Arthropod Tunnel Systems

Due to their relatively weak appendages, trilobites were ill-suited for deep burrowing. Only few of them produced permanent tunnels, in contrast to decapod *crustaceans* such as crabs and shrimps, whose legs are not only stiffer, but also have more freedom to bend in various directions. The differentiation of only five pairs of legs into pereiopods also allowed them to be operated individually, rather than collectively, in locomotion and burrowing. So it is not surprising that crustaceans had less difficulty than trilobites to excavate more compact mud and to produce open tunnels as permanent domiciles. This ability also gave them a lead in the competitive trend to penetrate the sediment to deeper and deeper levels (infaunal tiering). In addition, this trend (and the ability to actively reinforce tunnel walls in looser sediments; Pl. 18) increased the preservation potential of the crustacean burrows, because they (1) remained open long enough to be passively filled with different (mostly coarser) sediment; (2) they were unlikely to become eroded and (3) they were not erased by deeper burrows during the upward shift of tiers following sedimentation. Whereas trilobite burrows are commonly penetrated by deeper-tier worm burrows (often misinterpreted as prey; Pl. 74), bioturbational overprints on crustacean tunnels are restricted to exploitation of their sedimentary fill by *Chondrites* (Pl. 74). As another preservational advantage, the relatively lose fill was a preferred site for concretionary prefossilization. The resulting calcareous, sideritic, or chertified casts are resistant enough to become secondarily reworked, or to weather out, without losing the details of scratch patterns (Pl. 16). Open tunnels also acted as traps, in which delicate microfossils are preferentially preserved in three dimensions.

The tunnel systems of terrestrial *insects* have a much lower preservation potential. An exception are domiciles whose walls became actively solidified by an organic cement. This is the case in the nests of soil bees, in the depositories of dung beetles, and in pupa chambers (Pl. 3). The latter are so resistant that they may survive reworking and limited transport, just as body fossils.

There is also the question, whether insect nests should be classified as trace fossils? It becomes critical in objects like bee or wasp nests constructed above ground, or in the minings made by larvae in leaves or bark. Coprolites and cololites are a similar case. Such objects are fossilized and their interpretation poses the same problems as ordinary trace fossils. Still they are not covered by the present text, which only deals with traces in the sense of biogenic *sedimentary* structures.

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Chapter IV

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Plate 16: Crab and Shrimp Burrows

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Plate 19: Rhizocoralliids

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Schloz W (1968) Über Beobachtungen zur Ichnofazies und über umgelagerte Rhizocorallien im Lias alpha Schwabens. N Jb Palaeont Mh 11:691–698 (*Rhizocorallium* diagenesis)

Uchman A, Buniak I, Bubniak A (2000) The *Glossifungites* ichnofacies in the area of its nomenclatural archetype. Ichnos 7: 183–193 (*Glossifungites* at its type locality resembles *Rhizocorallium*)

Valenzuela M, García-Ramos JC, Gonzalez Lastra J, Suarez De Centi C (1985) Sedimentación ciclica margo-calcárea de plataforma en el Lías de Asturias. Trabajos de Geología, Univ. de Oviedo 15, pp 45–52 (Fig. 5: *Glossifungites* in Jurassic firmground)

Veevers JJ (1962) *Rhizocorallium* in the Lower Cretaceous rocks of Australia. BMR Bull 62(2):3–14, 3 pls. (Pl. 1: *Glossifungites* preservation)

■ *Thalassinoides* (U. Triassic, Italy)

Plate 16
Crab and Shrimp Burrows

Crab Burrows. On tropical beaches today, the dominant tunnel builders are brachyuran crabs. Their tail is folded under the body, so that the animals are wider than long. They can run *sideways*, and reverse gears, at considerable speed. In tube-dwelling species (e.g., fiddler crabs), body length has become even further reduced, so that the now cigar-shaped animal fits perfectly into the cylindrical tunnel, as shown in the diagram. These crabs are active during low tide, grazing the algae that develop at the sediment surface. While scraping the sediment with the pincers in a medio-posterior direction, they employ a *forward* gear in order to scan a broader surface (like *Dimorphichnus*, Pl. 9), but upon the slightest disturbance they switch to sideward running and retreat into the burrow. Other activities also take place at the surface, such as defense of the territory against neighbors, or courtship. For this purpose male fiddler crabs (*Uca*) have enlarged one of their two claws into a colorful flag waved according to specific codes. For a patient observer willing to remain motionless in spite of mosquito bites, these activities provide a fascinating spectacle. They also leave a record in the form of tracks and scratchways radiating from burrow entrances, but this protocol does not survive the next flood and never enters the fossil record, because the algal skin does not resist erosion. What we find are the vertical burrows. Only in exceptional cases – as in the figured chertified cast from the **Cretaceous chalk** of northern Germany – are leg scratches preserved on their surfaces. Their pattern registered by rolling the cast over clay like a cylinder seal reflects a brachyuran tracemaker. Otherwise burrow morphologies show little variation, because most brachyuran galleries serve the single purpose of shelter against enemies, high tides and storms.

Shrimp Burrows. The great majority of post-Paleozoic crustacean burrows can be ascribed to *ghost shrimps*, as represented by modern species of *Callianassa* and *Upogebia* (Pl. 18). These are relatives of the hermit crabs whose exoskeleton is weakly mineralized (and hence transparent: "ghost" shrimps) except for the claws, which are the only body parts likely to be fossilized. In modern environments, ghost shrimp are rarely seen because of their truly troglodytic existence; like moles, they spend all their lives in the underground tunnel systems. Only the expert recognizes their presence from the volcano-like cones of flushed-out sediment (Pl. 18). On these mounds, one may also find the characteristic faecal pellets, whose complex internal structure makes them stratigraphically useful in the fossil record (*Favreina*). More recently, paleontologists working in modern mud flats managed to make epoxy casts of complete burrow systems and dig them out by underwater "vacuum cleaners". By their size and complexity, such casts would deserve a place in a gallery of modern art, but for the biologist they express complex behavioral programs and reveal functions that different parts of the tunnel system had in the life of the inhabitant shrimp family.

Fossil examples show similar morphologies, but they also provide additional information. In the figured specimen from the Miocene of Spain, for instance, pointed ends and claw traces running at a slight angle to the burrow axis reflect a certain digging technique, in which the pincers probably made headway, while the other pereiopods widened the tunnel by scraping the wall in tailward direction. As the scratch pattern is the same all around the cast, the animal must have also rotated along its axis while excavating (a trilobite would have had difficulties in doing this). There are also finer "brushings" on both sides of the branching points. They were probably made by the setate tail appendages, which serve as gills and also ventilate and flush the tunnel system. Such details cannot be seen in a modern cast, which depicts the wall after it has been lined with mucus. Behavioral modifications will be discussed in Pl. 18.

Neglecting that through Earth history shrimplike crustaceans other than *Callianassa* probably produced similar burrows (the earliest known examples are from the Paleozoic), one may informally group all branching crustacean tunnels into one ichnofamily, Ophiomorphidae (name derived from the most familiar representative, *Ophiomorpha*). Even if they are taxonomically heterogeneous, they share a number of characters:

1. They maintain a deeper tier than other burrows and are therefore preferentially preserved.
2. Vertical shafts tend to branch at depth into a boxwork of largely horizontal tunnels.
3. At the dichotomous branching points, tunnel diameter increases as in elk antlers, in order to provide space for the animal to turn around by somersaulting.
4. If scratches are preserved, they run at a slight angle in two directions, so that their overcrossing produces a rhombic network.

Plate 16 · Crab and Ghost-Shrimp Burrows   51

Scratch Patterns
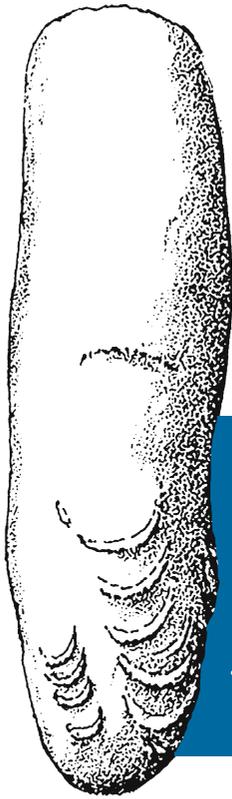
chertified crab burrow,
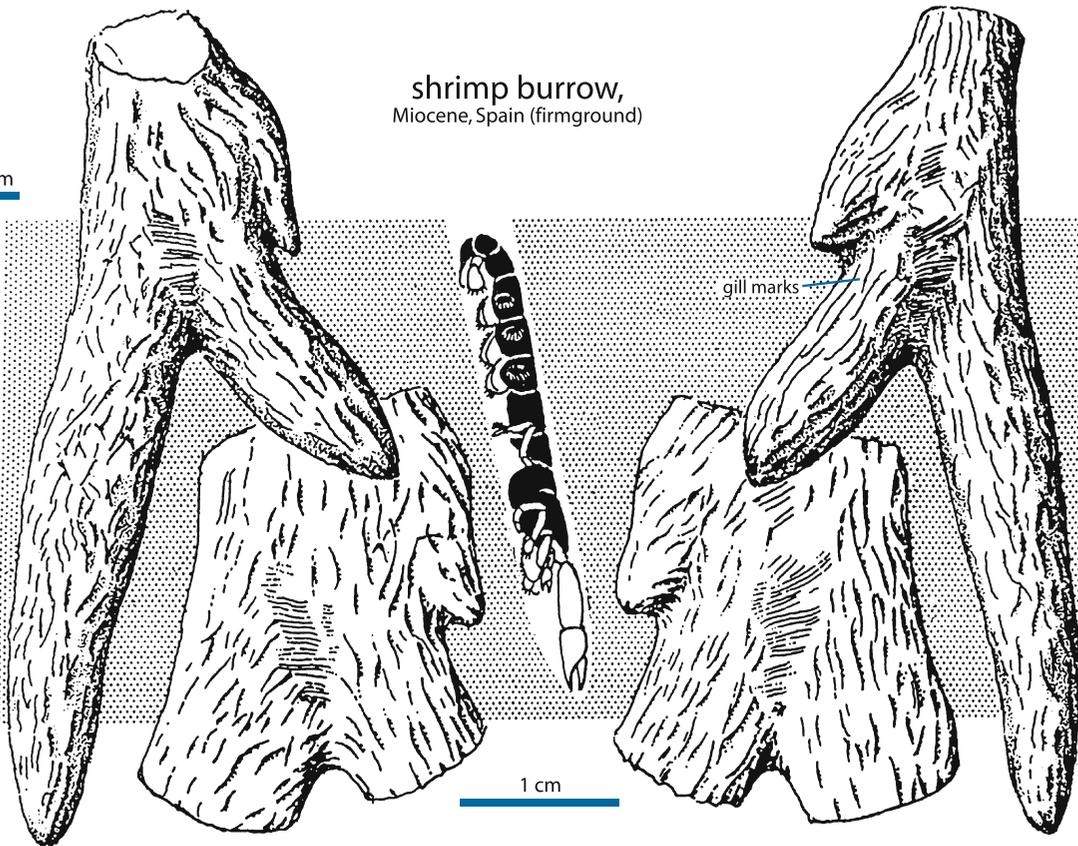U. Cret. Chalk, Rügen, Germany

Uca

1 cm
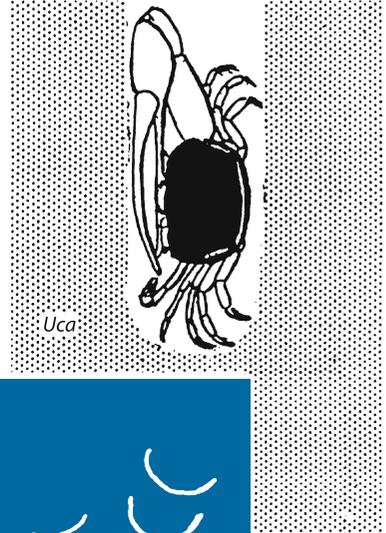
rolling on clay

shrimp burrow,
Miocene, Spain (firmground)

1 cm

gill marks

1 cm

Plate 17
Other Arthropod Tunnels and Nests

The previous examples made it clear that the architecture of a particular tunnel system is not sufficient to identify the owner, because different groups of animals may have independently evolved the same burrowing techniques and behavioral programs. Thus additional clues are necessary to single out rhizocoralliids made by crustaceans (Pts. 19–20), but due to preservational constraints only few of the potential criteria are available in any single occurrence. This dilemma increases with regard to less known, or less distinctive, burrow morphologies. This chapter presents cases, in which at least an arthropod origin may be assumed.

Teichichnoid Forms. One may question whether this group of burrows should be referred to *Teichichnus* (Pl. 41), whose arthropod affiliation rests on the weakest of all criteria: size. Yet the Cambrian *Teichichnus rectus* well represents the basic architectural principle. Even though only the retrusive spreite is preserved, there was clearly a generating tunnel. While functioning as a U-tube, it had no vertical shafts and more closely resembled an inverted arch. Unfortunately no scratches or faecal pellets are preserved in *T. rectus*; nevertheless its thumb-like diameter (as in all following examples) is the only argument for a crustacean, rather than a wormlike, tracemaker.

A form from the Middle Cambrian sandstones of Öland, Sweden (not figured) looks very much like *Teichichnus* in vertical outcrops, but as the retrusive spreite lamellae are bilobed, it may represent trilobite-made tunnels. It would be worth the effort to search for a specimen penetrating into an underlying shale in order to corroborate such an interpretation by *Cruziana*-like scratches.

In the architecturally similar *Trichophycus* from Ordovician limestones, such scratches are preserved (hence the name, meaning "hairy seaweed") and sometimes occur in sets of up to six parallel scratches. They suggest a trilobite maker (e.g., *Cryptolithus*); but scratch patterns in other occurrences are more likely made by crustaceans.

Serial Teichichnids. Besides providing only limited protection, shallow teichichnid burrow systems have the disadvantage that retrusive spreite production must end when the tunnel gets too close to the sediment surface. Therefore it is not surprising that some forms tend to expand their mines by intermittent dislocation of one tunnel exit. This results in a more complex spreite structure: while backfills are retrusive at every station, expansion must proceed in a protrusive mode. New fields may be opened also in *Trichophycus*, but in the following forms this was done in a regular fashion.

The earliest example is *Ctenopholeus* from the Lower Devonian Hunsrück Slates. In *Margaritichnus* from the Lower Carboniferous (Colorado, Kansas, and Morocco), the shafts follow in line at short distances, but instead of opening to the surface, they appear to end blindly like upside-down elephant feet, but still this may result from only the spreite being preserved. In material from Morocco, openings proceed protrusively and in one case alternate, as in the Irish *Intexalvichnus* of the same age. All these forms must be studied by serial sectioning before the underlying programs can be fully understood.

Pholeus abomasoformis from the Muschelkalk of northern Germany (Pl. 18) appears to stem from a crustacean unrelated to ghost shrimps. Probably the inhabitant used the wider chamber as shelter, but added a narrower vertical shaft for easier ventilation. Otherwise the fossil appears to be a simple internal cast of the cavity, without a backfill body.

Insect Burrows. In terrestrial habitats, insects make domiciles in various substrates, some of which also provide food (wood or leaves). In the present context we focus on wet-sediment burrows made by insect larvae. They are usually backstuffed behind the animal, rather than forming transversal backfills as in rhizocoralliid and teichichnid burrows. As one would expect, insect burrows are generally restricted to nonmarine sediments.

Scoyenia (Pl. 32) occurs in redbeds of Permian and younger ages, where it forms straight ridges on the soles of thin sand layers. In this mode it may preserve delicate longitudinal scratches which are arranged in groups and give the tunnel cast a somewhat "segmented" appearance. In stretches where the animal happened to backfill mud instead of sand, the hypichnial ridges may also switch into sharp-edged grooves. Potential makers are insect larvae that bulldoze below microbial mats in the style of "undermat miners" (Pl. 45).

In mud puddles, insect burrows appear as elevated ridges tracing the course of the tunnel underneath. The figured *modern* spiral trace was observed in such a puddle. In a fabricational sense, it reflects a program, in which probings are made only to one side and stop short before hitting a previous tunnel. When there is no more space left, the larva turns into a pupa, from which the fly emerges after metamorphosis. So the function of this complex pattern is probably that of a protective fence around the most vulnerable stage of the insect's life cycle. The beehive-shaped wall of *Tambia* from the Oligocene titanothere beds of Wyoming, in another preservation and associated with Permian vertebrate tracks (Pl. 3), reflects a similar strategy. Similar pupal chambers are known from the Tertiary of South America and Australia.

Plate 17 · Other Arthropod Tunnels and Nests   53

Backfilled Arthropod Tunnels
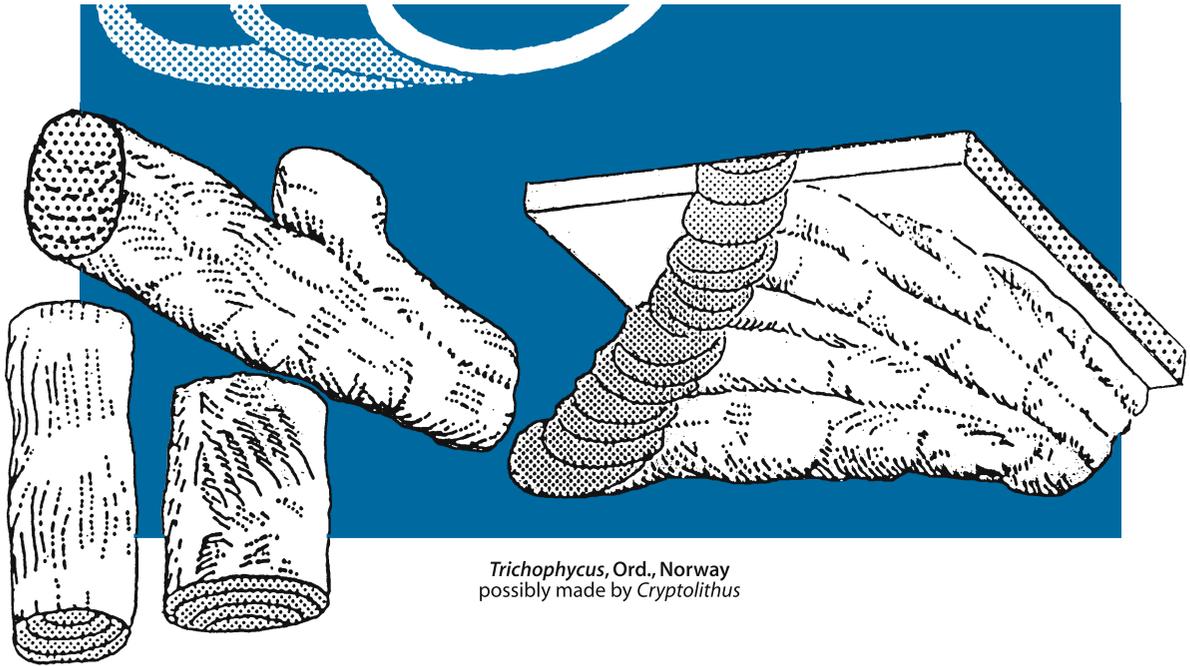
Trichophycus, **Ord., Norway**
possibly made by *Cryptolithus*
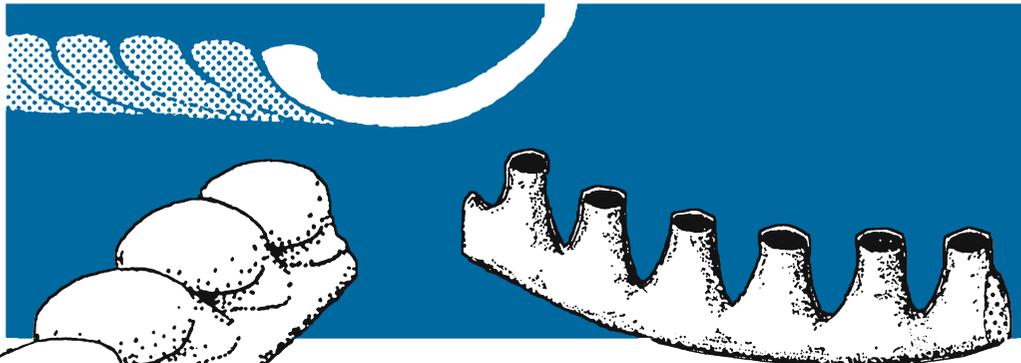
Margaritichnus, **Carb., USA**

Ctenopholeus, **L. Dev., Germany**

defence
zones
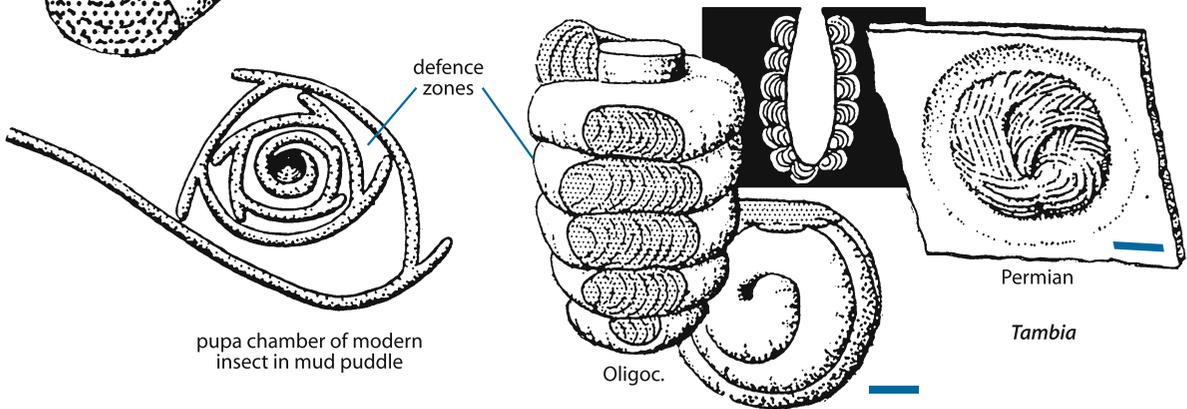
pupa chamber of modern
insect in mud puddle

Oligoc.

Permian

Tambia

Plate 18
Ophiomorphids

Tunnel Systems. We have already talked about ghost shrimp burrows in the text to Pl. 16. Basically there are several *shafts* connected at depth by a horizontal **gallery system**. The tunnels may reach 10 cm in diameter and anastomose into hexagonal meshes (the figured *Thalassinoides suevicus* comes from the Lower Jurassic). There may also be bulb-shaped "**turnarounds**" between branchings, as well as a **corkscrew** extension to lower levels (*Gyrolithes*), whose function will be discussed below.

At first glance, *Granularia* from Late Cretaceous (and younger) deepsea turbidites (flysch facies) looks very different. It reaches only the diameter of a pencil and the branchings are sparse and form angles smaller than 120°. Yet, the presence of turnarounds, scratches and pelletoidal linings (from which the name is derived) suggest an ophiomorphid relationship. Therefore this may be another example for the general onshore → offshore trend. In the deepsea environment the shrimp responsible became not only miniaturized, but also penetrated more deeply (possibly several meters; see Pl. 72). This behavior allowed them to reach the nutrient-rich bases of new sandy turbidites. At the same time, the original boxwork changed into a more centralized system with a reduced number of shafts and long probes along the turbidite sole.

Preservational Modifications. On Pl. 16 we discussed scratch patterns (*Spongeliomorpha* preservation). They are preserved in the cast if the tunnel was dug in stiff mud or as it crossed the interface between sand and an underlying mud layer, but due to secondary wall linings they may not be seen on the inside of the actual tunnel (*Thalassinoides* preservation). In clean sand, however, the shrimp has to protect the wall against collapse and against erosion by its own ventilatory current. This is done with distinctive *mud pellets*. As they are globular and much larger than thalassinid fecal pellets, they probably consist of material sorted out and shaped by the mouth parts like the sand balls of modern ghost crabs (*Ocypode*). Because these balls tend to become diagenetically mineralized, specimens weathered out from loose sands show a typical cobblestone pattern (*Ophiomorpha* preservation). In other cases the modification of the fossil burrow is strictly diagenetic: shafts served as a conduit, so that a concretionary halo formed in the surrounding sediment. In less consolidated matrix, such as the Cretaceous Chalk, a weathered-out "*Paramoudra*" may be several meters high and by far exceed the diameter of the burrow nucleus.

In consolidated storm sands, horizontal gallery systems are exposed on bedding planes. On top surfaces, they form positive **epireliefs** with smooth surfaces (casts of inner tunnel) and rims of weathered-out mud pellets. On sole surfaces they occur either as three-dimensional *Thalassinoides*, or as **washed** *out* hyporeliefs without sharp margins, i.e. tunnels dug in stiff mud became uncovered and buried again during a storm.

In micritic limestones, one commonly observes a cylindrical tube running along the crest of the shrimp burrow, as if a worm had been creeping along the already filled tunnel. In reality it is an artifact related to the filling process itself. Comparable **draft fill** channels are known in ceratite steinkerns, in which the phragmocone chambers became gradually mud-filled by draft currents. Eventually only a channel with the diameter of the narrow siphuncular passages is left on top of the fill. This principle can be applied to *Callianassa* burrows, because their openings are always narrower than the tunnel and its inhabitant, who never leaves its burrow voluntarily.

Functional Modifications. The micritic *Krebsscheren-Kalke* in the Upper Jurassic of southern Germany must have been a paradise for ghost shrimps: their pincers (the only well-calcified parts of their exoskeleton) are so common that the formation was named after them and that contemporary tube-worms used them for constructing their walls. Ophiomorphids show not only draft fills, but also modifications that are clearly biological. One variant looking like the base of a candle holder is difficult to explain. It may have served for food *storage* (some modern *Callianassa* species store plant material for fermentation), as a brood chamber, or simply as a terminal turnaround.

A typical *Thalassinoides* in the Cretaceous of **Texas** has a stack of teichichnoid lamellae (Pl. 41) below the horizontal tunnels. Such backfill structures are actually more common, but have escaped attention in other occurrences.

In an occurrence in the Miocene of **Borneo**, burrows are selectively sideritized. During this process the internal structure got lost, but the whole backfill bodies weather out with perfectly preserved surface patterns. What resembles the turnaround swellings in ophiomorphid burrows was in reality a *sanitary dump* for faecal pellets, whose ellipsoidal shape (enlarged picture) suggests that the maker was not a ghost shrimp.

A last modification are the corkscrew tunnels (*Gyrolithes*). Their connection with *Ophiomorpha* is shown by the specimen from **Switzerland**. Vertical sections in Miocene sands of **New Zealand** look like puppet faces, because the lining of mud pellets is restricted to the roofs, where it was most essential. Another cast from Tertiary limestones in **Venezuela** (Univ. of Caracas coll.) has a draft-**fill channel**. It indicates that the spiral section was not dead-ended, but connected with the surface at both ends, in spite of being at the deepest level of the boxwork.

Consequently, *Gyrolithes* may be a farming burrow. Being actively flushed by oxygenated surface water from above, and supplied with reduced pore water from below, the floor of the corkscrew tunnel would have been an ideal place to farm sulfuric bacteria. Regarding the functional significance, comparison with the much larger *Daimonelix* in Miocene paleosols of Nebraska and the Permian of South Africa is pointless: these were made by tetrapods (rodents and therapsids, respectively), for whom a spiral staircase is more convenient than climbing up and down in a chimney. Ghost shrimps, in contrast, are able to bend their legs to the dorsal side, and have no problem moving in a vertical shaft.
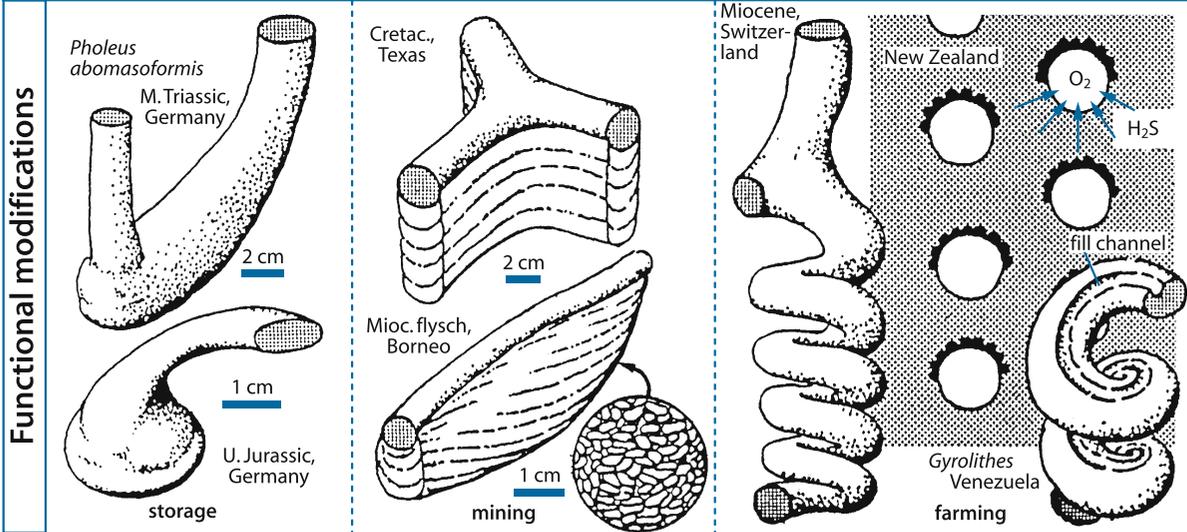
Plate 18 · Ophiomorphids   55

Tunnel systems

fecal pellets
com-
mensal
crab

shafts

turnarounds

gallery system

cork screw

Callianassa seilacheri

10 cm

1 cm

Thalassinoides, Jur., Germany

Granularia, Tertiary flysch

Ophiomorphids

Preservational modifications

Spongeliomorpha (stiff mud)

Ophiomorpha (sand)

"Paramoudra" (concretionary mummy)

L. Jur., Germany

U. Jur., Germany

mud pellets

U. Jur., France

draft fill

epirelief

washout

Functional modifications

Pholeus abomasoformis
M. Triassic, Germany

Cretac., Texas

Miocene, Switzer-land

New Zealand

O_2

H_2S

2 cm

2 cm

fill channel

1 cm

Mioc. flysch, Borneo

U. Jurassic, Germany

1 cm

Gyrolithes Venezuela
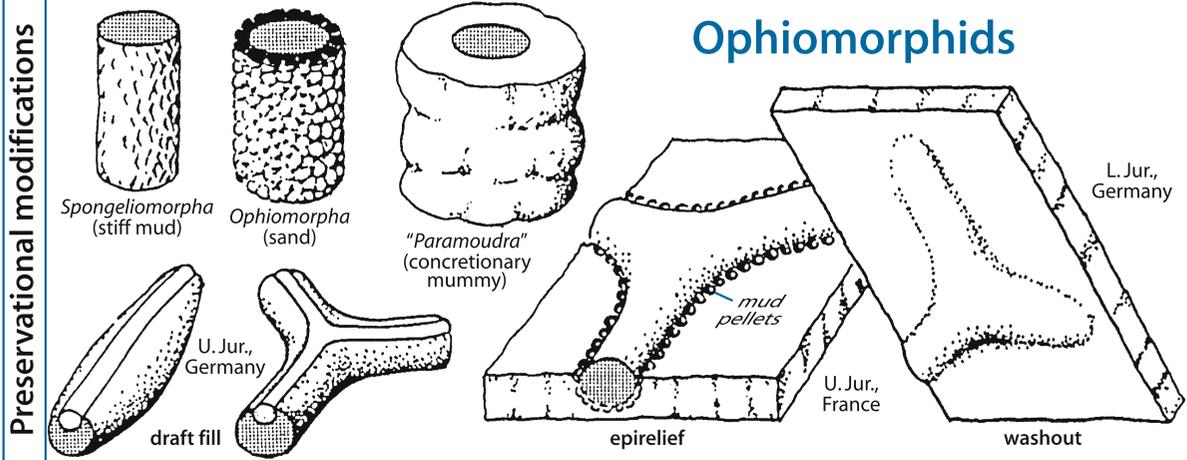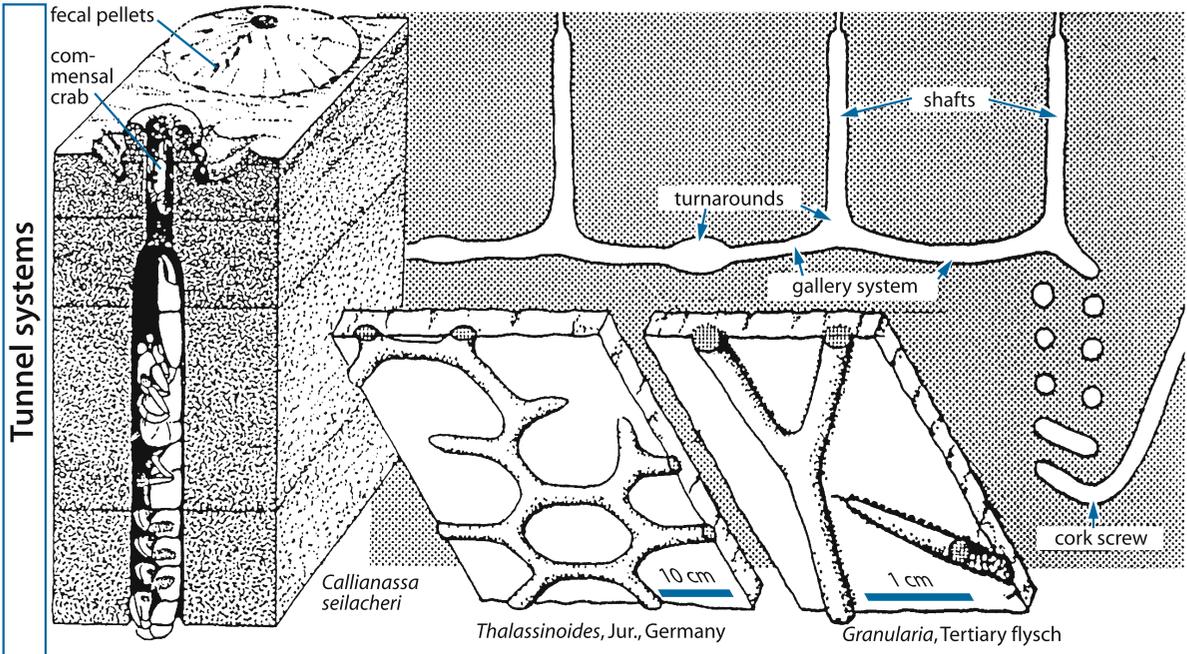
storage

mining

farming

Plate 19
Rhizocoralliids

So far we have been able to relate trace fossils to certain groups of animals – at least at the level of classes and phyla. In the group of fossils that may informally be called rhizocoralliids, such distinction cannot be consistently made, because their main character is a particular technique of burrow construction rather than kinship. Today it is practiced by unrelated aquatic animals, such as worms, crustaceans and insect larvae (Pl. 17); so the producer can only be inferred in fossil forms.

Polydora. The polychaete worm *Polydora* certainly does not fit the heading of this chapter. Yet its borings in hard substrates are well suited as a model for the much larger rhizocoralliids, the majority of which was probably made by shrimplike crustaceans.

Polydora burrows are most familiar as bioerosional shell borings. As fossils, they are known as *Caulostrepsis* and may also be found in calcareous rock grounds. Essentially they are U-tubes in the shape of an old-fashioned hairpin. What makes them distinctive is that the area between the two limbs is filled with weakly cemented sediment grains. After the inhabitant has died, this backfill becomes readily washed out, so that the burrow transforms into a slit with a dumbbell-shaped cross section. By breaking it open, or making a resin cast and freeing it with hydrochloric acid, one can also see traces of former U-tubes between the two shafts. They record the gradual deepening of the U (Pl. 36) required by the growth of the tenant.

In order to maximize safety against predators and erosion, penetration should be perpendicular to the surface of the substrate, but in mollusk shells the limited thickness of the substrate forces the borer to deviate parallel to the surface. The figured example from a Red Sea **pearl oyster** shows some interesting modifications.

1. The original hairpin first turned flat and then developed two separate lobes at a deeper level. Did lengthening only serve to accommodate the growing length of the worm? Alternatively, it could be related to foraging on organic components or on microscopic borers, such as algae, within the shell.
2. Between two lobes there is a backfill structure ("sprerite") on the wrong side (asterisk). This suggests that the worm mistook the sharp bend as a cue and penetrated its own backfill.
3. One of the apertures followed the growth of the host shell by extending into a shallow radial groove that ends at the shell margin. The animal probably parasitized on the inhaling current of the host for its own ventilation and possibly for suspended food. The other opening stayed behind and functioned as an exhaustor.

Polydora (perhaps even the same species!) may also dig into **stiff mud** exposed along tidal channels. In this case, the hairpin tubes are always perpendicular to the surface and never become lobate. The block diagram shows the animal at the base of such a tunnel. Note that the parapodial setae of the fifth body segment are modified into a nearly horizontal shovel operated by muscles. As shown by steeply oblique scratches in the burrow wall, they remove sediment from the floor of the tunnel and transport it to the ceiling, where it is plastered with mucus secreted by the body wall.
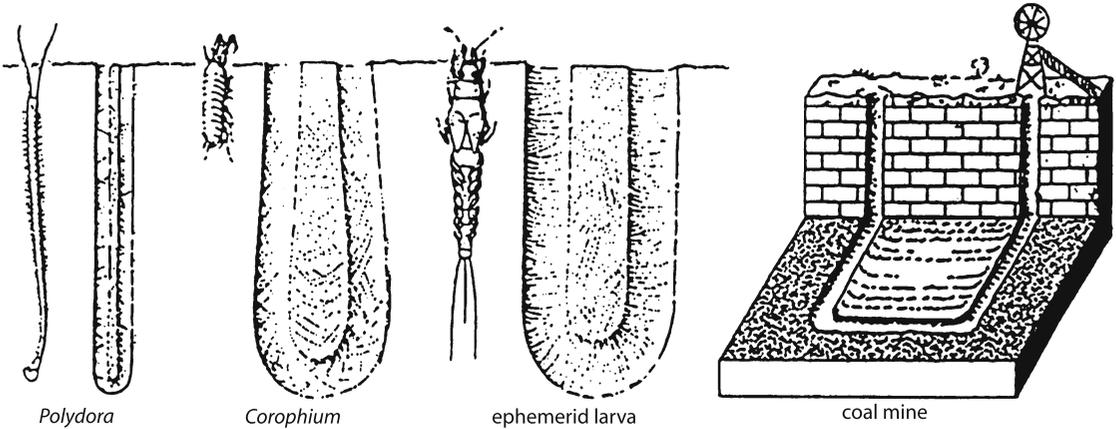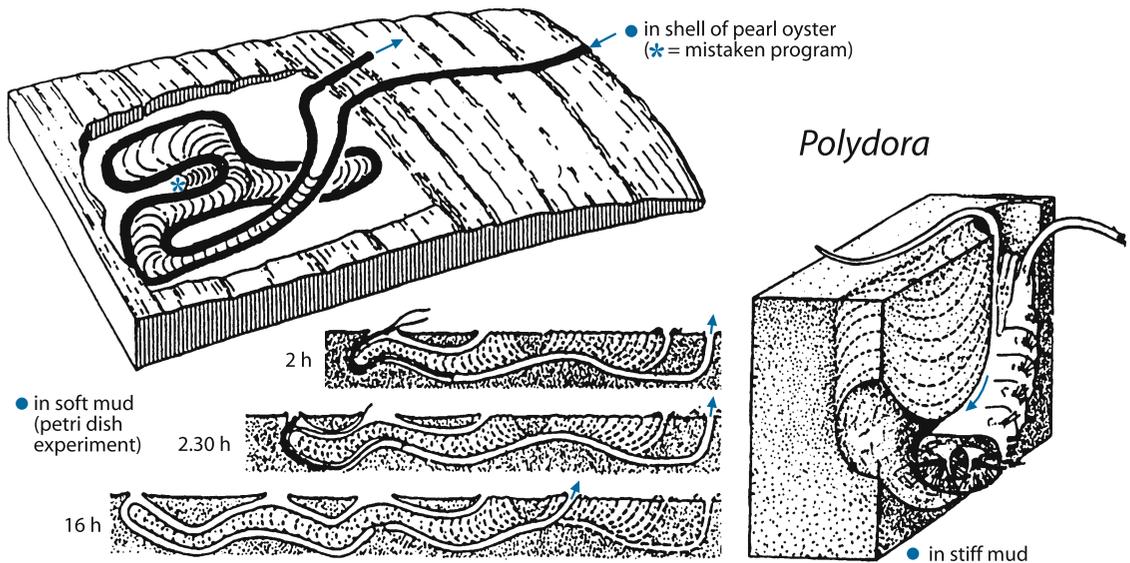
How can this technique transform into shell boring? The answer is probably that the mucus is acid enough to chemically soften the substrate for subsequent mechanical removal in the described fashion.

The third picture shows the behavior of *Polydora* after it was placed into a petri dish filled with a layer of very **soft mud**. In this experimental situation, the animal could not burrow vertically; instead it dug along the glass wall, so that the burrowing process could be directly observed over several hours.

Fossil Rhizocoralliids. Being larger (tube diameters reach more than a centimeter) and lithified, fossil examples are much more suitable for the study of backfill structures than modern ones. The term "*sprerite*" used for them (as well as the name *Rhizocorallium*) comes from the time when fossil burrows were considered as seaweeds: for German botanists, **sprerite** is the part spreading between the veins of a plant leaf. Sections reveal that the rhizocoralliid sprerite consists of stacked lamellae of reworked sediment whose shapes correspond to the ceiling of the U-bend, i.e. they resemble the rim of a bicycle wheel, whose curvature is opposite in longitudinal and cross sections. Such a structure is called **protrusive**, indicating that the U became deeper at every stage. This applies to most occurrences of the vertical *Diplocraterion*, but in the Rhaetic Sandstone (Upper Triassic, southern Germany), the sprerite is always **retrusive**, with the lamellae looking like the fender of a bicycle and the terminal tunnel being on top. In a Devonian sandstone, the late Roland Goldring observed a combination of the two structures. The name he gave, *Diplocraterion yoyo*, well describes the down and up motion of the U-tube. As the switch to the retrusive mode (and vice versa) implies reworking of the former backfill, the up and down was probably a response to erosion and sedimentation. In other words, *Diplocraterion* was not a feeding burrow, but the easily flushable domicile of a suspension feeder. *Rhizocorallium* itself follows the same principle, but the plane of its sprerite is inclined or bends into the bedding plane at depth. It also is never retrusive and may become excessively long without gaining increased security. The conclusion that its maker was a sediment feeder is corroborated by rod-like fecal **pellets** lining the tunnel wall and making up most of the sprerite. As the ratio between pellet and tunnel diameters (the latter corresponding to the circle in drawings) is the same in large and small *Rhizocorallium*, they must be the products of the owner, whose narrow anus matches a crustacean better than a worm.

Plate 19 · Rhizocoralliids   57

Rhizocoralliids

in shell of pearl oyster
(✱ = mistaken program)

Polydora

Modern counterparts

in soft mud
(petri dish
experiment)

2 h

2.30 h

16 h

in stiff mud

Polydora   Corophium   ephemerid larva   coal mine

Spreite structure

Diplocraterion

L. Jurassic   M. Triassic

Rhizo-corallium

pellet lining in spreite
relative to tube
diameter

protrusive   yoyo   retrusive

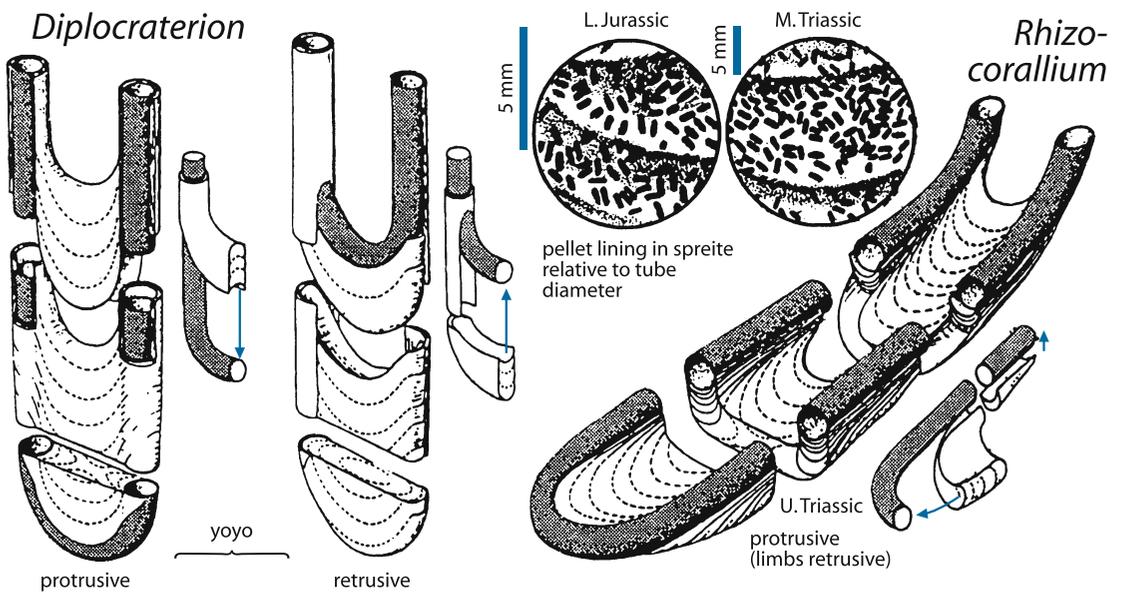U. Triassic
protrusive
(limbs retrusive)

Plate 20
Rhizocoralliid Modifications

Through the Phanerozoic, the basic rhizocoralliid program has been modified in ways that can be explained by changes in function (dwelling versus feeding burrows) and fabrication (behavioral programs), while other differences are due to preservation. Yet, it often remains uncertain whether the makers were arthropods or worms.

Functional Modifications in Softgrounds. Rhizocoralliid burrows are primarily flushable domiciles that can be adapted to the growth of the inhabitant without it having to leave, but the same technique can also be used to mine the sediment for food. Modifications indicate whether or not this additional function was important.

Rhizocorallium. Excessive length of the tube (with more energy required for flushing), inclined or horizontal burrowing (with little gain in security), and faecal pellets suggest that *Rhizocorallium* was a feeding burrow, whose effectiveness could be improved by modified programs.

A large form found in highly bioturbated sands of the Upper Jurassic (Boulogne, France) is **slipper-shaped**. In contrast to the diagram in Pl. 19 (based on specimens from the Upper Triassic of the German Alps), the retrusive teichichnoid spreite structures below the terminal tunnel are not the accidental product of sediment falling from the roof of the U-tunnel. Rather, the slipper shape reflects a fixed two-stage program: the animal first increased tube length by constructing an inclined *protrusive* spreite and then switched to an upward *retrusive* mode. In this phase the tube became again shorter, but without reworking parts of the earlier spreite. However, this process could not be continued indefinitely; it is a kind of count-down program.

A corkscrew version (**Lapispira bispiralis**, Lower Jurassic; spreite hypothetical) was possible because it maintains the inclination of the spreite. In contrast to spiral worm burrows (*Zoophycos*, Pl. 38; *Daedalus*, Pl. 44) its central shaft is not straight, but forms a steeper screw. Wider horizontal circles occur in the **Permian** (*Bellerophon* Limestone) of Austria.

On the other hand an irregularly winding course within the bedding plane (Triassic and Jurassic) often leads to a *lobate* spreite: without a gravitational compass, the animal relied on the signal of its own body flexure to induce spreite construction. Thereby it interpreted accidental bends in the primary limb tunnels as a signal to produce secondary lobes. The gain of new exploration fields evidently outweighed the disadvantage of a longer ventilation tunnel.

All these variants support the view that *Rhizocorallium* was basically a feeding burrow; but its irregular stratigraphic distribution does not (yet) allow to establish a behavioral genealogy.
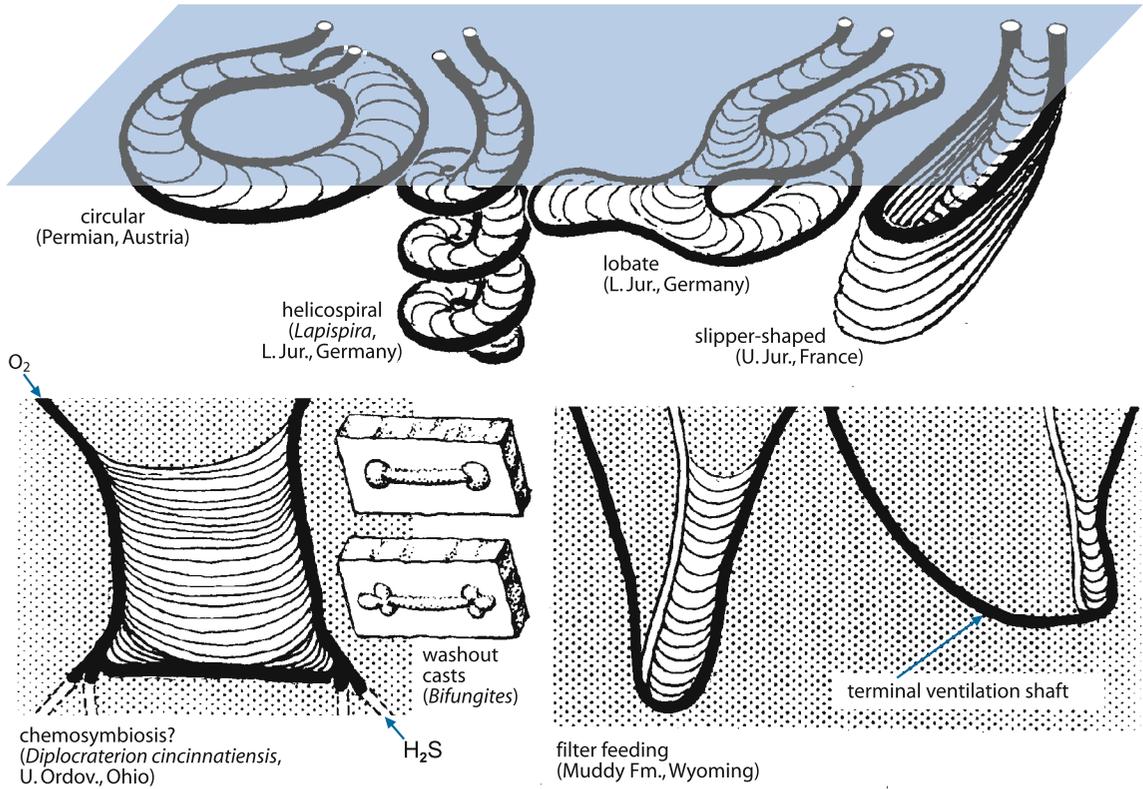
Diplocraterion. The occurrence in high-energy sands, vertical orientation, and the response to sedimentation (*Diplocraterion yoyo*, Pl. 19) fit the paradigm of simple domiciles. Yet *Diplocraterion* is also found in silts and muds deposited in quiet waters. One ichnospecies (*Diplocraterion cincinnatiensis*) occurs in finely laminated silt beds and its tunnel resembles the outline of an elephant's foot rather than a U. As these burrows usually end at the base of the silt bed, it seemed reasonable to assume that the encounter with the underlying mud was responsible for the deformation. Occasional specimens, however, end in the same fashion at a higher level. This supports a *chemosymbiotic* function: the two lower corners were the pumping stations for H_2S water from the mud and their interference was reduced by distancing them beyond the regular width of the spreite. This view is corroborated by the fact that the only associated trace fossil is *Chondrites* (Pl. 48), another suspect for chemosymbiosis. Additional information comes from a different kind of preservation: on the soles of tempestites, *Diplocraterion* may be expressed by casts in the shape of a dumb bell (**Bifungites**). They formed when a previous silt layer became stripped away to its mud base and reburied during the same event. In the Ordovician, however, the swollen ends are trifoliate, rather than simple globes resulting from erosion of a marginal tunnel. In conclusion, there were probably three probes radiating from each corner of *Bifungites biclavatum*.

In Cretaceous shallowmarine sandstones (**Wyoming**; Germany) one commonly observes small spreite burrows that could well have been made by *Corophium* (Pl. 19). However there is an additional "escape hatch" rising obliquely from the base of the U-tube. More likely it was made by a suspension feeder for distancing the two openings in the final state, i.e. to place the sewage outlet further away from the eating table. This also tells us that the animal had a three-stage burrowing program: (1) head-on piercing used to make the initial U-tube; (2) vertical spreite construction to accommodate growth; (3) head-on construction of the terminal **ventilation shaft**.
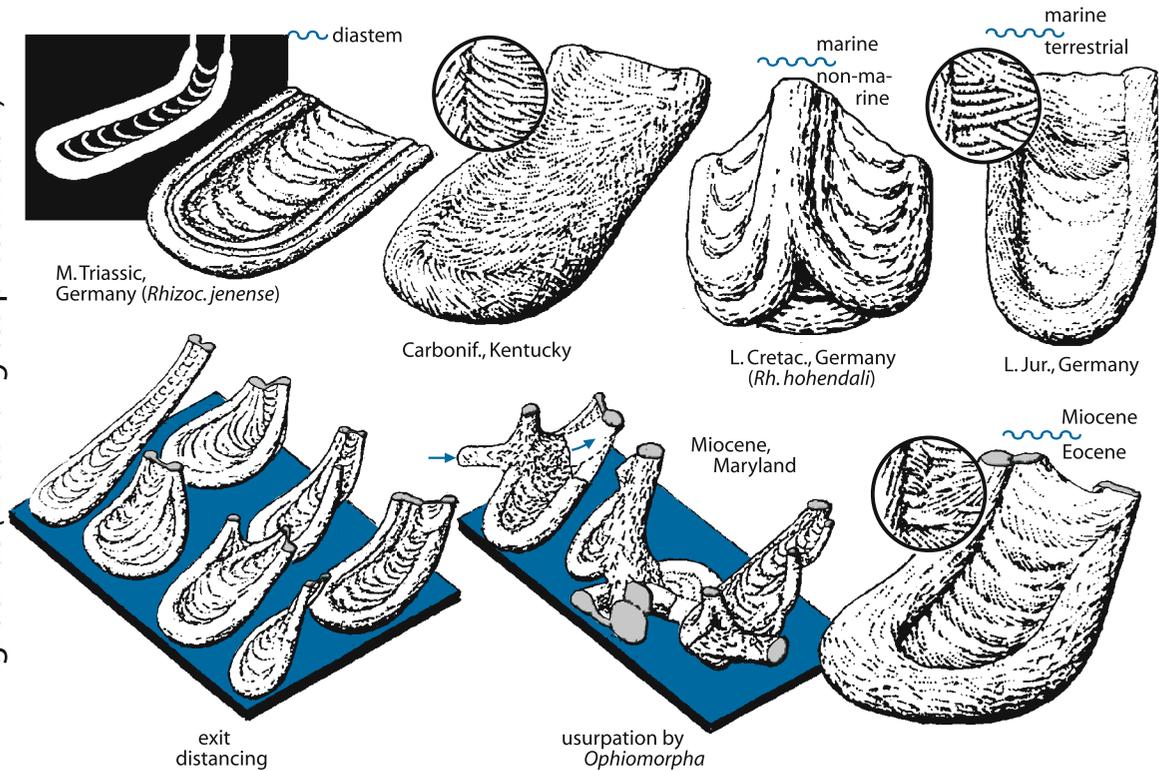
Modifications in Firmgrounds. Firmgrounds result from erosion of muddy sediment to a level, at which it had already become sufficiently stiffened by compaction; i.e. they trace a stratigraphic gap (diastem) on the order of hundred years (Pl. 73). Burrowing in stiff mud poses, first, a fabricational problem: the animal has to work hard and be equipped with strong claws or setae (trilobite limbs would not do). Accordingly, firmground burrows functioned as mere domiciles, because their construction is overly expensive relative to the nutrient content of the substrate. Second, a stiff substrate provides better protection than soft sediment against predators and erosion, so that burrows need not be as deep and not perfectly vertical. Firmground burrows also have preservational ▶

Plate 20 · Rhizocoralliid Modifications   59

Rhizocoralliid Modifications

Softgrounds

circular
(Permian, Austria)

helicospiral
(*Lapispira*,
L. Jur., Germany)

lobate
(L. Jur., Germany)

slipper-shaped
(U. Jur., France)

O$_2$

washout
casts
(*Bifungites*)

terminal ventilation shaft

chemosymbiosis?
(*Diplocraterion cincinnatiensis*,
U. Ordov., Ohio)

H$_2$S

filter feeding
(Muddy Fm., Wyoming)

Firmgrounds (*Glossifungites* preservation)

diastem

marine
non-ma-
rine

marine
terrestrial

M. Triassic,
Germany (*Rhizoc. jenense*)

Carbonif., Kentucky

L. Cretac., Germany
(*Rh. hohendali*)

L. Jur., Germany

Miocene
Eocene

Miocene,
Maryland

exit
distancing

usurpation by
Ophiomorpha

advantages. As they do not readily collapse, the open tunnels become passively filled with looser sediment that becomes preferentially cemented during early diagenesis.

Our first example is a horizontal *Rhizocorallium jenense* from a low-grade firmground in the Middle **Triassic** limestone of Germany. Along the crest of its marginal tunnel commonly runs a fill channel, as in ophiomorphids from a similar facies (Pl. 18). So we may conclude that – at least in softer mud – the openings of a *Rhizocorallium* burrow were also constricted and that the inhabitant did not normally emerge at the surface.

The other figured specimens from the Carboniferous of **Kentucky** and the Miocene of **Maryland** differ from softground *Rhizocorallium* in various respects. (1) Their outline resembles a rabbit ear rather than a U with parallel limbs. This is to be expected in domichnial rhizocoralliids: if flexure of the body was the signal for burrowing, the spreite became automatically wider as the animal grew larger. (2) As concretionary cementation of the fill sediment stopped at the interface with the dense host mud, the surface of the casts preserves scratches in considerable detail. Their pattern suggests a crustacean maker. (3) Despite of being dwelling burrows like *Diplocraterion*, they are inclined like the feeding burrow *Rhizocorallium*. Inclination, however, facilitates not only the exploitation of nutrient-rich horizons, but also climbing up and down the tube. As the inhabitant allowed itself such comfort, its burrow became similar to *Rhizocorallium* in spite of not being a feeding burrow. For this

reason, one should maintain the old name *Glossifungites* for firmground versions of rhizocoralliid burrows, whether vertical or inclined. This applies also to the specimens from the **Lower Cretaceous** and the **lowermost Jurassic** of Germany. Both were produced by marine crustaceans penetrating into muds deposited in a different regime. The former one regularly produced three *Diplocraterion*-like spreite bodies linking three vertical shafts ("tripods"). The simpler burrow from the boundary between a Triassic red-bed and a Jurassic limestone bed is much smaller (only a few millimeters wide) and could well have been made by *Corophium*. Still it preserves the typical scratch pattern observed in modern examples (Pl. 19).

The lower row shows specimens collected at a locality (Susquehanna River, Maryland, USA), where Eocene shales are disconformably overlain by bioclastic sands of Miocene age. But while the Eocene bioturbation of the shale is hardly recognizable, the burrows dug into the same bed during the Miocene transgression can be easily collected, because they weather out as ear-shaped casts. Firmground conditions are also expressed by associated burrows of pholadid bivalves and of ghost shrimps, which are other characteristic members of the *Glossifungites* Ichnofacies (Pl. 71). Belonging to a deeper tier, the *Spongeliomorpha* tunnels were probably made after *Glossifungites*, so the ghost shrimps could reduce their burrowing effort by partly using the shafts of their rhizocoralliid predecessors.

■ Fecal pellets of *Rhizocorallium* (U. Muschelkalk, Germany)