Fig. 4. Infilled clavate borings interspersed with horizontal burrows of *Thalassinoides* along *in situ* basal contact of the Isidro Formation at CSUN loc. 1495. Square end of hammer is 2 cm in width.

100 per square meter in the central part of the study area. With increasing density, there is a pronounced tendency for infilled borings to become longer with more bulbous ends, for the infilled borings to display directional changes, and for penetration angles of the infilled borings to deviate from vertical and become as much as 45 degrees from the vertical to nearly horizontal. Infilled borings do not intersect each other, even where they are crowded.

According to Kelly and Bromley (1984), the geologic range for clavate borings in lithic substrates is Jurassic to Recent. Miocene reports of infilled clavate borings are common, and examples that resemble those from the Isidro Formation have been reported from Japan (Uozumi and Fujie 1956), California (Adegoke 1966), the Gulf of Mexico (Warme and McHuron 1978), Poland (Radwanski 1977) and New Zealand (Bradshaw 1980). Modern borings that resemble those from the Isidro Formation have been reported from Oregon by Evans (1970), from San Diego by Warme (1970), and from the Texas Gulf Coast by McHuron (1976). The resemblance involves size and shape, substrate affected, presumed environment of creation, and associated trace fossils. Based on these similarities, the infilled clavate borings at CSUN loc. 1495 are identified as *Gastrochaenolites.* Kelly and Bromley (1984) provided a detailed review of this ichnogenus.

Horizontal burrows.—Approximately five percent of the infilled clavate borings are connected by horizontal burrows (Fig. 4) with circular cross sections whose diameters range from 1.5 to 2.5 cm. The fill in these burrows is similar to that in the infilled clavate borings. Most of these burrows have walls which exhibit extensive scratch marks, although a few bear no sculpture. In the cases where burrows branch, they usually do so at a 60-degree angle. Some burrows loop out from and then re-enter an individual infilled boring. The sculptured horizontal burrows are assigned to *Spongeliomorpha* on the basis of comparison to descriptions by Ekdale et al. (1984, pp. 31, 33, 192), and the unsculptured horizontal burrows are assigned to *Thalassinoides* on the basis of comparison to illustrations in Ekdale et al. (1984, figs. 3-5, 15-5).

Ichnofacies

According to Ekdale et al. (1984), firm but uncemented substrates are associated with the ichnofacies *Glossifungites,* which is characterized by the ichnogenera *Gastrochaenolites, Spongeliomorpha,* and *Thalassinoides.* Pemberton and Frey (1985) asserted that the *Glossifungites* ichnofacies typically is associated with dewatered muds. They also noted that thalassinoidean traces in this ichnofacies commonly display well-developed cheliped sculptings. The *Trypanites* ichnofacies, as described by Ekdale et al. (1984), is associated with fully lithified substrates (generally a relict surface) and can also contain the ichnogenus *Gastrochaenolites.* Recognizing that the two ichnofacies are intergradational, we assign the trace-fossil assemblage at the base of the Isidro Formation to the *Glossifungites* ichnofacies on the basis of the ichnogenera present and the lack of complete cementation of the Eocene substrate.

Discussion

On the basis of their strong resemblance to the morphology of modern borings described by McHuron (1976), Evans (1970), and Warme (1970), as well as to fossil borings whose producers have been positively identified (see references on Miocene borers in "Sediment-infilled clavate borings" section), we believe that the organisms responsible for the Isidro Formation borings were pholadid bivalves. Several other lines of evidence support this conclusion.

According to Pemberton and Frey (1985), pholadids dominate foreshore-like, wave-influenced deposits. Evans (1968a) noted that morphology of pholadid borings in a given substrate is controlled by population density, with greater crowding producing greater variability. McHuron (1976) observed that the same species of pholadids could produce borings with or without bioglyphic ornamentation (i.e., serrated tool marks), depending on the substrate hardness (harder substrates tend to diminish sculpture). Kennedy (1974) pointed out that pholadid borings in an open-coast marine environment tend to be filled with coarser sediments and that some secondary nestlers extract calcium carbonate from pholadid shells, thereby dissolving them. He also distinguished pholadid from mytilid borings on the basis of the virtually constant cross-sectional area of mytilid borings and the fact that they are bilaterally symmetrical, in contrast with the conical body and circular cross sections of pholadid borings.

Given the evidence at hand and the assumption that pholadid bivalves produced the clavate borings, it is possible to interpret the environmental conditions at the base of the Isidro Formation. Incompletely cemented Eocene deposits of the Bateque Formation were subaerially exposed and eroded. Subsequent transgression by the Miocene seas provided a relatively hard surface which was colonized by pholadid borers. Ekdale et al. (1984) stated that heavy infestation of lithic substrates by ichnogenus *Gastrochaenolites* is large a shallow-water phenomenon. A shallow-water environment for the Isidro Formation borers is also indicated by the shell-hash infill of the boreholes. The shell-hash contains remains of near-shore animals that do not show evidence of significant post-mortem transport. As pholadid colonization progressed, secondary inhabitants took advantage of the pioneering efforts of the pholadids and became nestlers in the borings. At this point, a departure from "textbook" descriptions takes place.

According to Warme and McHuron (1978), the species richness of modern-marine hardgrounds is due to borers that open the substrate "frontier" for secondary settlers. They stated that abandoned borings become inhabited and modified by an assortment of organisms. Warme (1970) noted that in advanced stages, borings become interconnected to form networks of passageways. Kennedy (1974) remarked that erosion rates are higher where pholadids colonize, due to a weakened substrate and wave action. Evans (1968b) found that erosion in such areas increased by a factor of 24. However, in the assemblage studied at Arroyo Mezquital, there is no ichnologic evidence of species richness. Nor is there evidence of significant erosion of the substrate, even in the populous central area of study.

Our interpretation is that the set of environmental conditions that gave rise to the pholadid community was very short-lived. The central, "seed" area of the colony reached a population maximum and the secondary settling by horizontal-burrowing crustacean opportunists then began while the pholadids were in the process of peripheral expansion. Abruptly, a sediment influx overwhelmed the filter-feeding pholadids. The few borings that extend upward into the overlying strata represent the efforts of surviving crustaceans. Ultimately, in a regimen of increasing storm-generated sedimentation, they too perished.

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