from the Late Precambrian sediments of Vindhyan Supergroup⁵. The decreasing diversity of microplanktons and medium size leiosphaerids of sphaeromorphida acritarch as well as few acanthomorphs in the present assemblage favours Vendian age to these sediments⁶. The rhodophytes, viz. Wengania and Thallophyca are also known from the Terminal Proterozoic Doushantuo Formation of South China^{7,8}. Thus, the recovered microfossil assemblage from the phosphatic chert lenticles and shale of Chambaghat Formation and available data from the overlying and underlying formations⁹⁻¹⁶ indicate Terminal Neoproterozoic age to these sediments.

The presence of medium-size ornamented acritarchs, rhodophytes, viz. Wengania and Thallophyca and cyanobacterial remains with mucilaginous sheath¹⁷ and coiling of filaments^{18,19}, small size of cells in coccoidal forms²⁰ associated with phosphatic chert lenticles and shale indicates moderate deep marine environment under stable shelf conditions. However, the dominant lithology consists of quartz arenite, which is deposited in shallow-water environment, such as tidal flat or lagoonal complexes. The present assemblage and its diversity suggest amalgamation of two environments (desiccating in the stagnant water body affected by storms) by any natural obstacle8,21 for the deposition of phosphatic black chert lenticles and shale associated with quartz arenite of Chambaghat (Krol Sandstone) Formation, Krol Group.

- Shanker, R., Kumar, G., Mathur, V. K. and Joshi, A., J. Pet. Geol., 1993, 2, 99–136.
- 2. Joshi, V. K., *Indian Miner.*, 1970, **24**, 358–363.
- Kumar, G., Shanker, R., Mathur, V. K. and Maithy, P. K., Geosci. J., 2000, XXI, 1– 10.
- Jiang, G., Sohl, L. E. and Christie Blick, N., Geology, 2003, 31, 917–920.
- 5. Maithy, P. K. and Babu, R., *Palaeobotanist*, 1988, **37**, 77–80.
- Vidal, G. and Knoll, A. H., Nature, 1982, 297, 57–60.
- Yuan, X. and Hofmann, H. J., Alcheringa, 1998, 22, 189–222.
- Zhang, Y., Yin, L., Xiao, S. and Knoll, A. H., J. Paleontol. Suppl. Mem., 1998, 72, 1-52.
- Tiwari, M. and Knoll, A. H., Himalayan Geol., 1994, 5, 193–201.
- 10. Tiwari, M., Curr. Sci., 1996, **71**, 718–719.
- 11. Mathur, V. K. and Shanker, R., J. Geol. Soc. India, 1989, 34, 245–254.
- 12. Mathur, V. K. and Shanker, R., J. Geol. Soc. India, 1990, **36**, 274–278.
- 13. Shanker, R. and Mathur, V. K., *Geophytology*, 1992, **22**, 27–39.
- Shanker, R., Mathur, V. K., Kumar, G. and Srivastava, M. C., Geosci. J., 1997, XVIII, 79–94.

- Shanker, R., Bhattacharya, D. D., Pande,
 R. C. and Mathur, V. K., J. Geol. Soc. India, 2004, 63, 649–654.
- Shukla, M., Babu, R., Mathur, V. K. and Srivastava, D. K., Curr. Sci., 2004, 87, 868–870.
- 17. Knoll, A. H. and Swett, K., Am. J. Sci. A, 1990, **290**, 104–132.
- Knoll, A. H., Blick, N. and Awramik, S. M., Am. J. Sci., 1981, 281, 247–263.
- 19. Mansuy, C. and Vidal, G., *Nature*, 1983, **302**, 606–607.
- Semina, H. J., The Micropaleontology of Oceans (eds Funnel, B. M. and Riedel, W. R.), Proceedings of the Symposium on Micropalaeontology of marine bottom sediments, Cambridge University Press, UK, 1971, p. 89.
- 21. Wall, D., *Micropalaeontology*, 1965, **11**, 151–190.
- 22. Auden, J. B., Rec. Geol. Surv. India, 1934, **67**, 357–433.

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Pseudovivipary in two rupestrian endemic species (Leiothrix spiralis and Leiothrix vivipara)

Pseudovivipary is a rare phenomenon described for approximately 50 species of angiosperms¹. It describes plants that produce asexual propagules in place of the sexual reproductive structure. Several authors² have argued that pseudovivipary has evolved in response to a short growing season, enabling plants to complete the cycle of offspring production, germination and establishment during the brief periods favourable to growth and reproduction in markedly seasonal environments¹.

Though pseudovivipary was known in plants belonging to many families (Alliaceae, Liliaceae, Agavaceae, Poaceae, Saxifragaceae and Polygonaceae)¹, the Eriocaulaceae family was not cited in the revision made by Elmqvist and Cox¹. Most

species in the Eriocaulaceae family occur in the rupestrian grasslands in the Espinhaço mountain chain, above 1000-1100 m, up shallow and sandy soils, and rocks mostly of quartzites and sandstones³ (Figure 1 a). The genus Leiothrix is restricted to South America and contains 37 species with 25 in the Espinhaço mountain chain. Many Eriocaulaceae species possess the capacity for inflorescence proliferation⁴; however pseudovivipary is not always observed. This suggests that for some species pseudovivipary is an ecological phenomenon, which depends on environmental influences. However, all species of Leiothrix subg. Stephanophyllum are pseudoviviparous and some of them (L. spiralis and L. vivipara) are endemic to

the state of Minas Gerais, Brazil (19°12′–19°20′S and 40°30′–43°40′W)⁵. These species occur in areas where the soils are usually shallow and sandy, with rocky outcroppings throughout³, and inflorescence proliferation is always observed in their life cycle, indicating that pseudovivipary in these species could be genetically determined.

Individuals of *Leiothrix* are small-rosette plants whose inflorescences on flower heads are supported by scapes. The scapes in pseudoviviparous species function like stolons when the flower heads of rosettes proliferate giving rise to plantlets or ramets.

L. vivipara is a pseudoviviparous species that occurs in dry, sandy soil, sometimes densely covered by a herbaceous layer.

Majority of the formed ramets remain supported by the scapes or are intertwined with herbaceous leaves (Figure 1 b). These ramets are much more numerous than those attached to the ground. For each 100 supported ramets we recorded only one attached ramete, in sites crowding from

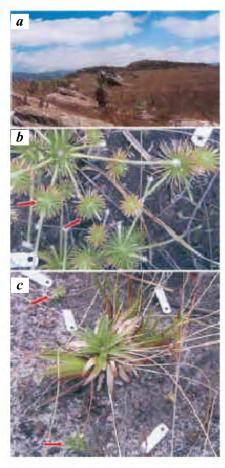


Figure 1. *a*, Typical landscape of rupestrian grasslands where *Leiothrix* is quite common. *b*, Rosettes of *Leiothrix vivipara* with scapes. Note ramets suspended without touching the ground (red arrow). *c*, Rosettes of *L. spiralis* with scapes. Note ramets attached to parent plant by way of scapes (red arrow).

herbaceous plants. This 100:1 proportion diminishes to 100:10 in sites with low-density herbaceous plants. Despite this decrease in proportion, the supported versus attached proportion is still high, indicating that a scandent habit developed in this species. Ramets formation from flower heads is precocious and occurs without touching the ground soon after the formation of flower heads. The flower heads of the suspended ramets also proliferate giving rise to new ramets. This process may repeat itself several times.

Besides being a rhizomatous species, *L. spiralis* is also pseudoviviparous. Nevertheless, in this species the ramets are formed late, only after the flower heads touch the ground. Few rosettes grow amongst herbaceous plants, even if these are sparse. In addition, practically all of ramets formed are attached to the ground (Figure 1 c). Contrary to *L. vivipara*, formation of suspended ramets is extremely rare in *L. spiralis*.

Both L. vivipara and L. spiralis grow in nutrient and water-poor soil. Such conditions are unfavourable for sexual reproduction. Hence, it is not surprising that pseudoviviparous species of Leiothrix can successfully grow and reproduce in these sites. Furthermore, pseudoviviparity should evolve in sites with extreme environmental conditions. Thus, it is remarkable that pseudoviviparity did not evolve in all species of Leiothrix from the south of the Espinhaço mountain range. The typical environmental heterogeneity of the rupestrian grasslands promotes a variety of microhabitats available for the Leiothrix species to grow. Leiothrix species occur in areas that display small differences in patch quality rather than abrupt discontinuities. Such habitats are heterogeneous for resident plants exerting different kinds of selective pressure, probably favouring the origin of mixed reproductive strategies⁶. The adaptations of pseudoviviparous species to poor environmental conditions are not clear⁷. If pseudoviviparity does represent an advantage for *Leiothrix* in the ruspestrian grasslands, then it have to be tested.

- 1. Elmqvist, T. and Cox, P. A., *Oikos*, 1996, **77**, 3–9.
- 2. Lee, J. A. and Harmer, R., *Oikos*, 1980, **35**, 254–265.
- Giulietti, A. M., Menezes, N. L., Pirani, J. R., Meguro, M. and Wanderley, M. G. L., Biol. Bot. Univ. Sao Paulo, 1987, 9, 1–151.
- Monteiro-Scanavacca, W. R. and Mazzoni, S. C., Bol. Bot. Univ. Sao Paulo, 1976, 4, 23–30.
- 5. Giulietti, A. M., Ph D thesis, Univ. Sao Paulo, 1978.
- 6. Yoshimura, J. and Clark, C. W., *Evol. Ecol.*, 1991, **5**, 173–192.
- Sarapul'tsev, I. E., Russ. J. Ecol., 2001, 3, 188–196.

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