707, Pl. 1, fig. 15.

2018 *P. varius*; di Pasquo et al., p. 154, fig. 11.D, p. 155, fig. 12.N.

2018 *Protohaploxylinus* sp. cf. *goraiensis*; di Pasquo et al., p. 156, fig. 13.B.

DIAGNOSTIC CHARACTERS. Haploxylinoid to slightly diploxylinoid, amboval to subrectangular. Cappa bearing less than 12 striae, generally 8-12, subparallel and occasionally branched/wedged. Central body subcircular to slightly oval in transverse section barely distinct. Cappula rectangular 1/2 to 1/3. Lateral ridges somewhat present (see description in Utting 1994).

COMPARISON. This species bears morphological characters like a broad rectangular cappa, somewhat lateral ridges and subparallel to wedge – shape striae being transitional to *P. limpidus* and *P. perfectus*. The diagnostic features of *P. chaloneri* and its holotype illustrated by Clarke (1965, Pl. 42, Fig. 4) agree with the morphological description of *P. latissimus* and support our reassignment to this species. The same argument is applied to the specimens illustrated as *P. varius* by Balme (1970) and *Protohaploxylinus* sp. cf. *P. goraiensis* by di Pasquo et al. (2018, transitional to *P. haigii*). Hence, they are transferred to *P. latissimus*. Two specimens illustrated as *P. latissimus* by MacRae (1988, Pl. 25, figs. 13, 14) that are confirmed herein.

Protohaploxylinus limpidus (Balme & Hennelly) Balme & Playford, 1967

Figures 2.1, 3.5, 4.3, 5.9, 5.10, 5.15, 6.2, 6.7, 8.6

BASIONYM. *Lueckisporites limpidus* Balme & Hennelly, pars., p. 94, Pl. 3, fig. 29 (designated by Balme & Playford 1967).

1962 *Faunipollenites varius* Bharadwaj, p. 95, Pl. 18, fig. 230.

1964 *Protohaploxylinus micros* Hart, p. 29, text-fig. 60.

1965 *P. jacobii* Jansonius (auct. non); Clarke, p. 337, Pl. 41, fig. 1.

1972 *Faunipollenites singrauliensis* Sinha, p. 195, Pl. 7, fig. 105.

1979 *Protohaploxylinus jacobii* Jansonius; Foster, p. 89, Pl. 30, Fig. 12.

1988 *Protohaploxylinus suchonensis* (Sedova) Hart (auct. non); MacRae, p. 63, Pl. 25, fig. 16.

(Auct. non) 2018 *P. limpidus*; di Pasquo et al., p. 155, Fig. 15.M.

See Balme (1970), Foster (1979) and MacRae (1988) for additional synonymy.

DIAGNOSTIC CHARACTERS. Bilaterally oval to subrectangular haploxylinoid amb, central body outline distinct ± subcircular to slightly oval in horizontal-vertical shape, cappa with more than 4 to 8 striae parallel, distal saccus attachment ill-defined occasionally with folds and a broad cappa bearing somewhat a median, vertical slit or groove can be present. Holotype measure 95 x 67 µm.

ORIGINAL DIAGNOSIS OF *F. singrauliensis*. Horizontally oval, bilateral pollen grains. Size 64 x 50 µm-100 x 70 µm. Central body ill defined, proximally bearing well defined horizontal striations, 5-10 in number. Sacci haploxylinoid, zone of distal saccus attachment diffused, a median vertical groove or slit present.

COMPARISON. The holotypes of *F. varius* (type species) and *F. singrauliensis* are synonymized with *P. limpidus* based on equal number of (5-10) striations, narrow cappa and occasional folds along the cappa. Ill- defined nature of central body of the holotype is not

Table 1. Main morphological characters of the accepted species of *Protohaploxypinus* revised in this contribution. Abbreviations. AMB: H= haploxylonoid, Ds= slightly diploxylonoid, Lr=Lateral ridges present. CORPUS AMB: C= circular, Sc= sub-circular, Ov= oval in length (vertical), Oh= oval in width (horizontal). CAPPULA- WIDTH: Broad (B) (½ or larger), Medium (M) (1/3-1/4), Narrow (N) (1/5 or less). CAPPULA- AMB: Rectangular (R), Lensoid (L), Expanded laterally (E). STRIATIONS TYPE: S= stright and parallel, W= partly wedged/branched, (W)= occasionally w/b. DIMENSIONS (original specific diagnosis): Total Breadth (TB), corpus breadth (CB), corpus heith (CH), cappula breadth (BC).

GROUPS	NAME OF SPECIES	AMB (GRAIN)	AMB (corpus)	CENTRAL BODY			FOLDS		CAPPULA= WIDTH - AMB			STRIATIONS		DIMENSIONS
				Distinct	Indistinct	Transitional	Present	Absent	(B) (M) (N)	(L) (R) (E)	Number	Type		
1	P. latissimus	H-Ds-Lr Srectang- oval	Sc	X					X	B	R	6-12	S-W	TB= 66(82)110µ; CB= 22(39)44µ; CH=27(45)64µ; BC= 7(18)24µ
	P. limpidus	H Srectang- oval	Oh-C	X			X			B/M	R	5-8	S (W)	TB=43(63)85µ; CB= 22(39)57µ; CH= 22(39)50µ; BC= 5(10)15µ
P. perfectus	H-Ds-Lr Srectang- oval	Oh-Ov- Sc	X			X			B/M	R	7-10	S-W	TB= 83(94)120µ; CB= 36(53)70µ; CH= 55(64)75µ; BC=6(12)20µ	
P. hagii	H rectang	Oh (broad)	X			X			B	R	5-9	S	TB=73(85)120µ; CB= 39(49)60µ; CH= 25(34)44µ; BC= 7(15)25µ	
2	P. perexiguus	H Scirc	Ov	X			Occasional	X	N	R/L	5-10	S-W (barely distinct)	TB= 57(79)110µ; CB= 22(44)50µ; CH= 50(66)87µ; BC= 0.5-16µ	
P. diagonalis	H-Ds (Lr) Scirc-oval	Oh	X					X	M	R	4-8	S-W (diagonal)	TB= 40(49)60µ; CB= 23(28)33µ; CH= 32(41)51µ; BC= 2-9µ	

Table I. (Continuation).

3	<i>P. pennatulus</i>	H-Ds Srectang-oval	Ov						very N	R/E	8-12	S (W)	TB=56(88)115µ; CB= 35(50)57µ; CH=53(65)80µ; BC=0.5-5µ
	<i>P. baradwajii</i>	H-Ds-Lr oval	Ov (narrow)	X					M	R/L	5-11	S (W)	TB=55(83)105µ; CB= 25(39)50µ; CH= 42(62)75µ; BC= 5-16µ
	<i>P. microcorpus</i>	H-Ds (Lr) Srectang-oval	Ov		X				M	R/L	10-16	S-W	TB= 92(105)121µ; CB= 43(51)58µ; CH=64(75)84µ; BC=18-25µ
	<i>P. hartii</i>	H-Ds rectang	Ov						B	R	5-8	S-W	TB= 51(70)89µ; CB= 27(34)44µ; CH= 35(43)54µ; BC= 11(15)20µ
	<i>P. samoilovichii</i>	Ds (H) Srectang-oval	Oh-Ov-Sc	X					B/M	R	6-8	S (Well-marked)	TB= 71(76)82µ; CB= 40(44)48µ; CH= 45(49)56µ; BC= 14-18µ

taken into consideration herein since the nature of central body is doubtful due to the treatment with HNO₃ applied to the Indian materials as it was explained. Size is also discarded to separate species of *Protohaploxylinus*. The specimens illustrated as *P. jacobii* by Foster (1979, Pl. 30, Fig. 12), as *P. jacobii* by Clarke (1965, Pl. 41 Fig. 1), and *P. suchonensis* (Sedova) Hart by MacRae (p. 63, Pl. 25, fig. 16) are relocated into *P. limpidus* based on sharing the same diagnostic features with this taxon described above.

Protohaploxylinus microcorpus (Schaarschmidt) Clarke, 1965

Figures 3.6, 6.3, 8.2

BASIONYM. *Striatites microcorpus* Schaarschmidt (p. 55, Pl. 14, figs. 6-7)

1979 *Faunipollenites multistriatus* Srivastava; p. 86, Pl. 3, Fig. 16.

For other synonymies see Foster (1979), di Pasquo et al. (2018).

DIAGNOSTIC CHARACTERS. Amb haplo- to slightly diploxytonoid, subrectangular to oval in shape, narrow lateral ridges occasionally present, corpus vertically oval, cappula rectangular to lensoid, variably broad, distal attachment usually with folds, cappa with more than 10 striae mostly parallel and lesser in wedge-shaped.

ORIGINAL DIAGNOSIS OF *F. multistriatus*. Size range 104-120 µm x 70-80 µm; central body obscure, circular to horizontally oval, 58-64 x 60-68 µm; horizontal striations 12-18 µm, branched, sulcus 20-24 µm wide.

ORIGINAL DESCRIPTION. Bilateral, disaccate diploxytonoid; body thin, intra-microreticulate; sacci hemispherical, attachment full, straight to convex, intra-reticulation fine.

REMARKS. This species is haplo to weakly diploxytonoid oval amb, central body indistinct, cappa with 10 to 20 taeniae commonly branched, discontinuous or wedge-shaped, sacci cappula

1/2-1/3 rectangular to lensoid. Total diameter 92-121 µm (after Foster, 1979).

COMPARISON. *F. multistriatus* is synonymized with *P. microcorpus* based on similarities in size, the number of striations (12-18) and lensoid cappula. Our morphological description and illustrations of *P. microcorpus* agrees with the one provided by Foster (1979, p. 91). *Striatites richterii* Jansonius (1962, Pl. 14, figs. 21-22) and *Striatopodocarpites magnicarpus* Bharadwaj & Tiwari (1964) illustrated by Murthy et al. (2010), are quite diploxytonoid differing from the haplo to slightly diploxytonoid amb of *P. microcorpus*. Hence, a reassignment to *Striatopodocarpites* is proposed. *P. microcorpus* is considered transitional to *P. bharadwajii* and *P. pennatulus*, and also, to *Striatoabieites multistriatus* in the case of specimens having a horizontally oval corpus and smaller sacchi (see also *P. seawardi* after Hart 1964).

Protohaploxylinus pennatulus (Andreyeva) Hart, 1964

Figures 2.7, 2.9, 3.3, 4.1, 4.2

BASIONYM. *Coniferaletes pennatulus* Andreyeva et al. (Lectotype selected by Hart 1964).

1961 *Lunatisporites goraiensis* Potonié & Lele, p. 32, Pl. 3, figs. 70-72.

1964 *P. kumaonensis* (Lankhapal, Sah & Dube) Hart, p. 29, text-fig. 62.

1965 *Faunipollenites copiosus* Bharadwaj & Salujha, p. 36-37, Pl. 2, fig. 40.

1967 *Faunipollenites bharadwajii* Maheshwari, p. 275, Pl. 8, fig. 63 [auct. non *P. bharadwajii* Foster 1979].

1988 *P. goraiensis*; MacRae, Pl. 25, figs. 17, 19, 25.

1991 *P. amplus*; Backhouse, Pl. 17, fig. 11.

DIAGNOSTIC CHARACTERS. Amb horizontal (transversely) oval to subcircular, haplo to slightly diploxytonoid, with narrow lateral ridges, little discernible central body of subcircular to slightly longitudinal oval form. Cappa with

more than 8 well- marked taenia, parallel to occasionally wedge. Relatively narrow capula (1/5-1/10) with rectangular to irregular shape enlarging at the lateral ends (i.e. narrower in the central part, Table I).

ORIGINAL DIAGNOSIS OF *F. copiosus*. Central body vertically oval, outline hardly discernible, exine intra-microreticulate, horizontal striations 9-11, coarsely intra-reticulate bladders, 25-32 µm apart distally. Size 148-162 µm in width (Bharadwaj & Salujha 1965, p. 36-37).

ORIGINAL DESCRIPTION. Bisaccate, bilateral, golden yellow pollen grains; holotype 162 µm. Central body vertically oval, 70-76 µm x 88-98 µm, slightly bigger in height than the bladders, outline hardly discernible, striation ends distinct. Exine intra-microreticulate, proximally bearing 9-11 horizontal striations without any vertical partitions. Bladders subspherical, coarsely intrareticulate attaching distally and leaving a 25-32 µm wide thin bladder free area (Bharadwaj & Salujha 1965, p. 36-37).

ORIGINAL DIAGNOSIS OF *F. bharadwajii*. Pollen grains disaccate, bilateral, haploxytonoid, 152-180 µm long, holotype 179 µm. Central body ill-defined, proximally bearing 7-10 simple or forked striations, exine in between the striations intra-microreticulate. Sacchi hemispherical, distally inclined leaving a narrow, ill-defined distal sulcus; saccus intra-reticulation coarse.

COMPARISON. Both *Protohaploxylinus pennatulus* and the holotype of *Faunipollenites copiosus* are characterized by haploxytonoid to slightly diploxytonoid saccus construction, circular to oval central body (oval in *F. copiosus*) with a slight transverse or longitudinal elongation with 8-12 striations and a thin straight narrow cappa. *F. bharadwajii* and *Lunatisporites goraiensis* are reassigned to *P. pennatulus* because of their similarity especially based on the number of striations (7-10 in *F. bharadwajii*) and narrow cappa. It is interesting to note that

Foster (1979, page 87, pl. 29, figs. 6-10) erected a new species of *Protohaploxylinus* with the same epithet "*bharadwajii*", but he did not mention that it was used by Maheshwari (1967) for a new species of *Faunipollenites*. The synonymization of *F. bharadwajii* to *Protohaploxylinus pennatulus* allows us to retain Foster's epithet. Interestingly, Playford & Dino (2000) among others that described *P. bharadwajii* Foster, did not notice this situation since some Permian papers published by Indian researchers were ignored due to inaccessibility or not considered by researchers outside India.

Protohaploxylinus perexiguus (Bharadwaj & Salujha) Foster, 1979

Figures 3.4, 4.8, 5.14, 6.4, 6.9, 6.12

BASIONYM. *F. perexiguus* Bharadwaj & Salujha, 1965.

See Foster (1979) for additional synonymy.

1965 *Faunipollenites parvus* Tiwari, p. 200, Pl. 7, Fig. 158.

1965 *Faunipollenites minor* Salujha, p. 232, Pl. 2, Fig. 30.

1969 *Protohaploxylinus rugatus* Segroves, p. 200-201, Pl. 7, Figs. G-H.

1979 *P. rugatus* Jansonius; Foster, p. 92, Pl. 33, figs. 5-6.

1988 *P. limpidus*; MacRae, p. 61, Pl. 25, fig. 7.

1988 *P. goraiensis*; MacRae, p. 64, Pl. 25, fig. 24.

1988 *P. microcorpus*; MacRae, p. 64, Pl. 25, figs. 21-22.

1989 *Faunipollenites congoensis* (Bose & Kar) Tiwari, Srivastava, Tripathi & Vijaya, p. 259, Text Fig. 9.

1989 *Faunipollenites magnus* (Bose & Kar) Tiwari, Srivastava, Tripathi & Vijaya, p. 259; Text Fig. 10.

1991 *P. rugatus*; Backhouse, p. 289, Pl. 17, figs. 1-5.

1994 *Protohaploxylinus panaki* Utting, p. 55, Pl. 6, figs. 30, 31, Pl. 7, figs. 1-3.

2010 *P. singrauliensis*; Murthy et al., p. 707, Pl. 1, fig. 14.

2012 *P. rugatus*; di Pasquo & Grader, Pl. 7, figs. 3, 5.

DIAGNOSTIC CHARACTERS. Amb haploxylinoid, subcircular to vertically oval, central body indistinct, circular- subcircular to vertically oval. Cappa with taenia not well-defined, more or less parallel to wedge/ branching in shape into central part, *sensu stricto* than 8 in number and more distinct in the central part of the body in general. Cappula narrow (mostly 1/10), rectangular to weakly widening at the lateral ends, without distal folds or occasionally narrow folds. Sacchi semicircular scarcely developed in longitudinal width, without lateral ridges. Total diameter 29-40 µm to 110 µm (Foster 1979).

ORIGINAL DIAGNOSIS OF *F. parvus*. Small, bilaterally oval pollen grains, known size 53-70 µm x 33-51 µm. Central body small, thin, obscure, apparently subcircular; known number of horizontal striations 5-7, without vertical partitions; distal channel narrow poorly defined, 8-9 µm broad when slightly apparent; sacchi ± hemispherical finely intrareticulate.

ORIGINAL DESCRIPTION. Holotype 60 x 37 µm. Pollen grains small bilaterally oval; central body almost ill-defined, apparently subcircular thin, finely intra-microreticulate. Horizontal striations unbranched without any vertical partitions. Distally, saccus free area thin, narrow and uniformly broad, only in few cases measurable, 8-9 µm broad. Sacchi small, ± hemispherical, finely intrareticulate.

ORIGINAL DIAGNOSIS OF *F. minor*. Overall size 36-62 µm. Central body indistinct, exine intra-microreticulate; distal sulcus 8-12 µm broad, bladder intra-reticulation small sized.

ORIGINAL DESCRIPTION. Yellow, bisaccate, bilateral pollen grains, holotype 46 µm. Central body vertically oval, outline indistinct made out by striation ends; exine intra-microreticulate, proximally bearing 5-7 horizontal striations

without any vertical partitions in between them. Bladders semi-spherical with small sized meshwork, attaching distally leaving 8-12 µm wide bladder free thin area.

COMPARISONS. The original diagnosis of the holotype of *F. parvus* states it is characterized by an obscure central body. However, the holotype does not support this view. Foster (1979) considered *F. parvus* and *F. minor* as junior synonyms of *P. limpidus* and included small, distinctly haploxylinoid end members of *P. limpidus* and *P. perexiguus* under *P. rugatus*. He said the latter differs only on their limboid sacchi margins and narrow cappulae slit like, rectangular or slightly expanded at lateral extremities. However, *F. parvus* and *F. minor* are closely similar to *P. rugatus* even in their small size. Tiwari et al. (1989) synonymized *F. parvus* with *F. perexiguus*, whilst Millstead (1999) considered them as junior synonyms of *P. limpidus*. Balarino (2012) considered *P. perexiguus* and *P. rugatus* as junior synonyms of *P. goraiensis* also agreeing with the criteria of size stated by Lindström et al. (1997). MacRae (1988) proposed to maintain *P. goraiensis* separated from *P. pennatulus* because of a slight difference in the number of striae and size, which are here considered not enough arguments in agreement with Foster (1979). In this work we accept the validity of *P. pennatulus* as senior synonym of *P. goraiensis* (holotype) preventing its usage as a valid species (with priority), and we consider the holotypes of *Faunipollenites parvus*, *F. minor*, *Protohaploxylinus rugatus* and *P. panaki* as junior synonyms of *P. perexiguus*, because they are all morphologically similar to *P. perexiguus* beyond differences in size, in agreement with Lindström et al. (1997), who said it should not be used to differentiate species.

On the other hand, Tiwari et al. (1989) made two new combinations, *Faunipollenites congoensis* and *F. magnus*. They transferred

the species of *Striatopiceites congoensis* Bose & Kar 1966 to *F. congoensis* due to bearing ill-defined central body contrary to a well-defined central body that characterized the genus *Striatopiceites*. Nevertheless, when Foster (1979) made a new combination of *Protohaploxylinus perexiguus* (Bharadwaj & Salujha), he stated that *S. congoensis* is undoubtedly closely related to *P. perexiguus* but is distinguished only by its larger size (154-192 µm) than *P. perexiguus* (57-110 µm). Further, the type specimens of *P. perexiguus* fall within the morphological limits of *Striatopiceites* Zoricheva & Sedova ex Sedova. Foster (1979) reassigned *Striatopiceites* to *Protohaploxylinus* since it is a less restricted form genera. On these grounds, we re-assign *Faunipollenites congoensis* and also *Faunipollenites magnus* to *Protohaploxylinus perexiguus*.

From the above, it is evident that there are many difficulties to differentiate the mentioned species because of the overlapping of almost all their characters. Hence, this reinforces the proposal of considering *P. perexiguus* as senior synonym of those species with overlapping features such as the size. It is not discarded that some specimens can show intermediate morphologies with other species of *Protohaploxylinus* like *P. diagonalis* and *P. pennatulus*.

Protohaploxylinus perfectus (Naumova) Samoilovich, 1953

Figures 2.3, 2.5, 3.7, 3.8, 4.6, 4.7, 5.3, 5.16, 6.1, 6.8, 7.3, 8.1

LECTOTYPE. Samoilovich (1953, work translated in 1959 and edited in march 1961).

Additional synonymy see Utting (1994, p. 55) and Foster (1979, p. 86) as *P. amplus*.

1962 *Striatites jacobii* Jansonius, p. 67-68, Pl. 14, Figs. 16-17.

1965 *Strotersporites indicus* Tiwari, p. 199, Pl. 6, figs. 139-141 (holotype fig. 140).

1970 *Protohaploxylinus goraiensis* (Potonié & Lele) Balme, p. 362, Pl. 11, figs 1-3.

1979 *Protohaploxylinus amplus*; Foster, p. 86, Pl. 29, Figs. 11-13.

1979 *Protohaploxylinus jacobii*; Foster, p. 89, Pl. 30, Fig. 11.

1991 *Protohaploxylinus amplus*; Backhouse, Pl. 17, fig. 12.

1999 *Protohaploxylinus goraiensis*; Millstead, Pl. 13, figs. 4, 10, 11.

2000 *Protohaploxylinus amplus*; Playford & Dino, p. 108, Pl. 10, figs. 1-4.

2012 *Protohaploxylinus amplus*; di Pasquo & Grader, Pl. 6, fig. 15.

2015 *Protohaploxylinus amplus*; Stephenson, p. 224, Pl. 4, fig. 8.

DIAGNOSTIC CHARACTERS. Striate pollen bilaterally symmetrical, amb oval to sub-rectangular, haploxylinoid, lateral ridges are often present. Corpus circular to slightly elongate oval (in both ways), frequently distinct, cappa with 7–10 taeniae straight to occasionally branched. Cappula parallel-sided to oval-shaped, width $\frac{1}{2}$ to $\frac{1}{4}$ of the corpus, distal intexinal folds generally present.

REMARKS. We follow the taxonomic status of *P. perfectus* by Utting (1994). It seems that he cited or considered common species in palynofloras from Northern Hemisphere especially in Russia, as he did not mention *P. amplus*, widely known in Gondwana, even their close similarity as stated by Foster (1979, p. 87) that further support the synonymy list above.

COMPARISON. *Protohaploxylinus baradwajii* Foster 1979 differs from *P. perfectus* in its t-a elongated central body with rhomboidal amb. The holotypes of *Protohaploxylinus jacobii* and *Strotersporites indicus* Tiwari, 1965 are considered junior synonyms of *P. perfectus*; the same occurs with specimens illustrated in the literature revised (see list above), all because of their similarity. We accept herein the proposal

of Hart (1964, p. 32), who considered the genus *Strotersporites* Wilson 1962 as a junior synonym of *Striatopodocarpites* Sedova emend. Hart 1964, and the combination of its type species *S. communis* (Wilson) Hart, based on the grounds of its diploxylinoid amb with striate cappa. However, we do not agree with the argument used by Stephenson (2015, p. 224) of having a monolete mark to maintain *Strotersporites* separated from *Striatopodocarpites*.

Finally, the specimen akin to *P. jacobii* by Foster (1979, Pl. 30, Fig. 12) is better relocated into *P. limpidus*, and the specimens illustrated as *Striatopodocarpites rarus* (Bharadwaj & Salujha) Balme (auct. non), by Foster (1979, Pl. 36, figs. 4-5) look morphologically transitional to *P. perfectus*.

Protohaploxylinus samoilovichii (Jansonius) Hart, 1964

Figures 2.4, 3.1, 6.11, 8.3

BASIONYM. *Striatites samoilovichii* Jansonius, p. 67, Pl. 14, figs. 9-11.

1991 *P. amplus*; Backhouse, Pl. 17, fig. 10.

2010 *Crescentipollenites fuscus* Bharadwaj et al. (auct. non); Murthy et al., p. 707, Pl. 1, fig. 16.

For additional synonymy see Foster (1979).

DIAGNOSTIC CHARACTERS. Amb slightly diploxylinoid, corpus subcircular to slightly oval in both directions, cappa with well-defined taenia and striae (6-8), cappula broad, rectangular to lensoid in shape, frequently with folds in saccus attachment.

COMPARISON. *Crescentipollenites fuscus* illustrated by Murthy et al. (2010) and *P. amplus* in Backhouse (1991) are reassigned to the current species due to its haploxylinoid amb, corpus vertically oval and lensoid cappula. It is noticed that the original diagnosis of *Crescentipollenites* includes diploxylinoid forms with folds in their attachment zones (Bharadwaj et al. 1974) and it is a junior synonym of *Striatopodocarpites* (Foster 1979).

Species and specimens rejected herein for *Protohaploxylinus*

- 1- *Faunipollenites enigmatus* Maheshwari (1969), *F. circumstriatites* Maheshwari (1969), *F. gopadensis* Bharadawaj & Srivastava (1969) and the specimens illustrated as *Protohaploxylinus suchonensis* and *P. limpidus* by MacRae (1988, in Pl. 25, Figs. 15 and 12 respectively)
- 2- Those species and specimens differ from species of *Protohaploxylinus* in having striations encircled by a marginal striae that is a main feature of *Illinites*, and they are likely similar to *Illinites unicus*.
- 3- *Striatites rugosus* Jansonius, 1962 (p. 69, Pl. 14, figs. 18-19). This species was combined without certainty with *Protohaploxylinus rugosus* (Jansonius) Foster (1979, Pl. 33, fig. 7). The description and the specimens illustrated support their reassignment to *Striatopodocarpites* due to a diploxylinoid amb and cappa with 4 taenia, although *P. hartii* could be a transitional form as well (see description in Foster 1979).
- 4- The specimen illustrated as *P. limpidus* by di Pasquo et al. (2018, p. 155, Fig. 15.M) is reassigned herein to *Lunatisporites variesectus* Archangelsky & Gamero (1979).
- 5- *Protohaploxylinus suchonensis* (Sedova) Hart (1964, text-fig. 54) is likely *Striatoabieites multistriatus* or a species of *Vittatina*.

DISCUSSION

Since the first palynological studies on Permian rocks began, many striate taxa have been instituted and their classification soon became unreasonable. Hart (1964) proposed the first attempt to improve the Infraturma Striatiti Pant 1954 in which many genera and species were reassigned to validly published taxa with priority

over another and discarding *nomen nudum* taxa. This kind of taxonomic changes applied to morpho-taxa of fossil palynomorphs are in agreement with the rules recommended in the International Code of Botanical Nomenclature. This important morpho-taxonomic contribution was followed by other palynologists such as Balme (1970), Scheuring (1970), de Jersey (1972), Morbey (1975), amongst others. Foster (1979) presented a taxonomic revision of striate pollen grains of genera like *Protohaploxylinus*, *Lunatisporites* and *Striatopodocarpites* including combinations and large synonymy lists. In those contributions, the synonymization of *Faunipollenites* Bharadwaj 1962 with *Protohaploxylinus* has been a subject of debate since it was initially proposed by Hart (1964). This synonymization was rejected and criticized by Indian workers such as Venkatachala & Kar (1968), Sinha (1972), Tiwari (1974) and Tiwari et al. (1989). They argued that the genus *Faunipollenites* is distinguished from *Protohaploxylinus* by “the diffused nature of intra-microreticulate central body, common haploxylinoid organization of sacci, merging zones of sacci attachment on distal side, the free ends of striations simulating the body limit and the protosaccate nature of sacci” (Tiwari et al. 1989). Therefore, they claimed that it cannot be synonymized with *Protohaploxylinus* at any level. Balme (1970) provisionally accepted Hart’s (1964) view since *Faunipollenites* by definition included haploxylinoid taeniate grains. Foster (1979) further reviewed species of *Faunipollenites* that were synonymized to species of *Protohaploxylinus* with variable confidence. This contribution was the basement for most of palynologists especially working in the Permian of Gondwana.

Concerning morphologic variations found in species of this striate genus among others, Foster (1979) explained that striations may have worked preventing their dehydration in response

to environmental conditions. The shrinkage and expansion of the exine is favored by the harmomegathic mechanism protecting its distal germinal area (see also Crane 1986, 1996, Vijaya 1990, Chaloner 2013). Another interpretation was presented by Tiwari (1982), who analyzed striate grains from the early Triassic under SEM, and found two different organizations described as follows: 1- taeniate grains with endexine widely exposed in the zone between the taeniae, called *platea* sensu Vijaya (1990, p. 86), and 2- the striate grains where the ectexine cover all the cappa, reduced in the narrow striae or grooves and without marked taeniae. These two features would have been related to the change in polarity of the germinal area, i.e. in the striate grains the germination occurred through the cappa, whereas in the taeniate ones, from its distal face. Tiwari (1982) considered it was a global morphological event relatively short lasting up to the end of Triassic. Vijaya (1990) proposed an evolutionary pattern of striation (striae and taeniae) through the Permian and Triassic succession in India, and discussed the climatic influence on their morphological variations and diversity. Even it is evident the morphologic distinction between those two groups, striate and taeniate taxa, we reinforce the necessity of constraining most of the generic taxa and species into well-recognizable entities to prevent superfluous proliferation such as many of the genera figured by Vijaya (1990, p. 87, text-fig. 2).

Protohaploxylinus is documented from Pennsylvanian (likely Moscovian) up to Triassic palynofloras of the World. Some discrepancies exist today about the function of both harmomegathy and polarity change of germinal area in morphological variations of striate pollen grains due to the lack of modern examples to help in its understanding. Harmomegathia could explain the frequent intermediate forms found

between species of the same genus or between genera (Foster 1979). This is also noticed in our analysis of species of *Protohaploxylinus*, thus, four morpho- groups of taxa supported by intermediate forms in between are proposed as follows: **1** – *Protohaploxylinus perfectus* - *limpidus* – *latissimus* – *haigii*, **2** - *Protohaploxylinus perexiguus* (*P. rugatus*) – *diagonalis*, **3** – *Protohaploxylinus pennatulus* – *microcorpus* - *baradwajii*, **4** – *Protohaploxylinus hartii* – *samoilovichii*. Other intermediate forms are also shared with other genera (e.g. *Striatopodocarpites*, *Striatoabieites*, *Illinites*, *Lunatisporites*).

On the other side, the polarity change of germinal area could have had importance especially in the first steps of the evolution of the gymnosperms during the latest Mississippian-earliest Pennsylvanian (e.g. Foster 1979, Ouyang 1996, Chaloner 2013). In the Permian, the ever-present striate/taeniate taxa and their related floras are used in local to global scale correlations and attested warmer and semiarid climates especially in Gondwana proved by its movement to lower latitudes. In northern Hemisphere they are related to Coniferalean and Peltasperms and in southern Hemisphere to Coniferalean, Glossopterids and also, Peltasperms (Crane 1988, Zhou 1994, Balme 1995, Césari & Gutiérrez 2001, Zavialova et al. 2001, Tripathi 2002, Zhu et al. 2005, Chaloner 2013, Zavialova & Karasev 2015). Its diversity and abundance increased during the Permian, as most of taeniate forms (e.g. *Lunatisporites*, *Lueckisporites*) appeared in the early Cisuralian/ or latest Pennsylvanian and soon after, their diversity and abundance increased as well (e.g. Ravn 1986, Zhou 1994, Jones & Truswell 1992, Utting 1994, Loboziak et al. 1997, Playford & Dino 2000, Césari & Gutiérrez 2001, Azcuay et al. 2002, Souza 2006, di Pasquo 2009, di Pasquo et al. 2015, Stephenson 2018). Studies of fructifications summarized by Balme (1995) show

a great variety of striate pollen grain genera although few are related with *Protohaploxyipinus*. Instead, synangia of a Permian glossopterid of Antarctica yielded several striate genera such as *Protohaploxyipinus*, *Striatopodocarpites*, *Striomonosaccites*, *Crustaesporites* (Lindström et al. 1997, McLoughlin et al. 1997). Another example corresponds to Late Permian isolated synangia *Permotheca striatifer* (Peltasperm?) from Russia in which several morphotypes of *Protohaploxyipinus* were found (Zavialova & Karasev 2015).

Those morphological variations could have been enhanced due to another interesting argument proposed by Crane (1986). He referred to the possibility that some gymnosperms were wind-pollinated plants and not obligately anemophilous. Hence, many could have been facultatively entomophilous, as shown by the occurrence of large amounts of typically anemophilous pollen in bee loads. Krassilov et al. (1999) analyzed and illustrated the pollen content in the gut of a primitive booklouse from the Urals. In the latter, striate pollen grains mainly of *Protohaploxyipinus* and *Lunatisporites* genera were recovered, and some monosaccate pollen grains were scarcely found as well. Krassilov et al. (1999) have found that several insects in the Permian of Urals may be pollinivores on *Protohaploxyipinus*, *Lunatisporites* and *Vittatina* pollen grains that correspond to Ullmaniaceae-Peltasperm fossil plant community. Therefore, one possibility is that these pollinivorous insects could have acted as pollination vectors *sensu stricto*, and the striae-taeniae (bands) present on their proximal face have facilitated to be stuck to insects or directly, they fed on the pollen grains before being released from the fructification. Considering any of the possible interpretations, it is evident they could have contributed to preserve high amounts of pollen grains into the sediments (i.e., fecal pellets,

insects buried into sediments). It follows from what has been said that intra and intergeneric and specific transitional morphologies documented in striate pollen grains could have been triggered either by paleoclimatic changes and/or co-evolution of insect-plants since their appearance (see Crane 1986, Vijaya 1990, Krassilov et al. 1999). These are also recognized between species of *Protohaploxyipinus* as confirmed herein (Table I, Fig. 9) and strengthened the necessity of eliminating more superfluous species documented in the literature from India and elsewhere.

Future perspectives

We aim to emphasize the usage of *Protohaploxyipinus* and its species instead of *Faunipollenites* in future studies of Permian and Triassic successions in India. The former is well-represented in the Permian as well as in the Pennsylvanian to Triassic of the World. In India, a wider revision of illustrated specimens assigned to *Faunipollenites* needs to be done. This will improve the stratigraphic ranges of species of *Protohaploxyipinus* in India and globally and will contribute to the knowledge of paleobiogeographic distribution of Permian palynofloras in both northern and southern Hemispheres (e.g. Utting & Piasecki 1995, Tripathi 2002, Chaloner 2013, di Pasquo et al. 2015, Stephenson 2018, and references therein). Another consequence of the present revision concerns to the updating of the epithet of palynozones such as the Cisuralian *Protohaploxyipinus goraiensis* Subzone of the *Vittatina costabilis* Zone of Brazil (see Souza 2006), which should be named as *Protohaploxyipinus pennatulus*. Although, this change does not affect its composition and age.

CONCLUSIONS

Specimens of both *Faunipollenites* and *Protohaploxylinus* obtained from palynoassemblages of India and Brazil, mounted after every stage of acid treatment (HCl, HF, HNO₃ between two hours and 24-28 hours and KOH), were carefully analyzed and compared under optic, CLSM and SEM microscopes. From this morpho- taxonomic evaluation, we affirm that a prolonged oxidation treatment (more than 24 hours) introduced morphological changes to the specimens leading to maintain *Faunipollenites* and *Protohaploxylinus* separated in Permian studies of India. Our study supported that *Protohaploxylinus* is the senior synonym of *Faunipollenites*. Species of *Faunipollenites* are synonymized with *Protohaploxylinus* species revised and confirmed herein (Table I, Fig. 9). Specimens bearing transitional features between species of *Protohaploxylinus* strengthen the necessity of eliminating superfluous species documented in the literature of India and elsewhere. Four morpho- groups of taxa are also recognized considering intermediate forms, joined as follows: **1** –*Protohaploxylinus perfectus* – *P. limpidus* – *P. latissimus* – *P. haigii*, **2**– *Protohaploxylinus perexiguus* (*P. rugatus*) – *P. diagonalis*, **3** – *Protohaploxylinus pennatulus* – *P. microcorpus* – *P. baradwajii*, **4** – *Protohaploxylinus hartii* – *P. samoilovichii*. Other intermediate forms are also shared with other genera (e.g. *Striatopodocarpites*, *Striatoabieites*, *Illinites*, *Lunatisporites*). The future re-assignment of specimens in any of the species of *Protohaploxylinus* herein confirmed, illustrated in Pennsylvanian to Permo-Triassic palynoassemblages of India and elsewhere will enable to refine intra-Gondwanan and global correlations and their palaeobiogeographic distribution in association to the respective megaflores.

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