



**FIGURE 1**—Deep-water Pleistocene gastropods from California found in shallow-water deposits. **A**) *Trophonopsis dalli* (Kobelt, 1878), Moonstone Beach, Humboldt Co., CAS loc. 124, shell height 14.8 mm. **B**) *Trophonopsis fleenerensis* Martin, 1914, Crannell Junction, Humboldt Co., CAS loc. 58202, shell height 14.2 mm. (CAS=California Academy of Sciences, San Francisco, CA; LACMIP=Los Angeles County Museum of Natural History Invertebrate Paleontology, Los Angeles, CA.)

(Boucot, 1981, p. 332). This consideration is in part because hermit crabs have a poor fossil record (Bishop, 1983) and therefore have not figured in paleoecological research. Even in modern communities, their ecological dynamics are not well known; research on hermit crabs in modern environments has focused chiefly on shell selection (Schembri, 1988; see Hazlett, 1981, for review).

I have reinterpreted the fossil and recent literature, with additions from my research, to provide a new synthesis of and perspective on how hermit crabs may potentially bias fossil accumulations. Seven preservational biases, under the rubric “anomalies” are codified here to call attention to the variety of biological taphonomic processes to which hermit crabs may contribute.

In environments where hermit crabs are common, they may be a significant taphonomic force, a source of bias generally not recognized in studies of the evolution and structure of fossil gastropod communities.

#### POTENTIAL TAPHONOMIC ANOMALIES CREATED BY HERMIT

Crabs Between Habitat Anomalies

##### Bathymetric

A perplexing problem in paleoecology is the occurrence of deep-water fossil gastropods found in shallow-water deposits. These anomalous bathymetric distributions may be explained by biological agents either transporting the shells into shallow water or maintaining the shells that have “washed” into shallow-water areas. Distinctions between shell “transport”

and “shell maintenance” are not clear and will be discussed in more detail later.

Most bathymetric anomalies are identified from Pleistocene deposits because the fossil gastropod shells have living analogues from which their fossil depth distributions are inferred. The California Pleistocene provides many examples of anomalous species (Table 1). Physical processes (such as storms), different thermal tolerances between modern and Pleistocene species, and reworked older shell deposits have been used to explain these anomalous distributions (e.g., Woodring et al., 1946; Emerson and Addicott, 1953; Emerson, 1956; Valentine and Mallory, 1965; Addicott, 1966, 1969; Zimmeister, 1974).

Biological factors, such as kelp and diving marine birds, may contribute to anomalous bathymetries. Kelp, washed up on beaches after storms, can carry deep-water shells (Valentine, 1961; Dell and Fleming, 1973). Neogene marine birds may have contributed to mixed molluscan fossil assemblages by bringing fish (that had eaten deep-water molluscs) to their nearshore rookeries (e.g., Teichert and Serventy, 1947; Smith, 1952; Lindberg and Carlton, 1969; Lindberg and Kellogg, 1982). Molluscivorous fish are size-selective in the type of prey they prefer and may transport shells inshore, thereby biasing shell accumulations (see Boucot, 1981, p. 220, 226-230, 235-236). Hermit crabs have also been implicated in shell transport (Kohl, 1974; Arntz et al., 1976). Kohl (1974) reported two anomalous deep-water gastropods, *Trophonopsis fleenerensis* and *Trophonopsis dalli*, from his Crannell Junction (Humboldt County, California) shallow-water Pleistocene locality. He suggested that hermit crabs and/or currents brought the deep-water shells into shallower water. Hermit crab body fossils were not present at his locality. In fact, only five localities in California are known to have pagurid body fossils (Rathbun, 1926). Is it possible to dismiss Kohl’s hermit crab hypothesis on the lack of body fossils at his locality?

No. The bathymetric distribution of Pacific Northwest hermit crabs are well within the range of deep-water snail species (Table 2). Seven species of hermit crabs range from shallow subtidal waters to deep water (>90m) off the coast of California (Table 2) and one could argue that most of these species may have lived in the Pleistocene. In addition, a unique trace fossil, *Helicotaphrichnus commensalis*, which occurs in the columella of only hermit crab-inhabited shells, is present in many Pleistocene localities and can be used to document the hermit crabs’ occurrence in those localities (Kern et al., 1974). I obtained specimens of *T. fleenerensis* (collected by Kohl from Crannell Junction) and *T. dalli* (collected from Moonstone Beach, a nearly fossil locality) and examined them for the occurrence of this trace fossil. Both specimens had *Helicotaphrichnus* bore holes in their columellae (Figs. 1A and 1B), indicating that these deep-water shells were previously occupied by a hermit crab.

It is clear that hermit crabs occupied these shells and maintained them in shallow water, but it is not known whether they physically transported the shells into the shallow habitat. Marine hermit crabs have the ability to transport tagged shells long distances (S. Gilchrist, pers. comm., 1988) but no studies have been done to address this question from a historical (taphonomic) perspective.

In addition to *Helicotaphrichnus* bore holes, there are many