Functional morphology of the cuticular terraces in burrowing terrestrial brachyuran decapods

ENRICO SAVAZZI

Observations on *Gecarcinus lateralis* and *Ocypode quadrata* from Bermuda show that their cuticular terraces are not functional as burrowing sculptures, as previously assumed. Instead, they increase the friction against the walls of the burrow when the animal wedges itself to avoid being extracted by predators. No significant increase in the number of terraces takes place during growth in the size interval available for this study. This is different from the situation described as usual in burrowing decapods, and is rather similar to that of crevice-dwelling crabs. The distribution of terraces and their ontogenetic pattern, therefore, are not reliable indicators of the life habits. □ *Functional morphology, ontogeny, cuticular sculptures, Decapoda, Crustacea.*

Enrico Savazzi, Paleontologiska Institutionen, Box 558, S-751 22 Uppsala, Sweden. Present address: Dept. of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.; 27th April, 1984.

Terrace lines, or terraces, are ridges with a sharp edge and one side consistently steeper than the other. Adjacent terraces are usually parallel, and their steeper faces are oriented in the same direction. The occurrence of comparable terrace patterns in several invertebrate groups (inarticulate brachiopods, bivalve and gastropod molluscs, trilobites, isopods, brachyuran and anomuran decapods, anomalocystitid echinoderms or calcichordates) and the apparently simple relationships between their morphology and adaptive significance have attracted the attention of biologists and paleontologists (Seilacher 1961, 1972, 1973, 1976; Stanley 1969, 1970, 1977, 1981; Miller 1975; Schmalfuss 1975, 1976, 1978, 1981; Signor 1980, 1982a, 1982b, 1982c, 1983; Savazzi 1981, 1982, 1983; Jefferies *et al.* 1981; Savazzi *et al.* 1982).

A consistent number of invertebrates which burrow in loose sediments possess terrace sculptures. Being asymmetrical in cross-section and oriented perpendicularly to the burrowing direction, the terraces exert a different friction against the substrate when pushed in opposite directions. The steeper terrace sides, which face away from the burrowing direction, wedge against the sediment particles and greatly increase the resistance against back-slippage. The gently sloping opposite sides, on the other hand, do not hinder progress through the sediment. In general, brachyuran and anomuran decapods burrow back-wards, and possess burrowing sculptures with the steeper faces directed anteriorly.

Efficient burrowing terraces should possess a high frictional asymmetry, i.e. they should display a high difference in the friction exerted in forward and backward direction. The efficiency of burrowing terraces depends on their physical size being proportional to the sediment grain-size (Seilacher 1972, 1973; Savazzi 1981, 1983).

Therefore, the size and spacing of burrowing terraces should remain constant during the growth of the organism, in order to stay proportionate to the unchanging granulometric composition of the sediment. In an arthropod, this requires that new terraces are introduced during ontogeny, to compensate for the overall increase in size of the organism. The constraints imposed by different growth patterns have been analyzed by Seilacher (1972, 1973), Savazzi (1981, 1983), Signor (1982a) and Savazzi *et al.* (1982).

In some brachyuran decapods that wedge themselves within rock crevices to avoid being extracted by predators, the terraces increase the friction against the surface of the rock. Schmalfuss (1978) showed that the number of terraces in these crabs does not increase during growth. Apparently, the efficiency of terraces acting as frictional anchors against a solid substrate does not depend on the size and number of terraces per unit of surface area, but on their total number, which does not have to change allometrically.
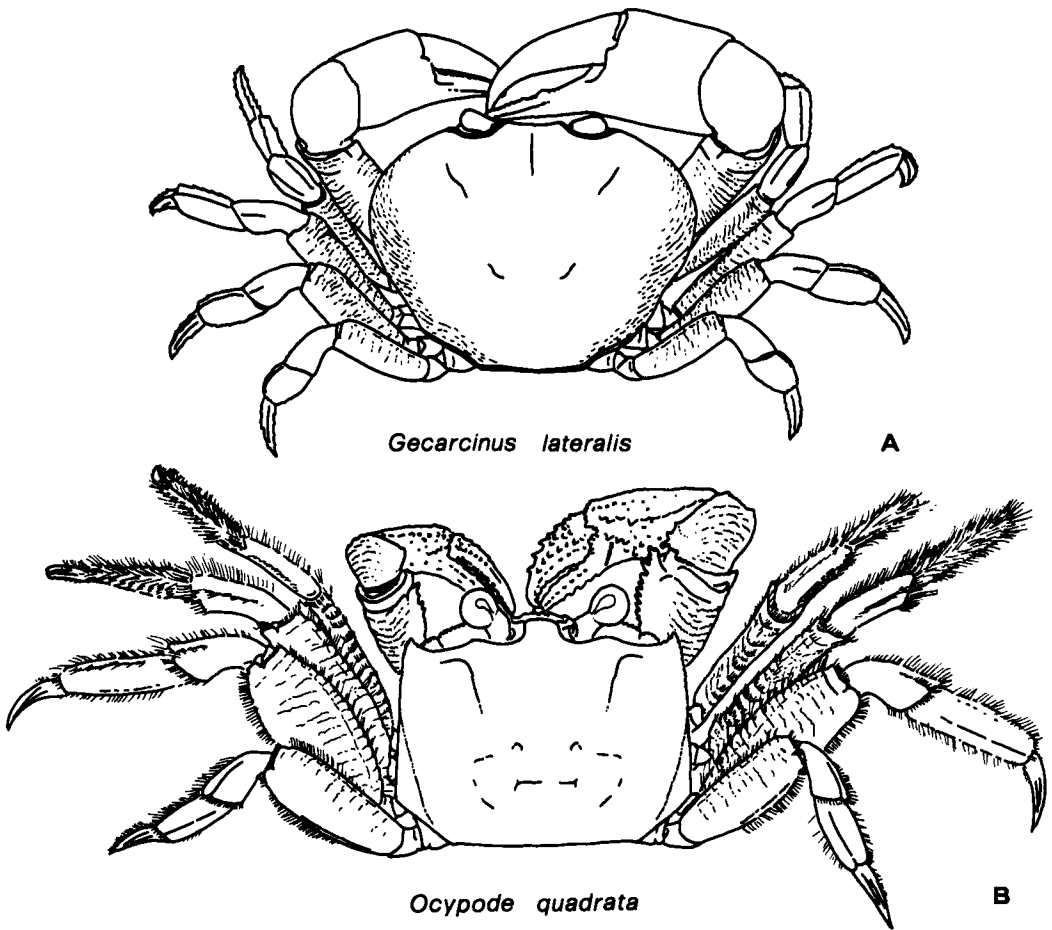
Fig. 1. Schematic drawing of *Gecarcinus lateralis* (A) and *Ocypode quadrata* (B) showing the distribution of terraces on the carapace and legs, approximately × 0.7.

The different ontogenetic patterns of burrowing and crevice-wedging terraces appeared to be potentially useful in assessing the life habits of fossil forms (Schmalfuss 1976, 1978). However, it has subsequently been found that the fossil brachyuran *Ranina (Lophoranina),* a burrower in sandy sediments, did not display an ontogenetic increase in the number of terraces (Savazzi 1981). The profile of the terraces became instead progressively modified during growth, to compensate for the diminishing burrowing efficiency.

In addition, the physical dimensions of burrowing terraces are related to characteristics of the burrowing process (e.g. hydraulic loosening of the sediment by water jets: Savazzi 1982). Coarse terraces are not necessarily indicative of life in coarse-grained sediments, but may suggest a combination of hydraulic and mechanical burrowing processes. It therefore appears that the relationships between morphology and function of terrace lines are much more complex than previously suspected. A larger sample of organisms must be studied, before general conclusions are attempted.

Material and methods

Two species of terraced brachyuran decapods, *Gecarcinus lateralis* (Freminville) (Gecarcinidae) and *Ocypode quadrata* (Fabricius) (Ocypodidae) were studied alive in the Bermuda Islands during the summer of 1982. No true growth series was obtained, but individuals at different growth

stages provided material for an analysis of the ontogenetic patterns.

Individuals of *Gecarcinus lateralis* ranging from 17 to 40 mm in carapace length were collected at Tucker's Town, around Harrington Sound and in several other localities in the Bermuda Islands, up to 0.5 km from the sea.

Ocypode quadrata was observed in the field on a beach near Tucker's town, in the supratidal zone. Individuals with carapace lengths ranging from 6 to 33 mm were collected.

Both species were allowed to burrow in the field and in the laboratory. The burrowing movements were recorded by time-lapse photography. As a rule, the nature of the substrate and the characteristics of the environment did not alter the basic burrowing behavior. As previously observed in several species of marine crabs (Savazzi 1982), the burrowing process consists of a rather stereotyped sequence of movements, ethologically distinctive at the generic or specific level and little affected by environmental conditions.

Fig. 2. Terraces on the lateral (A) and ventral (B) surface of the carapace of adult *Gecarcinus lateralis*, × 50. The terraces in B are modified to serve as part of a stridulatory apparatus.

Morphology, ontogeny and ecology

Gecarcinus lateralis is adapted to life in subaerial environments. It typically excavates permanent tunnels in compacted soil in grass-covered areas or among tree roots and boulders, from which it emerges at night for foraging. The preferred sediment type in Bermuda is unsorted, of prevalently fine grain size. *G. lateralis* possesses finely tuberculated terraces on the chelipeds, on the walking legs, and on a band around the sides of the carapace (Figs. 1A, 2, 3A–C). The steeper sides of the terraces on the legs are directed distally, while the carapace terraces are directed roughly upwards and anteriorly. At the center of the pterigostomial region (see Fig. 2B), the terraces are modified to serve as a stridulatory apparatus (Klaassen 1973; Schmalfuss 1978, Fig. 25). The individual tubercles forming the terraces in this region are more projecting and pointed than in other regions (Fig. 2).

Ocypode quadrata burrows above the high-water mark on medium to fine sand beaches. This species digs semi-permanent tunnels in moist sand. The ecology of *Ocypode* and the morphology of its burrows have been described by Cowles (1908), Hayasaka (1935), Crane (1941), Milne & Milne (1946). In *Ocypode quadrata*, terrace lines occur only on the chelipeds and walking legs (Figs. 1B, 3D). The terraces,
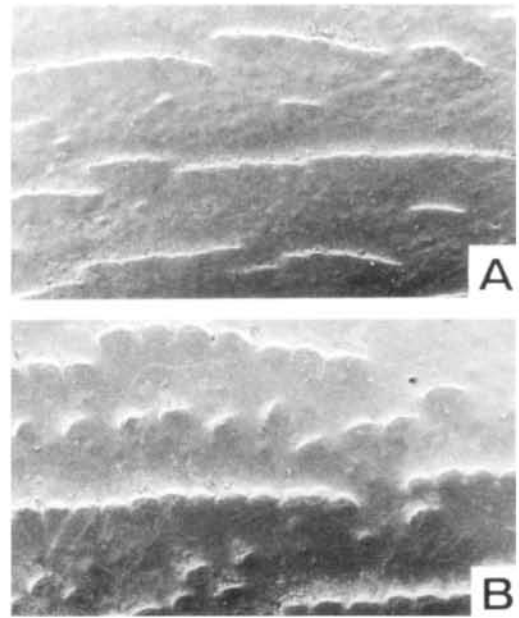
like in *G. lateralis*, consist of laterally aligned tubercles, and their steep faces are directed distally. The carapace bears round tubercles, which are symmetrical in cross-section. The sculpture in *O. quadrata* is representative of most species in the Ocypodidae.

A comparison of individuals of both species at different growth stages shows that the terrace sculptures become progressively reduced with age (Fig. 4). In addition, the leg terraces progressively lose their asymmetrical cross-sections and the sharp edges, until only rounded ribs may remain in the largest adults. In *O. quadrata*, degeneration of the terraces is accompanied by a marked increase in the number and length of the associated setae. In neither species does significant secondary increase in the number of terraces take place during growth in the size interval available for this study (Fig. 3), unlike what is reported by Schmalfuss (1978) for individuals of *G. lateralis* of smaller sizes. The carapace terraces in *G. lateralis* tend to increase in relative length during growth, but the general aspect of the adult carapace is not markedly different from that of juveniles (Fig. 3A). As a whole, there is a reduction of the extension of terrace sculptures during ontogeny (Fig. 4). This ontogenetic pat-
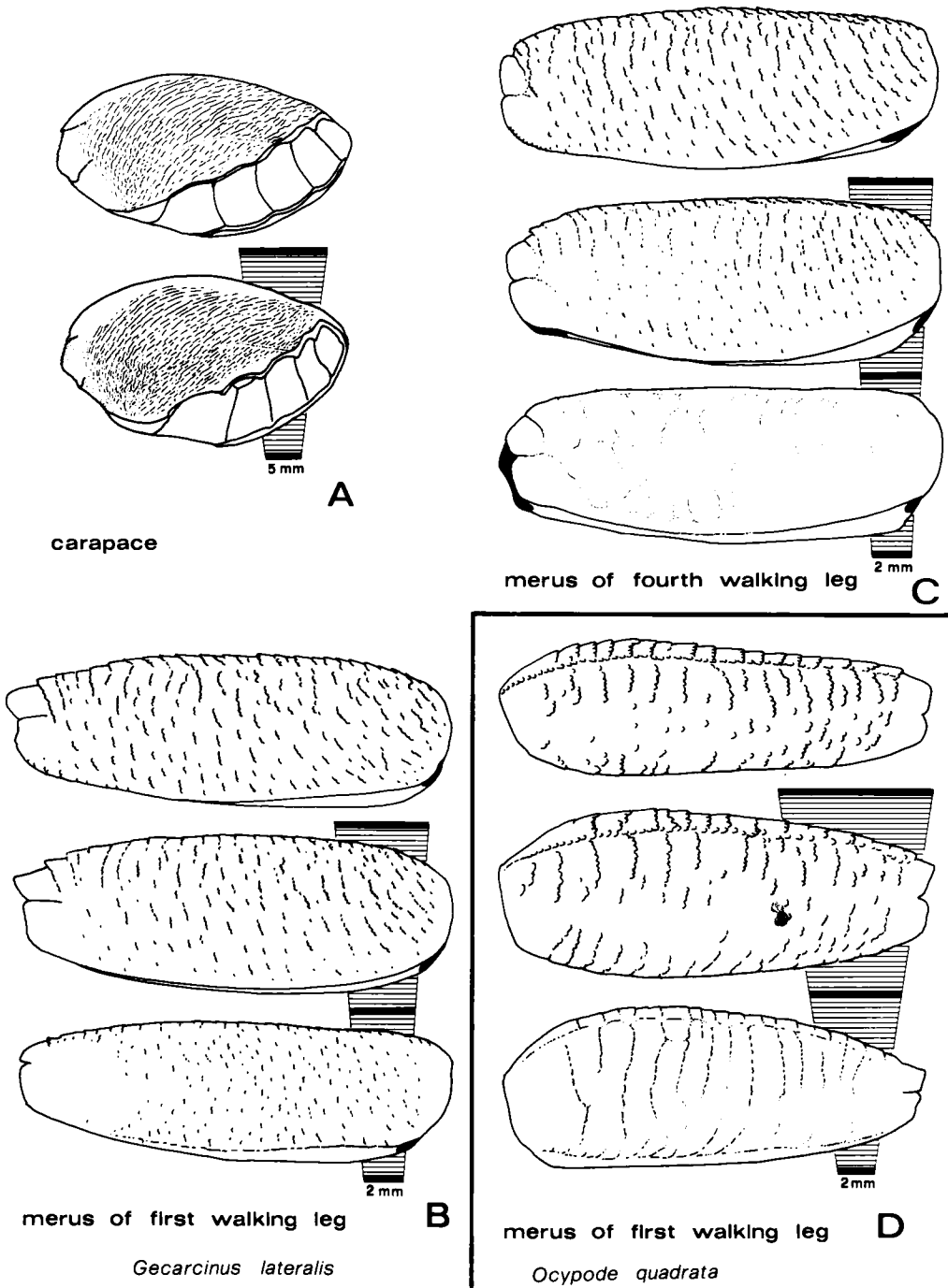
carapace

merus of fourth walking leg   **C**

merus of first walking leg   **B**

Gecarcinus lateralis

merus of first walking leg   **D**

Ocypode quadrata

Fig. 3. Growth pattern of the terraces on the carapace (A, left view) and on the anterior side of the merus of the walking legs (B–D) in the two species studied in this paper. The distal direction is to the left in B and C; to the right in D. See the text for details.
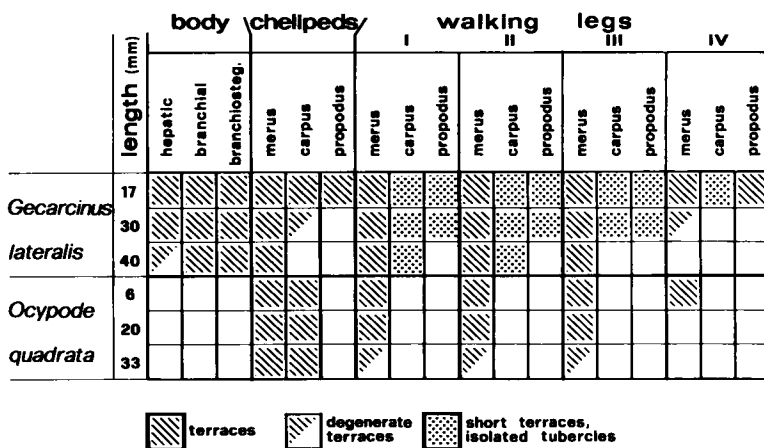
	length (mm)	body			chelipeds			walking legs I			II			III			IV		
		hepatic	branchial	branchiosteg.	merus	carpus	propodus	merus	carpus	propodus	merus	carpus	propodus	merus	carpus	propodus	merus	carpus	propodus
Gecarcinus	17																		
	30																		
lateralis	40																		
Ocypode	6																		
	20																		
quadrata	33																		

Fig. 4. Distribution of terraces and asymmetrical tubercles in *Gecarcinus lateralis* and *Ocypode quadrata* at different growth stages.

Legend: terraces — degenerate terraces — short terraces, isolated tubercles

tern contrasts with that described in other burrowing crabs (Seilacher 1976; Schmalfuss 1978).

Both *Ocypode quadrata* and *Gecarcinus lateralis* begin to burrow by scraping the soil with the dactyli of the first to third walking legs on one side. The legs on the opposite side anchor the crab to the ground. The fourth pair of walking legs, which is significantly smaller than the others, is only used to support the body. When a small amount of loose sediment has been collected beneath the animal, it is pushed away frontally by the chelipeds. As the burrow deepens, the material accumulating beneath the body of the crab is periodically collected between the chelipeds and the ventral surfaces (often also among the folded walking legs used for burrowing) and brought to the entrance of the tunnel (Fig. 5A, C).

Once outside the burrow, *Ocypode* throws the sediment a short distance with a rapid jerk of the body. *Gecarcinus*, on the other hand, tends to pile it close to the burrow entrance. From time to time, both species use the chelipeds to flatten the accumulating sediment mound. *Ocypode* was often observed to turn upside down within the tunnel while burrowing, in order to smooth the walls and ceiling. The flattened manus of *Ocypode* is well suited for holding the scarcely cohesive sandy sediments.

Discussion

According to Schmalfuss (1976, 1978), *Gecarcinus lateralis* carries the loosened sediment out of the burrow by holding it between the chelipeds and the pterigostomial regions. In his view, the terraces on the ventral surfaces of the carapace and on the merus of the chelipeds are functional in increasing the friction between the cuticle and the sediment, preventing it from slipping away.

From the above observations, it is apparent that the terraced regions in both species are not in contact with the sediment at any moment of the burrowing process. In no instance were the crabs observed to carry the sediment out of the burrows in the manner described by Schmalfuss (1978). When burrowing in dry ground, *Gecarcinus* may come out of the burrow with small amounts of sediment escaping between the chelipeds and the body, which may account for Schmalfuss's interpretation. However, the bulk of the sediment is always carried between the manus of both chelae and the antero-ventral surfaces. Furthermore, the extent of the terraced regions along the sides of the carapace largely exceeds the reach of the chelipeds, and the orientation of the terraces is not optimal to prevent sediment particles from slipping downwards (Fig. 5A). From these observations, it is concluded that the terraces on the carapace of *Gecarcinus lateralis* have no part in the burrowing process. The different behavior of *G. lateralis* reported by Schmalfuss (1978) may be due to the different size of the individuals (his observations were carried out on a juvenile population), and to possible genotypic, climatic, and substrate differences between the two populations. The observation that the nature of the substrate generally does not affect the burrowing dynamics (Savazzi 1982,
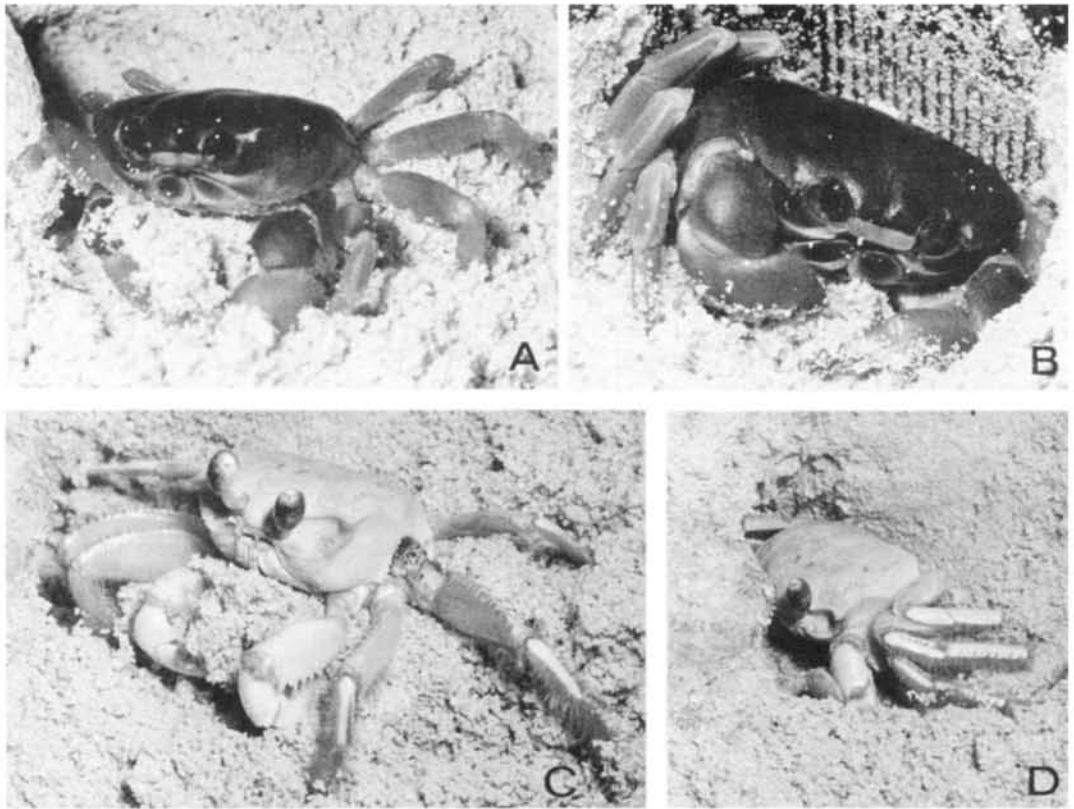
Fig. 5. Burrowing and wedged *Gecarcinus lateralis* (A and B, respectively) and *Ocypode quadrata* (C–D). The vertical lines in B are a feature of the plastic box used in the experiments. For photographic purposes, the crabs were induced to assume the wedged posture in shallow, incomplete burrows. Normally, wedging occurs much deeper within the burrows. Approximate scale: A, C–D: × 0.5; B: × 0.7.

and above) seems to exclude the latter possibility.

A sideways burrowing process can explain the lack of transversal terrace lines on the dorsal surfaces of the two species in discussion. Longitudinal terrace lines might be expected in this case. Decapod crustaceans do not seem to possess morphogenetic constraints limiting the distribution and orientation of terrace lines on the body and appendages. In fact, a few forms possess sculptures (not related to burrowing) consisting of complex convoluted lines with a sharp edge and an asymmetrical cross-section. The steep faces of these lines are directed anteriorly, posteriorly and laterally in different regions of the carapace. Therefore, it is legitimate to expect that the morphogenesis of longitudinal terrace lines in place of transversal lines is not prevented by constructional constraints. Rather, it may be

noted that burrowing terraces occur in decapods burrowing in loose sediments by alternately using the body and appendages as retraction and penetration anchors, respectively. Burrowing in a sediment with a shear strength sufficiently high to prevent the tunnel walls from collapsing is a considerably different process (see above), and constitutes a strong reason why burrowing sculptures should not be expected to occur in either species.

The behavior of the crabs within their burrows was studied to find possible adaptive values for the terrace sculptures. Both species, when scared, were often observed to fold the legs at the side of the body and wedge themselves against the walls of the burrow (Fig. 5B, D). Usually, the crabs also turned within the burrow to face the intruder. Since the body is much larger than long, this results in both sides of the

carapace wedging against the walls. One of the chelipeds was raised towards the intruder, or both were firmly pressed against the floor of the burrow.

The wedging behavior was easily triggered in *G. lateralis,* while *O. quadrata* often resorted to running out of the burrow, or fighting. Adult *O. quadrata,* in particular, usually assumed the wedging posture when alert, but immediately switched to the running or fighting behavior when directly touched. The distribution and orientation of the terraces on the legs in *G. lateralis* is consistent with a wedging function. An additional adaptive value of the wedging behavior may be that of bringing sensory setae in close contact with the sediment, thus enhancing the possibility of picking up vibrations of the substrate (this capability is possessed by both species). This function is not mutually exclusive with wedging to prevent removal from the burrow. Similarly, a primary wedging function does not automatically exclude a burrowing-related secondary function like the one described by Schmalfuss (1978).

Trying to dislodge a wedged *G. lateralis* by pulling at its appendages is often impossible without breaking them, as shown also by the numerous individuals observed in the field lacking one or more appendages. With respect to the wedging behavior, the shear strength of compacted soil is comparable with that of a solid substrate. The terraces on the carapace of *G. lateralis,* together with the leg terraces, form a redundant frictional apparatus ensuring that the loss of a few walking legs would not impair the effectiveness of the wedging behavior. Once one or more legs are lost, their wedging function is taken over by the terraced surfaces on the side of the carapace, pushed against the substrate by the legs on the opposite side.

The ontogenetic change in behavior of *O. quadrata* from wedging to active escape or fighting may also be related to the nature of the sediment, which in this case is scarcely cohesive wet sand. Its shear strength is low enough to make it likely that large individuals of this species, if relying on wedging as a defense against predators, could be extracted whole from their burrows by pulling on their legs. In both species, the terraces on the chelipeds are much coarser than on the rest of the body. This reflects the higher pressure exerted by these appendages, in comparison with the muscularly and mechanically weaker walking legs.

The wedging behavior is likely to be effective in discouraging predation by vertebrates, and may also be significant in intraspecific combat. In nature, individuals wandering at a distance from their own burrows may seek refuge in occupied burrows. In one instance, two males of *G. lateralis* were observed inside a burrow. The two individuals were locked with the chelae and wedged against the walls of the burrow, and were energetically trying to dislodge each other.

The reduction of the terraces during growth suggests that effective wedging sculptures become progressively less advantageous as the body size increases. However, this does not imply that the wedging behavior in general is less adaptive for adults than for juveniles. While adult *O. quadrata* prefer to run or fight, adult *G. lateralis* still wedge themselves within their burrows. In this case, the sheer increase in muscular strength resulting from the increase in size, together with a substrate unlikely to give way when subjected to mechanical stress, may render specialized sculptures unnecessary. As shown by Warne (1977) and Schmalfuss (1978), the formation of cuticular terraces in crabs is a complex process of selective resorption and resecretion of the exocuticle during the pre-molt stages. Since this process is certainly energy-consuming, terraces can be expected to degenerate, once they no longer constitute a significant selective advantage.

Conclusions

The primary function of the terraces in *Gecarcinus lateralis* and *Ocypode quadrata* is to increase the friction against the substrate when these organisms wedge themselves against the walls of the burrow. This behavior prevents the crabs from being extracted from their burrows by predators, and may also be advantageous in intraspecific fighting. The sculptural pattern and the associated behavior may prove to be common in terrestrial and semi-terrestrial crabs. Previous ideas on the function of terraces as burrowing sculptures in *G. lateralis* are not supported by the present study.

The reasons for the degeneration of the terraces during ontogeny may be different in the two species. Adults of *Ocypode quadrata* rely on their speed to escape predators, while adult *Gecarcinus lateralis* seem to rely on their muscular force and on the high shear strength of the sub-

strate to maintain the wedged posture. The terraces on the sides of the carapace in *G. lateralis* can be interpreted as a redundant feature, enabling this species to wedge within the burrow even if several legs are lost. The nature of the substrate, and the connected burrowing process, are also likely reasons why true burrowing sculptures do not occur, and should not be expected, in either species.

The function of the terraces is reflected in their ontogenetic pattern: like in crevice-dwelling crabs, there is no marked ontogenetic increase in the number of terraces, at least in the size interval available for this study.

Terrace patterns similar in general appearance to those occurring in the two species studied in this paper occur in many other Recent and fossil brachyuran decapods. These sculptural patterns are essentially similar in burrowing (e.g. *Cardisoma,* Ocypodidae, some Grapsidae) and crevice dwelling forms (*Cyclograpsus, Pachygrapsus, Grapsus*). Therefore, although a more detailed analysis may show characteristics useful in the inference of their autecology, their general aspect, distribution on the body and appendages, and ontogenetic pattern cannot be used as a reliable indicator of the life habits.

References

Cowles, R. P. 1908: Habits, reactions and associations in *Ocypoda arenaria. Pap. Tortugas Labor. Carnegie Inst. Washington 2,* 1–41.

Crane, J. 1941: On the growth and ecology of brachyuran crabs of the genus *Ocypode.* (Eastern Pacific Expedition of the New York Zoological Society XXIX). *Zoologica 26,* 297–310.

Hayasaka, I. 1935: The burrowing activities of certain crabs and their geologic significance. *Am. Midland Natur. 16,* 99–103.

Jefferies, R. P. S., Savazzi, E., Seilacher, A. & Signor, P. 1981: Grabskulpturen. *In* Reif, W.-E. (ed.): *Paläontologische Kursbücher 1, Funktionsmorphologie,* 111–140.

Klaassen, F. 1973: Stridulation und Kommunikation durch Substratschall bei *Gecarcinus lateralis* (Crustacea Decapoda). *J. Comp. Physiol. 83,* 73–79.

Miller, J. 1975: Structure and function of trilobite terrace lines. *Fossils and Strata 4,* 155–178.

Milne, L. J. & Milne, M. J. 1946: Notes on the behavior of the ghost crab. *Am. Naturalist 80,* 362–380.

Savazzi, E. 1981: Functional morphology of the cuticular terraces in *Ranina* (*Lophoranina*) (brachyuran decapods; Eocene of NE Italy). *Neues Jahrb. Geol. Paläont. Abh. 162,* 231–243.

Savazzi, E. 1982: Burrowing habits and cuticular sculptures in Recent sand-dwelling brachyuran decapods from the Northern Adriatic Sea (Mediterranean). *Neues Jahrb. Geol. Paläont. Abh. 163,* 369–388.

Savazzi, E. 1983: Aspects of the functional morphology of fossil and living invertebrates (bivalves and decapods). *Acta Universitatis Upsaliensis. Abstr. Uppsala Diss. Fac. Science 680,* 1–21.

Savazzi, E., Jefferies, R. P. S. & Signor, P. V. III 1982: Modifications of the paradigm for burrowing ribs in various gastropods, crustaceans and calcichordates. *In* Seilacher, A., Reif, W.-E. & Westphal, F. (eds.): Studies in paleoecology. *Neues Jahrb. Geol. Paläont. Abh. 164,* 206–217.

Schmalfuss, H. 1975: Morphologie, Funktion und Evolution der Tergithocker bei Landisopoden (Oniscoidea, Isopoda, Crustacea). *Zoomorphologie 80,* 287–316.

Schmalfuss, H. 1976: Panzerskulpturen bei Arthropoden. *Zbl. Geol. Paläont. II 1976,* 315–316.

Schmalfuss, H. 1978: Structure, patterns and function of cuticular terraces in Recent and fossil arthropods. I. Decapod crustaceans. *Zoomorph. 90,* 19–40.

Schmalfuss, H. 1981: Structure, patterns and function of cuticular terraces in trilobites. *Lethaia 14,* 311–341.

Seilacher, A. 1961: Krebse im Brandungssand. *Natur u. Volk 91,* 257–264.

Seilacher, A. 1972: Divaricate patterns in pelecypod shells. *Lethaia 5,* 325–343.

Seilacher, A. 1973: Fabricational noise in adaptive morphology. *Syst. Zool. 22,* 451–465.

Seilacher, A. 1976: Terrassenlinien des anomuren Krebses *Emerita. Zbl. Geol. Paläont. II 1976,* 313–314.

Signor, P. W. III 1980: Shell sculpture aids in burrowing in turritelliform gastropods. *Geol. Soc. Am. Abstr. Prog. 12,* 522.

Signor, P. W. III 1982a: Constructional morphology of gastropod ratchet sculpture. *Neues Jahrb. Geol. Paläont. Abh. 163,* 349–368.

Signor, P. W. III 1982b: Influence of shell shape on burrowing rates in infaunal turritelliform snails. *Third N. Am. Paleont. Conv. Proc. 2,* 483–487.

Signor, P. W. III 1982c: Resolution of life habits using multiple morphologic criteria: shell form and life-mode in turritelliform gastropods. *Paleobiology 8,* 378–388.

Signor, P. W. III 1983: Burrowing and the functional significance of ratchet sculpture in turritelliform gastropods. *Malacologia 23,* 313–320.

Stanley, S. M. 1969: Bivalve mollusk burrowing aided by discordant shell ornamentation. *Science 166,* 634–635.

Stanley, S. M. 1970: Relation of shell form to life habits in the Bivalvia (Mollusca). *Geol. Soc. Am. Mem. 125,* 1–296.

Stanley, S. M. 1977: Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. *Palaeontology 20,* 869–899.

Stanley, S. M. 1981: Infaunal survival: alternative functions of shell ornamentation in the Bivalvia (Mollusca). *Paleobiology 7,* 384–393.

Warne, G. F. 1977: *The Biology of Crabs.* 197 pp. Elek Science, London.