

## Lithophagic Snail from Southern British Honduras

**Abstract.** *A freshwater gastropod, Pachycheilus glaphyrus, responsible for unusual erosion in limestone has been located in southern British Honduras where it is abundant in streams flowing through areas of karst topography. These snails ingest algae that proliferate in solution grooves formed at the fluctuating air-water interface. Rasping action of the radula results in deepening of these grooves and appears to improve the algal habitat.*

Rock-eating snails are not commonly found in freshwater areas, although marine rock-boring gastropods are widespread and reasonably well known (1). There are occasional references in the literature to terrestrial examples, such as the remarks of Bunting (2) that snails are common in lime-rich soils and that they can wear deep holes in limestone. Preliminary investigation suggests that the lithophagic habits of *Pachycheilus glaphyrus* Morelet are an inadvertent result of feeding on blue-green algae that grow on the exposed surfaces of limestone outcrops along a number of small streams in southern British Honduras.

Repeated observations over a period of 2 months during the dry season (May to September) of 1957 indicate that these snails of the family *Pleuroceridae* are partly responsible for an unusual crenellate erosion pattern developed in limestone outcrops along the banks of Go-To-Hell Creek. This distinctive pattern of alternating grooves and ridges resembles the forms seen in penecontemporaneous ripple marks. Such an explanation of the origin is untenable in view of the conditions associated with the deposition of dense, aphanitic calcarenite approaching lithographic limestone in purity and uniformity. Dixon (3) has assigned the formation involved to the Upper Cretaceous, and from associated fossils it is evident that the beds were deposited in a low-energy backreef environment.

Solution activity of limestone has proceeded at an extremely rapid rate in this tropical area where more than 5100 mm of precipitation are received per year. Many of the streams that form the drainage systems of the larger rivers have their tributary headwaters in the broad, limestone plateau that occupies much of the southern British

Honduras. Numerous surface sinkholes and a complex of underground drainage have developed in the plateau so that stream discharge is largely governed by the continual blocking and opening of subterranean passages rather than by fluctuations in actual rainfall. These rapid changes in water flow have produced a band of solution-grooving approximately 1 m wide on limestone surfaces exposed to the oscillating air-water interface where solution activity is most vigorous.

Specimens of *P. glaphyrus* were particularly conspicuous where they were concentrated near the surface in the solution grooves. Density over the rocky bottom was estimated at 20 to 30 per square meter in favorable localities. The snails were noted only in streams flowing through limestone and were not found in adjacent areas where shale or alluvium comprised the stream bed material.

This preference for limestone is the basis for the distribution shown in

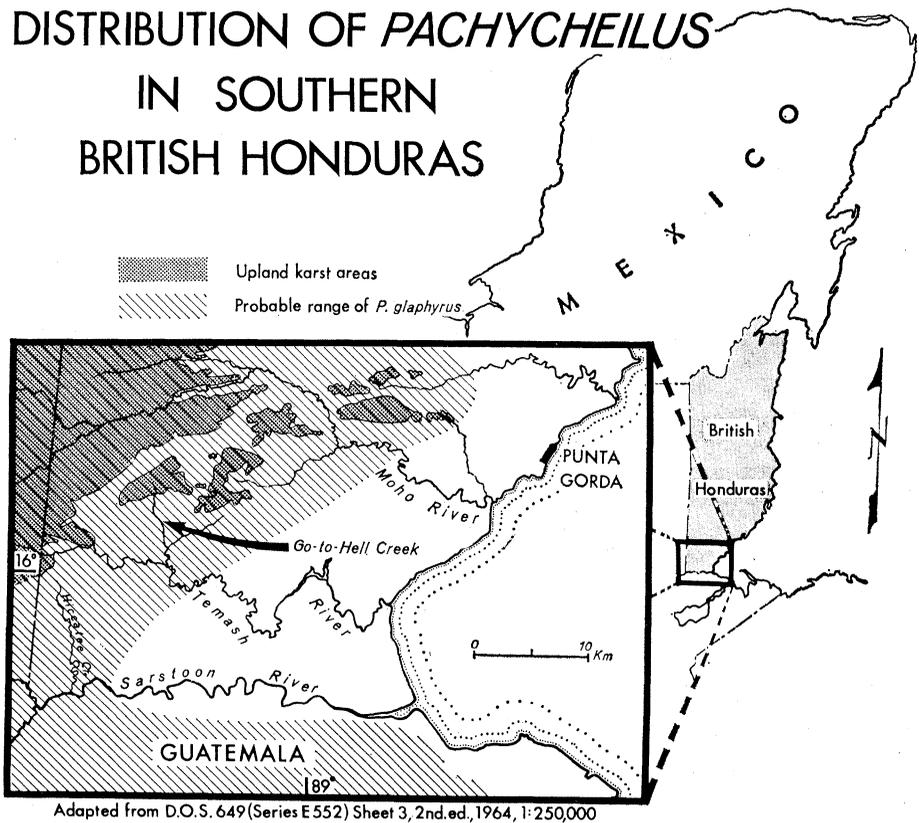


Fig. 1. Location map of study area showing distribution of *Pachycheilus glaphyrus* in southern British Honduras.

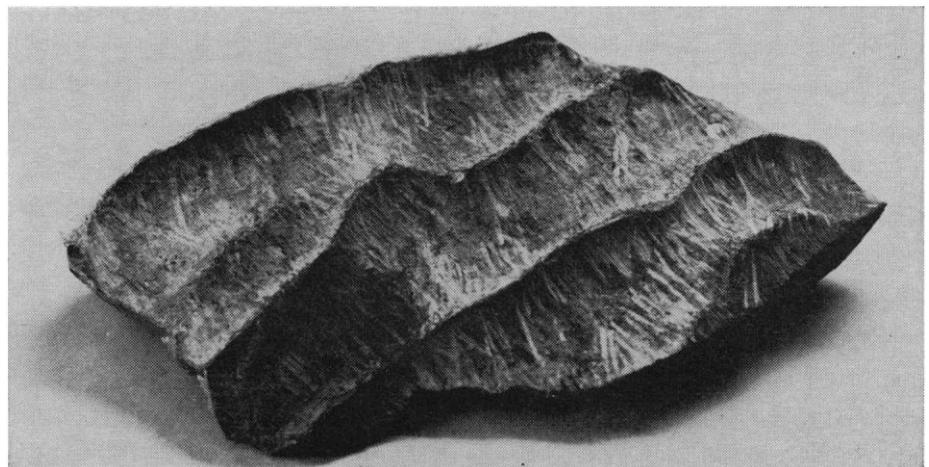


Fig. 2. Rasp marks and solution-grooving in limestone (actual size).

Fig. 1, which corresponds to known areas of limestone outcrop. Robertson (4) reports *P. obeliscus* from a similar habitat in the Rio Hondo of northern British Honduras.

Go-To-Hell Creek flows through a typical tropical rain forest environment and is not sufficiently large to develop a foliage-free corridor where sunlight can penetrate with ease. Nevertheless, sufficient available light is present to stimulate a subaqueous growth of blue-green algae on rock surfaces near the air-water interface. These plants proliferate in the relatively protected microhabitat of the horizontal solution grooves where they accumulate as a thick, palpable slime.

This concentrated algal growth affords a rich pasturage for the snails, which always align their shells parallel to the grooves. Ingestion of algae was observed to occur as a result of rasping action by radula strokes directly perpendicular to the longitudinal axis of the grooves. Closely spaced scratches made by the feeding snails can be seen with the unaided eye and are clearly defined in Fig. 2. These scratches extend through a thin, partially decomposed surface layer of chalky consistency to expose unweathered limestone. Continued rasping action thus enlarges

grooves initiated by solution activity, deepens the trough, and presents a fresh rock surface for carbonate solution as well as possible softening by the algae.

In describing a remarkably similar instance involving the tidewater snail *Nerita plicata*, Weins (5) cites Doty and Morrison (6) who suggest that blue-green algae have a very significant role in the decomposition of limestone. Their data indicate that the process involves local changes in pH brought about through metabolic activities of the algae.

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#### References and Notes

1. For example, the *Pholadidae* such as *Parapholas concamerita*, *Pholadidea melanura*, and *Pholadidea tridens*.
2. B. T. Bunting, *The Geography of Soil* (Aldine, Chicago, 1965), p. 43.
3. C. G. Dixon, *Geology of Southern British Honduras with Notes on Adjacent Areas* (The Government Printer, Belize, no date, about 1955), p. 23.
4. R. Robertson, *Phila. Shell Club Proc.* **1**, 20 (1963).
5. H. J. Weins, *Atoll Environment and Ecology* (Yale Univ. Press, New Haven, Conn., 1962), p. 264.
6. Herold J. Weins (5) cites Maxwell Doty and J. P. E. Morrison, "Interrelationships of the Organisms on Raroia Aside from Man," *Atoll Res. Bull.* No. 35.

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## "Twin Meiosis" and Other Ambivalences in the Life Cycle of *Schizosaccharomyces pombe*

**Abstract.** Diploid cells of the yeast *Schizosaccharomyces pombe* carrying the mating-type allele  $h^{90}$  are capable of sporulation and copulation. After copulation karyogamy does not always occur. In this case both nuclei will undergo meiosis separately (twin meiosis). Asci with eight haploid spores derive from this event. Diploid cells homozygous for the mating-type alleles  $h^+$  or  $h^-$  do not sporulate. However, their nuclei can perform meiosis when they are in a common cytoplasm with a diploid nucleus of compatible mating type.

In the life cycle of the fission yeast *Schizosaccharomyces pombe* Lindner a key role is played by the mating-type alleles. They control the abilities for copulation as well as for sporulation (1, 2). Below I report experiments with diploid *S. pombe* strains, which show some ambivalences in the course of events controlled by the mating-type alleles. For instance, after cell fusion nuclear fusion does not occur in part of the zygotes, and both nuclei undergo separate meioses (twin meiosis).

The vegetative cells of *S. pombe* are normally haploid. At the end of vegetative growth, cells of compatible mating type fuse pairwise (1, 2). In

the resulting zygotes, fusion of the nuclei (karyogamy) and meiosis take place, and four ascospores are formed within the cell wall of the original zygote (zygotic asci). Three alleles ( $h^{90}$ ,  $h^+$ ,  $h^-$ ) are known at the mating-type locus. They determine three different mating types (1-3): haploid strains having the allele  $h^{90}$  are homothallic, whereas strains with  $h^+$  or  $h^-$  are heterothallic (4). The following lists show which mating types are compatible and incompatible, respectively:

- 1) compatible (copulation):  $h^{90} \times h^{90}$ ,  $h^{90} \times h^+$ ,  $h^{90} \times h^-$ ,  $h^+ \times h^-$ ;
- 2) incompatible (no copulation):  $h^+ \times h^+$ ,  $h^- \times h^-$ .

Although the cells of *S. pombe* are normally haploid, it is possible to select diploid strains. An analysis of these strains has shown that the mating-type alleles not only determine the capability to copulate but also the capability to sporulate (2). Cells of the constitution  $h^{90}/h^{90}$ ,  $h^{90}/h^+$ ,  $h^{90}/h^-$ , and  $h^+/h^-$  undergo meiosis at the end of the period of vegetative growth and form directly four ascospores (azygotic asci). Diploid cells which are  $h^+/h^+$  or  $h^-/h^-$  do not sporulate but will copulate with either haploid or diploid cells of compatible mating type (2, 5). After copulation of diploid cells, in general four diploid ascospores are produced (6).

Two different complete culture media are used in experiments with *S. pombe*: YEA (7) and an incubation temperature of 30°C are suitable for vegetative growth, whereas MEA (7) and 25°C are favorable for copulation and sporulation. The results with diploid strains cited above (2, 6) were obtained with MEA (or beer wort) at 25°C.

In experiments using YEA at 30°C, I observed that  $h^{90}/h^{90}$  cells not only sporulate, but also frequently copulate with each other. After 2 to 4 days of incubation,  $h^{90}/h^{90}$  cultures show mainly azygotic asci, but a considerable number of giant zygotic asci are present too. The latter have either four large, apparently diploid spores, or they have six, seven, or, more frequently, eight spores of normal size (8). Spores from eight-spored asci were isolated by micromanipulation. Upon cultivation they gave rise to haploid cultures. This preliminary finding seemed to be consistent with the idea of "brachymeiosis" discussed in the earlier literature on Ascomycetes (9). It was therefore of interest to perform a more detailed analysis of the multisporous asci by means of strains with different genetic markers. In addition, the possible formation of eight-spored asci in mating-type combinations other than  $h^{90}/h^{90} \times h^{90}/h^{90}$  was examined.

I made nine different crosses with diploid strains on YEA and incubated them 2 to 4 days at 30°C. To avoid sporulation of the  $h^{90}/h^{90}$  and  $h^{90}/h^-$  strains before mating, the freshly selected diploids were grown in liquid yeast-extract medium on a shaker. In liquid medium only very few azygotic asci are formed, in contrast to cultures on agar. With respect to the mating-type combinations the crosses were of five different types (Table 1).