

IMPLICATIONS FOR THE GASTROPOD FOSSIL RECORD OF MISTAKEN CRAB PREDATION ON EMPTY MOLLUSC SHELLS

by SALLY E. WALKER *and* SYLVIA BEHRENS YAMADA

ABSTRACT. Durophagous crabs were found to make unusually high rates of predatory mistakes by attacking empty gastropods and models of intact bivalves. This mistaken predation is attributed to the crypticity of the shell: if a crab cannot readily determine whether a shell contains food, as is the case with gastropod shells, it will crush it. In contrast, empty bivalve shells (represented by half-shells) are readily examined by crabs and rejected. The taphonomic implications, and importance for the gastropod fossil record, are two-fold. First, where predatory crabs are abundant, shells of gastropods are prone to detrimental biological destruction at three levels: while alive, inhabited by hermit crabs and empty. Bivalves are subject to predation at only one level: while alive. Second, because empty gastropods are preyed upon, peel marks on fossil gastropods are therefore not a reliable indication of crab predation. Mistaken predation is a source of taphonomic bias that needs to be considered in interpreting predation events in fossil gastropods.

BIAS in the marine invertebrate fossil record stems from two main sources: (1) physical factors, such as varying sedimentation rates or current sorting; and (2) biological factors, such as rate of hard part production, secondary inhabitation of shells, or bioerosion (for reviews see Walker 1989, 1990, 1992; Parsons and Brett 1991; Kidwell and Bosence 1991). Our study addresses one potential source of biological bias: the impact of durophagous crabs on molluscan assemblages. Vertebrate predators, rather than invertebrate predators, have received the most attention in taphonomic studies (e.g. Zapfe 1939*a*, 1939*b*, 1939*c*; Davis 1959; Brain 1967, 1980; Sutcliffe 1970, 1973; Mellett 1974; Brothwell 1976; Hill 1976, 1980; Mayhew 1977; Dodson and Wexlar 1979; Behrensmeyer and Dechant-Boaz 1980; Haynes 1980; Shipman and Walker 1980; Steadman 1986). Additionally, vertebrate predators have been the focus, or suggested agents, of taphonomic anomalies in molluscan assemblages (e.g. Teichert and Serventy 1947; Carter 1974; Boucot 1981; Lindberg and Kellogg 1982; Cadée 1989). How have invertebrate predators, such as crabs, affected the potential fossil record of shelled prey (e.g. bivalves and gastropods)?

Unsuccessful predation on gastropods and subsequent shell repair by the living snail provide a record of predation events that can be tracked in the fossil record (Vermeij *et al.* 1981, 1982). Peeled apertures on gastropod shells, indicating crab predation, may also be used to infer predation intensity for some gastropods species (Vermeij 1983). However, crabs have been observed to attack model oyster shells (LaBarbera 1981) and empty gastropod shells in soft-sediment environments (Walker 1988). We have found that rocky shore crabs attack empty gastropod shells at relatively high rates, peeling or crushing the shells as if the shells contained prey. We have termed this phenomenon 'mistaken predation'. If rates of mistaken predation are high in modern intertidal communities, then predatory peel marks on fossil gastropods may not adequately represent the amount of live shelled prey attacked.

Gastropod shells are also inhabited by many species of invertebrates (for reviews see Vermeij 1987; Walker 1990). The evolutionary effects of predation on hermit crabs in contrast to living snails has been shown (LaBarbera and Merz 1992; see also Rossi and Parisi 1973; Vermeij 1977), but many other invertebrate species remain to be studied. Gastropod shells, then, are susceptible to destruction at three levels: while inhabited by the living snail, while occupied by secondary

occupants, and while empty. Bivalves are preyed upon only once, while alive. After the bivalve is dead, it gapes or disarticulates into two valves. A crab can readily discern if the bivalve shell is empty, but it cannot determine if a gastropod shell is empty. This disparity in predation may lead to differential preservation of bivalve shells over gastropod shells in habitats where durophagous crabs are abundant.

The object of our study was two-fold: (1) to determine the extent of mistaken predation by crabs in a modern environment; and (2) to determine whether bivalves and gastropods are equally susceptible to this preservational bias. Crabs use predominantly chemical cues in prey selection, but may also use tactile cues (Case 1964; Pearson *et al.* 1979; Vermeij 1983). We predict that live gastropod and bivalve prey (with both cues) should be attacked at a higher rate than model prey (only tactile cues). Empty bivalve shells, represented by single valves, will not be attacked by crabs, whereas empty gastropod shells will be attacked. If model or empty 'prey' are attacked at a rate that is at least 10 per cent that of live prey, then we consider mistaken predation to be an important factor in modification of gastropod death assemblages.

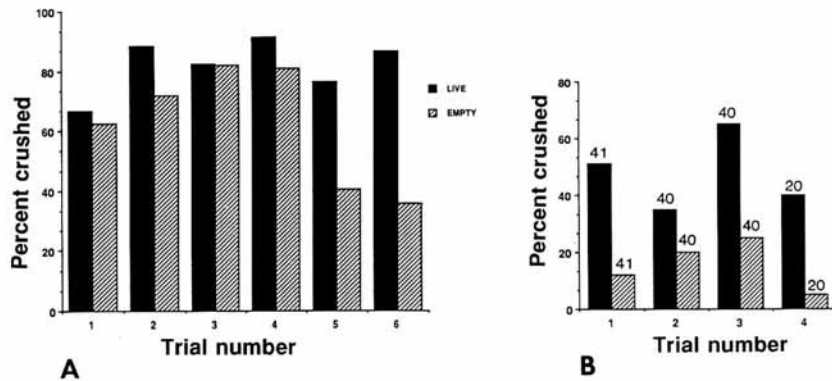
EXPERIMENTAL WORK

Field and laboratory experiments were conducted at Friday Harbor Marine Laboratory, San Juan Islands, Washington, in August 1990, when red rock crabs (*Cancer productus*) were most active. *Cancer productus* is an opportunistic forager that routinely feeds on bivalves and gastropods (Knudsen 1964; Boulding and Hay 1984; Robles *et al.* 1989). Of all the intertidal crabs, this species attains the largest size (up to 180 mm carapace width) and is the most voracious predator in the Pacific Northwest (Palmer 1985; Behrens Yamada and Boulding unpublished data). This species may be an important agent in structuring intertidal communities in the Pacific Northwest (Casilla and Paine 1987; Robles *et al.* 1989) but more studies are needed to determine the degree of importance. *Cancer productus* first appeared in the Pliocene of North America (Nations 1975, 1979). The propensity for biological modification of the gastropod fossil record, via shell destruction, is greater, however, as an additional twelve species of *Cancer* originated in North America between the Miocene and Pleistocene.

In the laboratory, live, empty and hermitted gastropod shells (*Littorina sitkana*: shell height range, 13–18 mm; mean, 14.7 mm) were given to fourteen red rock crabs, *Cancer productus* (carapace width range, 84–115 mm; mean, 99.8 mm) in the following manner: all crabs were housed in individual plastic containers (220 × 220 × 90 mm) with mesh holes to allow for water circulation. All containers were submerged in aquaria with a constant flow of sea water. The crabs were offered a series of three live *L. sitkana* and three empty *L. sitkana* for six trials (trial period of eight hours) to test if the crabs selectively attacked live or empty *L. sitkana*. Next, the same crabs were fed a series of three live *L. sitkana* and three hermitted (*Pagurus hirsutiusculus*) *L. sitkana* for seven trials (trial period of eight hours) to test if the crabs attacked both types of shelled prey. At the end of each trial, the shells were scored for predation. Only available shells were scored; snails or hermit crabs that crawled out of reach of the crab were deemed unavailable and were not used in the analysis.

To determine if the laboratory results were artefacts of confined crabs, gastropod shells were tethered in the field. Live and empty *L. sitkana* shells were tethered to fishing net lead line and placed in the low intertidal zone (1.5 foot level) in front of Friday Harbor Laboratories. Empty gastropod shells were plugged with plasticine clay to prevent hermit crab occupancy. A total of 141 live and 141 empty shells were used in iterations of 41 live:41 empty; 40 live:40 empty; 20 live:20 empty for four trials of 24 hours duration. At the end of each trial, each shell was scored whether it was crushed or peeled (for the purpose of this study both crushed and peeled shells were scored as 'crushed').

Live mussels (*Mytilus edulis*) were chosen for the bivalve experiment. Live ($n = 62$), model ($n = 76$) and half-shell ($n = 71$) mussels were attached to lead lines and placed in the low intertidal (1.5 foot level) for three trials (each trial was 24 hours). Model mussels were made from clean *M. edulis* shells that had been boiled and dried, plugged with plasticine clay and sealed with Z-spar



TEXT-FIG. 1. A, crab predation on live and empty *Littorina sitkana* for six laboratory trials. Only crabs in trials five and six attacked significantly more live snails than empty shells (trial five: $\chi^2 = 14.2$, $df = 1$, $P < 0.001$; trial six: $\chi^2 = 21.1$, $df = 1$, $P < 0.001$). B, frequency of crab attack on live and empty *L. sitkana* in field experiments. Numbers above columns represent sample size. Significantly more live than empty *L. sitkana* were crushed on trials one and three (trial 1: $\chi^2 = 14.4$, $df = 1$, $P < 0.001$; trial 3: $\chi^2 = 15.8$, $df = 1$, $P < 0.001$).

(splash-zone) epoxy. Mussels were tethered to the lead line with monofilament (15 lb) line. The tethered mussels were emplaced below the pier of the laboratory, so that observations on crab feeding could be monitored. At the end of each trial, crab-damaged shells were recorded.

RESULTS

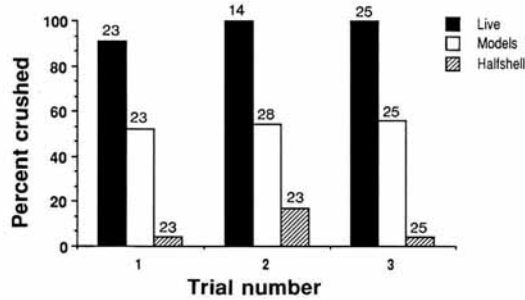
Cancer productus crushed over 50 per cent of live, empty, and hermitted *L. sitkana* shells in the laboratory (Table 1). This represents a high attack rate on all shelled 'prey'. Initially, the crabs did not discriminate between empty and living *Littorina sitkana*. However, after five trials (forty hours) three of the fourteen crabs significantly preferred live over empty shells (Text-fig. 1). This apparent learning skewed the overall results (Table 1) towards a significant difference in attack rate between live and empty shells.

TABLE 1. Fate of live, empty and hermitted *Littorina sitkana* offered to *Cancer productus*. When only available 'prey' are considered, significantly more live *L. sitkana* were attacked than empty shells ($\chi^2 = 26.2$, $df = 1$, $P < 0.001$) or hermitted shells ($\chi^2 = 26.0$, $df = 1$, $P < 0.001$). Frequency of crushed shells (number of crushed/number of available prey) is given in parentheses.

Laboratory experiments	Crushed shells	Intact shells	Unavailable prey	Total offered
Live <i>L. sitkana</i> vs Empty shells	162 (0.86)	27	33	222
Live <i>L. sitkana</i> vs Hermitted shells	131 (0.78)	37	123	291
Empty shells vs Hermitted shells	147 (0.54)	126	18	291

In the field, crab attacks on live *L. sitkana* varied from 35 to 60 per cent per day and on empty *L. sitkana* from 5 to 25 per cent per day (Text-fig. 2A). Therefore, even though crabs will attack empty gastropod shells in the field they exhibited a significant preference for live gastropods.

Crabs readily attacked live and empty (model) mussels in the field. Attack rates for the tethered mussels (*Mytilus edulis*) varied between 95 and 100 per cent for live and approximately 50 per cent for model mussels (Text-fig. 2B). Again, crabs showed a significant preference for live prey. Very few half-shell shells were chipped ($n = 4$), suggesting that the crabs could readily examine these shells and determined that the shells were empty. At high tide, up to fourteen red rock crabs foraged along the mussel lines at night, with most activity occurring between 11 p.m. and 2 a.m. Attacked model mussels were clearly seen through the water because of the bright green and blue of the plasticine clay.



TEXT-FIG. 2. Field experiments with live, model and half-shells of the mussel *Mytilus edulis*. Frequency of crushed live mussels was higher, and the frequency of crushed half-shells was lower, than expected by chance alone ($\chi^2 = 103.7$, $df = 2$, $P < 0.001$).

DISCUSSION

All three of our predictions were supported. First, *Cancer productus* crushed shells of *L. sitkana* whether they were empty, hermitted or live. However, significantly more living *Littorina* were selected over hermitted or empty shells of *Littorina*. Second, crabs attacked live mussels and model mussels in the field, further indicating that crabs are tactile foragers. In Florida, model bivalves made of resin also were not immune from attacks by the stone crab, *Menippe mercenaria*, and the blue crab, *Callinectes sapidus* (LaBarbera 1981). However, chemical cues must aid crabs in distinguishing between live and model mussels in our study. Crabs, as visual and tactile predators, are fooled by empty and model molluscs, but not necessarily all the time, because the rates of predation differed between live and model shells. The rate of predation on live mollusc shells in the field was extremely high. Crabs attacked over 95 per cent of the living mussels and 50 per cent of the model mussels. If crabs relied solely on tactile or visual cues, almost all the model shells would have been attacked. Lastly, mussel half-shells were rarely attacked. Crabs could readily distinguish that half shells had no meat in them and did not break them open.

Most individuals of *Cancer productus* in our laboratory experiments failed to distinguish between empty and live prey. It appears that crabs cannot determine if a gastropod shell is empty, thus the shells are cryptic in terms of their food resource. Shells that are not cryptic, like the mussel half-shells, can readily be explored by the crab and not damaged. Perhaps crabs learn to attack empty gastropod shells because they may contain a food resource, such as amphipods, hermit crabs, or a living snail deeply retracted in the shell. Crabs can learn better prey handling techniques (Hughes 1979; Cunningham and Hughes 1984) and thus, some crabs may learn as we suggest, to distinguish empty from food-rich, inhabited shells. Alternatively, not all behaviours are optimal from our human-based perspective (Rothstein 1982; Pyke 1984; Blaustein and Porter 1990) yet may persist as seemingly non-adaptive traits (Gould and Lewontin 1979). As Maynard-Smith (1978) suggested, we need to know the relative importance of the various processes affecting what we might call maladaptive or suboptimal behaviour.

In conclusion, from a taphonomic perspective, we propose that in habitats where crabs are common, the gastropod shell may be selected against, and the death assemblage will be extremely

biased towards peeled and fragmented shells. That is, crab predation not only occurs on the living snail and hermitted shells, but also on empty gastropod shells, creating an additional and important biological bias against gastropod representation in the fossil record. Additionally, peeled shells do not directly indicate predation on the primary food source (i.e. the living snail). Peeling and puncturing, characteristics of predatory crabs, can also occur in empty gastropod shells because of mistaken predation. Therefore, our results indicate that predation rates (based on peeled/crushed apertures) attributed to crabs in the fossil record may be anomalous.

Bivalves may not suffer from this bias for two reasons: first, empty (articulated) valves are not occupied by secondary inhabitants in a similar manner as gastropod shells (e.g. by hermit crabs, amphipods), and hence may not be attacked, and secondly, the gaping valves may readily be explored by a predatory crab. In conclusion, mistaken predation by crabs is a potential source of preservational bias between gastropods and bivalves, presently unaccounted for in the fossil record.

Acknowledgements. We would like to thank D. Willows, Director, and D. Duggins for access to Friday Harbor Marine Laboratories, H. Campbell for her invaluable field assistance, A. Blaustein for non-optimality argumentation, and A. J. Boucot, E. G. Boulding, M. Kowalewski, A. Olson, S. A. Navarrete, P. D. Taylor and anonymous reviewers for improving this manuscript. This research was supported, in part, by A. Boucot (S.E.W.), NSF grant EAR 900-4519 (S.E.W.) and the Oregon State University Research Council (S.B.Y.)

REFERENCES

- BEHRENSMEYER, A. K. and DECHANT-BOAZ, D. E. 1980. The recent bones of Amboseli Park, Kenya, in relation to East Africa paleoecology. 79–93. In BEHRENSMEYER, A. K. and HILL, A. P. (eds). *Fossils in the making*. University of Chicago Press, Chicago, Illinois, 338 pp.
- BLAUSTEIN, A. R. and PORTER, R. H. 1990. The ubiquitous concept of recognition with special reference to kin. 123–148. In BEKOFF, M. and JAMIESON, D. (eds). *Interpretation and explanation in the study of animal behaviour. Volume 1: Interpretation, intentionality, and communication*. Westview Press, Boulder, Colorado, 505 pp.
- BOUCOT, A. J. 1981. *Principles of benthic marine paleoecology*. Academic Press, New York, 463 pp.
- BOULDING, E. G. and HAY, T. K. 1984. Crab response to prey density can result in density-dependent mortality of clams. *Canadian Journal of Fisheries and Aquatic Science*, **41**, 521–525.
- BRAIN, C. K. 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Scientific Papers of the Namib Desert Research Station*, **32**, 1–11.
- 1980. Some criteria for the recognition of bone-collecting agencies in African caves. 107–130. In BEHRENSMEYER, A. K. and HILL, A. P. (eds). *Fossils in the making*. University of Chicago Press, Chicago, Illinois, 338 pp.
- BROTHWELL, D. R. 1976. Further evidence of bone chewing by ungulates: the sheep of North Ronaldsay, Orkney. *Journal of Archaeological Science*, **3**, 179–182.
- CADÉE, G. C. 1989. Size-selective transport of shells by birds and its palaeoecological implications. *Palaeontology*, **32**, 429–437.
- CARTER, R. W. G. 1974. Feeding sea birds as a factor in lamellibranch valve sorting patterns. *Journal of Sedimentary Petrology*, **44**, 689–692.
- CASE, J. 1964. Properties of the dactyl chemoreceptors of *Cancer antennarius* Stimpson and *C. productus* Randall. *Biological Bulletin*, **127**, 428–446.
- CASILLA, J. C. and PAINE, R. T. 1987. Predation and community organization on eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural*, **60**, 131–151.
- CUNNINGHAM, P. N. and HUGHES, R. N. 1984. Learning of predaceous skills by shorecrabs *Carcinus maenas* feeding on mussels and dogwhelks. *Marine Ecological Progress Series*, **16**, 21–26.
- DAVIS, D. H. S. 1959. The barn owl's contribution to ecology and palaeoecology. *Ostrich Supplement*, **3**, 144–153.
- DODSON, P. and WEXLAR, D. 1979. Taphonomic investigations of owl pellets. *Paleobiology*, **5**, 275–284.
- GOULD, S. J. and LEWONTIN, R. F. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London, Series B*, **205**, 581–598.
- HAYNES, G. 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. *Paleobiology*, **6**, 341–351.
- HILL, A. P. 1976. On carnivore and weathering damage to bones. *Current Anthropology*, **17**, 335–336.

- HILL, A. P. 1980. Early postmortem damage to the remains of some contemporary East African mammals. 131–152. In BEHRENSMEYER, A. K. and HILL, A. P. (eds). *Fossils in the making*. University of Chicago Press, Chicago, Illinois, 338 pp.
- HUGHES, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist*, **113**, 209–221.
- KIDWELL, S. M. and BOSENCE, D. W. J. 1991. Taphonomy and time-averaging of marine shelly faunas. 115–209. In ALLISON P. A. and BRIGGS, D. E. (eds). *Taphonomy: releasing the data locked in the fossil record*. Plenum Press, New York, 560 pp.
- KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crab-like Anomura of Puget Sound, Washington. *Pacific Science*, **18**, 3–33.
- LABARBERA, M. 1981. The ecology of Mesozoic Gryphaea, Exogyra, and Ilymatogyra (Bivalvia: Mollusca) in a modern ocean. *Paleobiology*, **7**, 510–526.
- and MERTZ, R. 1992. Postmortem changes in strength of gastropod shells: evolutionary implications for hermit crabs, snails, and their mutual predators. *Paleobiology*, **18**, 367–377.
- LINDBERG, D. and KELLOGG, M. 1982. Bathymetric anomalies in the Neogene fossil record: the role of diving marine birds. *Paleobiology*, **8**, 402–407.
- MAYHEW, D. F. 1977. Avian predators as accumulators of fossil mammal material. *Boreas*, **6**, 25–31.
- MAYNARD-SMITH, J. 1978. Optimization theory in evolution. *Annual Review of Ecology and Systematics*, **9**, 31–56.
- MELLETT, J. S. 1974. Scatological origins of microvertebrate fossil accumulations. *Science*, **185**, 349–350.
- NATIONS, G. D. 1975. The genus *Cancer* (Crustacea: Brachyura): systematics, biogeography and fossil record. *Science Bulletin of the Natural History Museum of Los Angeles County*, **23**, 1–104.
- 1979. The genus *Cancer* and its distribution in time and space. *Bulletin of the Biological Society of Washington*, **3**, 153–187.
- PALMER, A. R. 1985. Adaptive value of shell variation in *Thais lamellosa*: effects of thick shells on vulnerability to and preference by crabs. *Veliger*, **27**, 349–356.
- PARSONS, K. P. and BRETT, C. E. 1991. Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation. 22–65. In DONOVAN, S. K. (ed.). *The processes of fossilization*. Belhaven Press, London, 303 pp.
- PEARSON, W. H., SUGARMAN, P. C., WOODRUFF, D. L. and OLLA, B. 1979. Thresholds for detection and feeding behaviour in the Dungeness crab, *Cancer magister*. *Journal of Experimental Marine Biology and Ecology*, **39**, 65–78.
- PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–575.
- ROBLES, C., SWEETHAM, D. A. and DITTMAN, D. 1989. Diel variation of intertidal foraging by *Cancer productus* L. in British Columbia. *Journal of Natural History*, **23**, 1041–1049.
- ROSSI, A. C. and PARISI, V. 1973. Experimental studies of predation by the crab *Eriphia verrucosa* on both snail and hermit crab occupants of conspecific gastropod shells. *Bollettino di Zoologica*, **40**, 117–135.
- ROTHSTEIN, S. I. 1982. Successes and failure in avian egg and nestling recognition with comments on the utility of optimality reasoning. *American Zoologist*, **22**, 547–560.
- SHIPMAN, P. and WALKER, A. 1980. Bone-collecting by harvesting ants. *Paleobiology*, **6**, 496–502.
- STEADMAN, D. W. 1986. Holocene vertebrate fossils from Isla Floreana, Galápagos. *Smithsonian Contributions to Zoology*, **413**, 1–103.
- SUTCLIFFE, A. J. 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. *Nature*, **227**, 1110–1113.
- 1973. Similarity of bones and antlers gnawed by deer to human artefacts. *Nature*, **246**, 428–430.
- TEICHERT, C. and SERVENTY, D. L. 1947. Deposits of shells transported by birds. *American Journal of Science*, **245**, 322–328.
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: Gastropods, predators and grazers. *Paleobiology*, **3**, 245–258.
- 1983. Traces and trends of predation, with special reference to bivalved animals. *Palaentology*, **26**, 455–465.
- 1987. *Evolution and escalation*. Princeton University Press, Princeton, New Jersey, 527 pp.
- SCHINDEL, D. E. and ZIPSER, E. 1981. Predation through geological time: evidence from gastropod shell repair. *Science*, **214**, 1024–1026.
- ZIPSER, E. and ZARDINI, R. 1982. Breakage-induced shell repair in some gastropods from the Upper Triassic of Italy. *Journal of Paleontology*, **56**, 233–235.

- WALKER, S. E. 1988. Taphonomic significance of hermit crabs (Anomura: Paguroidea): epifaunal hermit crab-infaunal gastropod example. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **63**, 45-71.
- 1989. Hermit crabs as taphonomic agents. *Palaios*, **4**, 439-452.
- 1990. Biological taphonomy and gastropod temporal dynamics. 391-412. In MILLER, III, W. (ed.). *Paleocommunity temporal dynamics: the long-term development of multispecies assemblies. Paleontological Society Special Publication No. 5*, 421 pp.
- 1992. Criteria for recognizing marine hermit crabs in the fossil record using gastropod shells. *Journal of Paleontology*, **66**, 535-558.
- ZAPPE, H. 1939a. Lebensspuren der eiszeitlichen Hoehlenhyane; die urgeschichtliche Bedeutung der Lebensspuren knochenfressender Raubtiere. *Palaeobiologica*, **7**, 111-146.
- 1939b. Untersuchungen über die Lebensspuren knochenfressender Raubtiere, mit besonderer Berücksichtigung der Hyane. *Akademie der Wissenschaften, Wien. Mathematische Naturwissenschaftliche Klasse*, **76**, 33-35.
- 1939c. Lebensspuren der eiszeitlichen Hoehlenhyane und deren urgeschichtliche Bedeutung. *Forschungen und Fortschritte*, **15**, 269-270.

SALLY E. WALKER

Department of Geosciences
University of Arizona
Tucson, AZ 85721, USA

SYLVIA BEHRENS YAMADA

Department of Zoology
Oregon State University
Corvallis, OR 97731, USA

Typescript received 5 August 1992
Revised typescript received 22 October 1992