CHAPTER 19

RECENT LEBENSSPUREN IN NONMARINE AQUATIC ENVIRONMENTS

C. KENT CHAMBERLAIN
Department of Geology, Ohio University
Athens, Ohio, U.S.A.

SYNOPSIS

Diverse faunas exist in nonmarine aquatic environments, and the animals make distinctive tracks, trails, tubes, and burrows. For example, certain beetles make dwellings or feeding burrows and pupal chambers. Midgefly larvae and aquatic earthworms extensively rework lake bottoms and lentic parts of rivers. Caddisfly larvae use clastic grains and plant material to construct unique, mobile dwelling cases. Snails and clams make abundant surface traces and resting burrows. Distinctive shore tracks and trails, dwelling burrows and similar structures, hibernation burrows, feeding traces, and nesting structures are made by aquatic and semiaquatic, freshwater vertebrates of diverse types.

The principles of ecology and ichnology that apply to nonmarine aquatic animals and environments are the same as marine ones; only the parameters are different. Consequently, ichnological studies made on local streams or lakes can yield equally interesting and instructive results; and much work remains to be done.

INTRODUCTION

Traces of nonmarine aquatic animals are both abundant and diverse. Freshwater and other nonmarine aquatic animals, like marine animals, make dwelling structures, resting and crawling traces, and feeding burrows. Invertebrates make feeding traces and also pupal, brood, hibernation, and aestivation chambers, and vertebrates make hibernation burrows and nesting structures. As in the marine realm, the types of behavior are varied in shallow-water environments; but in deep waters, deposit feeding by invertebrates is most common.

The faunas responsible for the lebensspuren are also diverse. For example, shore beetles and crickets make extensive feeding burrows. Tiger-beetle larvae make deep dwelling burrows, and caddisfly larvae make dwelling cases by agglutinating organic debris or sediment grains together. The shape of many dwelling cases is diagnostic of a particular habitat and a particular species. Burrows in the substrate of deep lakes are made mainly by aquatic earthworms (oligochaetes) and amphipods. Some animals, such as the eubranchiopods, are diagnostic of ephemeral ponds, where they crawl upon or plough through the substrate and where only one or two species are found associated together. Even some dipterans (flies) make traces; for example, larvae of the midgefly make extensive dwelling burrows in lake sediments.

Vertebrates that make dwelling burrows in banks of rivers and lakes include muskrats, nutria, and the duck-billed platypus.

Beavers make dwelling structures (lodges) from wood and mud, and leave gnawed wood as evidence of their building and feeding activities. Shore tracks and trails are made in abundance by many vertebrates, particularly the numerous mammals. Among the lower vertebrates, sea lampreys build dwelling burrows and nesting structures.

The study of recent freshwater lebensspuren has some distinct advantages. The traces can be studied in local streams, rivers, lakes, or ponds, and the same principles can be applied there as in the generally more distant or otherwise inaccessible marine environments. Another advantage is that many new, original observations can be made, without the burden of too much previous information or possible dogmatic misconception.

At present, nonmarine aquatic environments have been studied so little by ichnologists that few reliable criteria are known for recognizing ancient analogs. Neither has the transition from marine to nonmarine environments been studied sufficiently.

My purpose in this chapter is to summarize the character of the lebensspuren of nonmarine aquatic animals as they are known at present, neglecting coprolites and fecal pellets, cysts and borings, and rasping traces (cf. Chapters 10 to 13).

Quantitative classifications (e.g., first- and second-order streams) and formal definitions are not necessary in describing nonmarine aquatic environments cited in this chapter, because the zoogeographic extents of trace-making animals are not precisely known. (Indeed, the animals seem to have a particular disdain for such artificial classifications.) Usually, "stream" refers to any body of flowing water. "Brook," "creek," and "river" imply successive increases in the size of a stream; "bayou" refers to a small, secondary, sluggish stream. "Lake" refers to any standing body of inland water, whether fresh, alkaline, or saline. A "pond" is a small, shallow lake, and a "pool" is a small, deep lake. "Lotic" refers to running water, and "lentic" to standing water. Streams are mostly lotic but have some lentic parts, and lakes are mostly lentic but have some lotic parts (e.g., wave-swept beaches).

NONMARINE AQUATIC INVERTEBRATES

Invertebrates living in freshwater environments are both numerous and diverse, although less so than in marine environments. Approximately 30 groups (phyla, classes, or orders) of invertebrates have representatives living in freshwater environments (Table 19.1). A few of these animals—eubranchiopods, nematomorphs, and hydracarins—are mainly or entirely freshwater denizens. The remaining groups are variably represented by a few to many species in freshwater environments, and generally have more species in marine waters (see Pennak, 1953, Table 2).

Insects and mollusks represent most of the species in the world. Only approximately 4 percent of the insects are aquatic or have aquatic stages, however, and only a small percentage of mollusks are freshwater forms. Nevertheless, insects and mollusks are among the major macroscopic invertebrates of benthic communities in lakes and streams, although amphipods and oligochaetes are also very abundant.

LEBENSSPUREN OF NONMARINE AQUATIC INVERTEBRATES

Although less than half of the freshwater invertebrates listed in Table 19.1 make lebensspuren, some groups include many species that are very active on or in the substrate; thus, abundant and interesting lebensspuren do exist in freshwater environments. Crayfish, gastropods, bivalves, aquatic earthworms, and certain insects are responsible for most of the lebensspuren. Nematodes, ostracods, amphipods, and eubranchiopods also make traces, although the extent of these is less well known.

TABLE 19.1 Invertebrates of Freshwater Environments.

- Phylum Protozoa (protozoans)
  - Class Mastigophora (flagellates)
  - Class Sarcodina (rhizopods)
  - Class Sporozoa (sporozoans)
  - Class Ciliata (ciliates)
  - Class Suctoria (suctoriales)
- Phylum Porifera (sponges)
- Phylum Coelenterata (jellyfish, sea anemones, corals)
  - Class Hydrozoa (hydrozoans)
- Phylum Platyhelmintha (flatworms)
  - Class Turbellaria (flatworms)
- Phylum Nemertea (proboscis worms)
- Phylum Gastrotricha (gastrotrichs)
- Phylum Rotatoria (rotifers)
- Phylum Nematoda (round worms)
- Phylum Nematomorpha (horsehair worms)
- Phylum Tardigrada (water bears)
- Phylum Ectoprocta (bryozoans)
- Phylum Endoprocta (endoprocts)
- Phylum Annelida (segmented worms)
  - Class Oligochaeta (aquatic earthworms)
  - Class Polychaeta (polychaetes)
  - Class Hirudinea (leeches)
- Phylum Arthropoda (arthropods)
  - Class Crustacea (crustaceans)
    - Order Eubranchiopoda (fairy, tadpole, and clam shrimps)
    - Order Cladocera (water fleas)
    - Order Ostracoda (seed shrimp)
    - Order Copepoda (copepods)
    - Order Mysidacea (opossum shrimp)
    - Order Isopoda (aquatic sow bugs)
    - Order Amphipoda (scuds)
    - Order Decapoda (crayfish, crabs, shrimp)
  - Class Hydracarina (water mites)
  - Class Arachnida (spiders)
  - Class Insecta (insects)
- Phylum Mollusca (mollusks)
  - Class Gastropoda (snails)
  - Class Bivalvia (pelecypods—clams, mussels)

Sponges, bryozoans, and most hydrozoans are sessile and consequently do not make traces. Certain animals, such as the opossum shrimp and water mites, are mainly nektonic and have little deliberate contact with the substrate. Other animals, such as the nemerteans and many turbellarians and insects, prefer a plant substrate rather than a clastic one. Protozoans, gastrotrichs, water bears, and rotifers are small enough that they probably do not leave an obvious trace when they move through or across the substrate; or at least, special techniques would be required to observe them. Among the intermediate-small animals, such as water fleas, rotifers, and copepods, whatever lebensspuren they might make have not been reported. Some of the rotifers do make small dwelling cases and tubes, by agglutinating clastic and woody grains together; but these inconspicuous structures range in size from less than 1 to about 5 mm across—even in colonial ones—and may easily be overlooked. (Such lebensspuren are nevertheless significant, as emphasized in Chapter 9, and warrant further study.) Water mites are very common in many freshwater bodies; the animals have been observed to make brush marks on the substrate of an aquarium, and plough marks on a drying substrate, but this sort of small feature probably would go unrecognized in natural situations.

The types of lebensspuren made by certain freshwater animals are summarized in Table 19.2. The table is deceptive in that not much is known about several of the groups of lebensspuren; the characteristics of some are inferred from the behavior of the animals and not from actual reports on observed traces. The type of lebensspur—resting trace, dwelling structure, etc.—corresponds generally to the classical behavioral types of trace fossils (see Chapter 3). Pupal, brood, hibernation, and aestivation chambers, however, are another category of lebensspuren. Unfortunately, not much information is available concerning these structures. Most of them are simple oval chambers corresponding to the size of the pupae or adults. The exact size, shape, depth, and habitat location of the trace, as well as the nature of the access tube, may

TABLE 19.2 Types of Lebensspuren Made by Nonmarine Aquatic Invertebrates.

Key
*—*the animals probably make this structure*
x—*the animals do make this structure*
a—*aestivation or hibernation chamber*
b—*brood chamber*
p—*pupal chamber*

	Resting Trace	*Dwelling Structure*	*Crawling Trail*	*Feeding Trail*	*Feeding Burrow*	*Chamber*
Platyhelmintha						
Turbellaria (flatworms)			*			
Nematoda (roundworms)			x			
Nematomorpha (horsehair worms)			*			
Annelida						
Oligochaeta (aquatic earthworms)				x		
Polychaeta (polychaetes)		x				
Hirudinea (leeches)			x			a
Arthropoda						
Crustacea						
Eubranchiopoda						
Conchostraca (clam shrimps)	x	*	x	*		
Notostraca (tadpole shrimps)	*	*	*	*		
Anostraca (fairy shrimps)	*		*			
Isopoda (aquatic sow bugs)	*					a
Ostracoda (seed shrimps)				x	x	
Amphipoda (scuds)	*	x	x		*	
Decapoda						
Astacidae (crayfish)	*	x	*			a
Potamidae (crabs)	*	x	*			
Atyidae and Paleomonidae (shrimps)	*		*			
Insecta						
Plectoptera (stoneflies)	*		*			
Ephemeroptera (mayflies)	*	x	*			
Odonata (dragonflies)	*	x	*			
Megaloptera (Alder and Dobson flies)	*		*			p
Hemiptera (bugs)		?				
Trichoptera (caddisflies)		x	x			
Coleoptera (beetles)						
Carabidae (carabs)		?				
Dytiscidae (predaceous diving beetle)	x					
Georýssidae (minute mud-loving beetles)	x					
Heteroceridae (variegated mud-loving beetles)					x	p
Hydraenidae (hydraenids)					?	
Gyrinidae (whirligig)						a

TABLE 19.2–Continued.

Key
**—the animals probably make this structure*
x—the animals do make this structure
a—aestivation or hibernation chamber
b—brood chamber
p—pupal chamber

	Resting Trace	*Dwelling Structure*	*Crawling Trail*	*Feeding Trail*	*Feeding Burrow*	*Chamber*
Hydrophilidae (water scavenger)	?		?			
Noteridae (burrowing water beetle)					x	
Ptilodactylidae (ptilodactylids)					x	
Staphylinidae (rove beetles)		x			?	
Cicindelidae (tiger beetles)		x				a, b, p
Diptera (flies)						
Syrphidae (hoverflies)	x					
Tabanidae (horseflies)					?	
Chironomidae (blood-worm)		x				
Hymenoptera						
Formicidae (ants)		x				
Sphecidae (mud daubers)			(excavation)			
Orthoptera (crickets)						
Gryllotalpinae (mole crickets)					x	
Tridactylidae (sand cricket)					x	
Dermaptera (earwigs)			x			
Mollusca						
Gastropoda (snails)	x		x			a
Bivalvia (clams and mussels)	x		x			a

be important in ultimately recognizing different traces when the animal is no longer present.

Pupal, brood, hibernation, and aestivation chambers are similar to agglutinated tests of the polychaete *Pectinaria* and arenaceous foraminiferans, but the chambers are true traces whereas the two tests are potential body fossils. (See Chapter 3.) Dwelling cases of caddisfly larvae are analogous to the latter and thus technically are "body parts" also.

An undetermined number of animals, particularly insects, commonly walk or creep along the shores of rivers or lakes, or through ephemeral puddles, but are not regular inhabitants of these environments. The crisscrossing furrows made through puddles by terrestrial earthworms, following a storm, are familiar to almost everyone. A reasonable attempt cannot be made at enumerating all of the lebensspuren possible under such fortuitous and random situations, particularly considering the thousands of active insects prone to tread hither and thither without regard to the plight of the neoichnologist. Perhaps the subdivision of these animals into major groups of treaders could be attempted after completion of additional careful field observation and some experimental neoichnology.

Experimental neoichnology has not been employed nearly often enough! (cf. Chapter 22). Based on the surprising complexity of insect locomotion traces reported by Graber (1884, 1886) and Demoor (1880, 1890), and salamander tracks by Evans (1946), further experimental neoichnology would be both interesting and replete with instructive surprises (Fig. 19.1A–C).

The burrow of a wasp and the trail of an earwig, each made in ephemeral storm puddles, are included in my descriptions. They are not aquatic in the sense of the other animals discussed here, but they typify forms that visit fresh muds. Some species, such as the mud-dauber wasp, come to gather building materials; but certain other forms, such as the earwig, come fortuitously. These particular ones were selected because they are distinctive, resemble other important lebensspuren, and information was already available on them.

Platyhelmintha: Turbellaria (Flatworms)

Freshwater turbellarians are widespread on many substrates. They range from a few to 30 mm in length, and are narrow. Some move by smooth, gliding movements of cilia on a thin coat of mucus; others crawl on the substrate by peristaltic waves of muscular contraction. These movements result in shallow, rounded furrows; further details are not known.

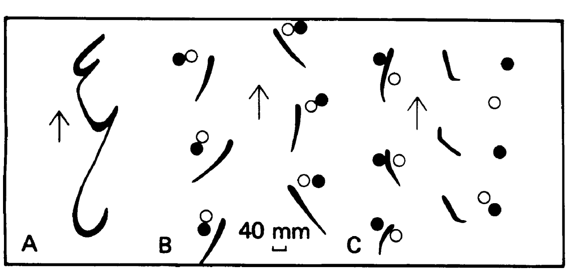


Fig. 19.1 Results of experimental ichnology, in which beetles were allowed to walk after treating each leg with different colors of paint. A, tibial spines of right hind leg of *Dyticus*, the swimming beetle. B, walking pattern of *Blaps mortisaga*; dots are tracks of the foreleg, circles of the middle leg, and slashes of the hind leg. C, *Trichodes*, using same codes as in B; beetle subjected to a 30° slope. (After Graber, 1884.)

Nematoda (Roundworms)

Nematodes are cosmopolitan in almost all waters and substrates. Under proper conditions, their small sinuous trails may be preserved in sediments or other substrates (e.g., Sandstedt et al., 1961; Gray and Lissmann, 1964; Wallace, 1968; Moussa, 1970). The trails range from 0.5 to 1 mm across, and have a sine-curve regularity (Figs. 19.4N, 19.6A). The trails are known from the Pleistocene (Tarr, 1935 = *Chironomous* larvae) and Tertiary (Moussa, 1970), but might well occur in much older rocks.

Nematomorpha (Horsehair or Gordian Worms)

Although horsehair worms are nowhere very abundant, they are fairly cosmopolitan —particularly in shallow, roadside water bodies—and are commonly found writhing about in damp shore sediments. They range from 0.3 to 2.5 mm across, and 10 to 70 cm in length. The swimming movements are feeble, slow undulations or writhings, and result in erratic brush and writhe marks against the substrate (Fig. 19.4O).

Annelida

Oligochaeta (Aquatic Earthworms)

Aquatic earthworms extensively rework sediments in many freshwater environments. They occur, sometimes in profusion, at all depths; but mainly they occur in shallow, quiet waters (less than 1 m deep). Some are most abundant in polluted waters. Oligochaetes construct small tubes, 1 to 2 mm across and projecting 2 to 5 mm above the substrate surface (Figs. 19.4M, 19.6C, 19.7I). The tubes are made of agglutinated mud, silt, or sand, depending on the substrate. Elongate fecal strings of ingested sediment are extruded to form mounds or circular ridges ranging from 5 to 20 mm across. Full details on the irregular, branching, feeding burrows are not known. They radiate from the surface tube, and most of them branch horizontally and continue a few centimeters laterally; others continue downward and simply fork at a wide angle. They have a fairly constant diameter; depending on the size or species, it ranges from less than 1 to more than 2 mm. Certain burrows are similar to the trace fossil *Chondrites*, except that they do not display phobotaxis (see Chapter 6). Irregular chambers are developed in some, apparently from complete mining of particularly nutritious areas.

Kozhov (1963) reported some large oligochaetes in Lake Baikal, Russia, that attain lengths of 12 to 20 cm and are 2 to 5 cm in diameter. One of these large forms occurs at the greatest depth of the lake; to know something of its burrowing behavior would be extremely interesting.

Polychaeta (Polychaetes)

Polychaetes have not become generally established in freshwater environments. Most of them are found in lakes or streams presently or recently joined with the ocean. A few have been found in high-altitude streams. Consequently, polychaetes are considered to have adapted only recently to the freshwater environment. Certainly their limited occurrence represents a low level of success at invading fresh waters through past eons.

Most freshwater polychaetes are small, ranging from 3 to 15 mm in length. They build small chitinous tubes containing agglutinated mud or silt, in silty bottoms, or moveable tubes on shore stones (Fig. 19.4L).

Hirudinea (Leeches)

Leeches generally do not live on a substrate suitable to form or retain lebensspuren, but some make creeping, looping, or inchworm movements on clastic substrates. These lebensspuren are not known in detail but probably are worth further study. Leeches are generally cosmopolitan, and range in length from 5 to 50 mm (Pennak, 1953).

Arthropoda: Crustacea: Eubranchiopoda

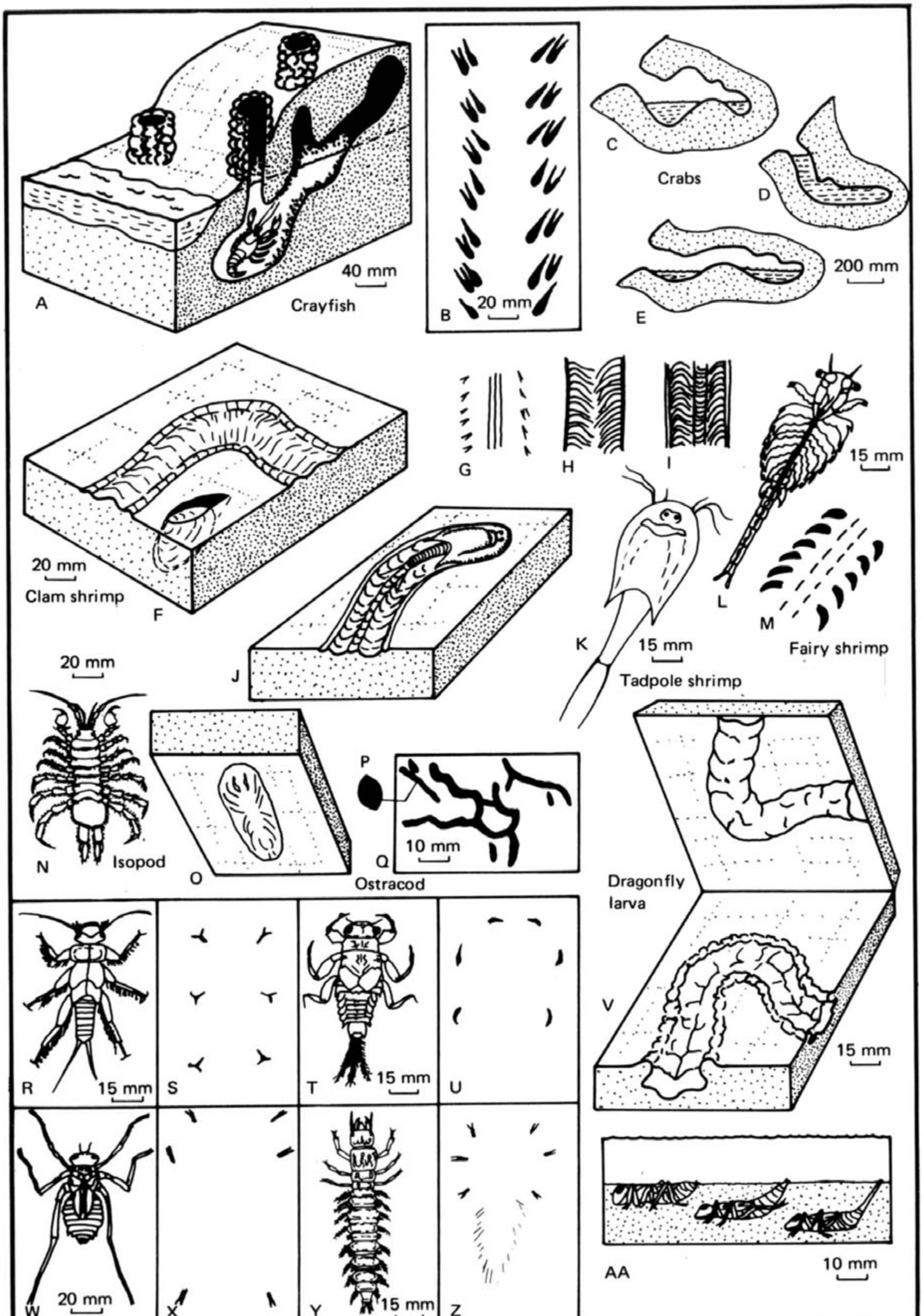
Conchostraca (Clam Shrimp)

Clam shrimp prefer vernal ponds and puddles, and seldom appear in lakes or ponds containing carnivorous animals. They range from Devonian to Holocene. Tasch (1964) illustrated and described crawling and resting lebensspuren of some extant species in an artificial environment. He observed a serpentine configuration approximately 2.6 mm wide. It had a median ridge at a lower elevation than the sides of the trails (Fig. 19.2F). At the bow of the looped area, the clam shrimp apparently crossed its previous trail. Another shorter, hairpin trail seemed to have been the older of the two trails. The parallel depressions of the trail, at a constant distance apart, indicated that they were excavated by the animal's paired appendages and that the sediment was moved posteriorly, as in burrowing. The width of the trail corresponded closely to the width of the animal's body.

Notostraca (Tadpole Shrimp)

Tadpole shrimp creep or burrow superficially in soft substrates much of the time (Pennak, 1953) and also spend much time swimming gracefully, by wave-like beating movements of the legs. Tadpole shrimp prefer vernal, alkaline, muddy waters in temperate-arctic regions, and range in age from Cambrian to Holocene.

For lack of specific data, I only conjecture here as to the nature of the lebensspuren left by tadpole shrimp (Fig. 19.2G–K; also see Bromley and Asgaard, 1972, Fig. 3). Resting, walking, and ploughing traces of tadpole shrimp would compare favorably with trace fossils made by trilobites, in


40 mm
A
Crayfish
B
20 mm
C
Crabs
D
200 mm
E
G
H
I
15 mm
20 mm
Clam shrimp
F
J
K
15 mm
Tadpole shrimp
L
M
Fairy shrimp
20 mm
N
Isopod
O
P
Q
10 mm
Ostracod
Dragonfly
larva
V
15 mm
R
15 mm
S
T
15 mm
U
W
20 mm
X
Y
15 mm
Z
AA
10 mm

which the body morphology is shown in various degrees of fidelity, depending mainly on the activities of the animal. Ploughing by means of the numerous paired legs would leave a striated, bilobate furrow. If the shield-like carapace is brought against the substrate, then lateral grooves would parallel the furrow. If the abdomen-telson is brought in contact with the substrate, a central concave groove would result; and with the paired caudal rami in contact, paired grooves would be produced. Savage (1971) described a resting trace and several crawling trails that compare very favorably with traces that would be left by tadpole shrimp.

Anostraca (Fairy Shrimp)

Fairy shrimp occupy ephemeral puddles and ponds, and include the brine shrimp *Artemia salina* of the Great Salt Lake. They range from Oligocene to Holocene. Fairy shrimp are swimmers that make graceful movements by wave-like beating of the legs; they normally swim on their backs.

Again, no specific information is available on their lebensspuren; my speculation is based on body morphology, in order to suggest something of possible traces. If these forms brushed the bottom, with the ventral side down rather than the dorsal, they would leave a series of paired appendage marks, and perhaps a median paired groove as the abdomen-telson dragged the substrate (Fig. 19.2L, M). These traces would be distinguishable from tadpole shrimp trails by having shorter and stouter appendage marks. The trace fossil *Umfolozia* (Savage, 1971, Figs. 5, 6) shows the type of trail one might expect from fairy shrimp.

Crustacea: Isopoda (Aquatic Sow Bugs)

Allee (1929) studied isopod aggregations in a stream. The animals oriented themselves up–current, making resting traces before they made another attempt against the current. The details of this lebensspur are not known; it would conform generally to the morphology of the isopod, and would have a bilobate, oval shape (Fig. 19.2N, O).

Crustacea: Ostracoda (Seed Shrimps)

Ostracods inhabit all types of waters and substrates, and are very cosmopolitan. Most species do prefer quiet mud bottoms, less than 1 m deep. Typical animals are less than 1 mm long and seldom more than 3 mm. One South African freshwater species attains a length of nearly 8 mm (Pennak, 1953).

Most species of ostracods are nektonic animals, but some creep or scurry along the substrate. Species of the Candoninae burrow as deeply as 5 cm in soft substrates, but most remain within 2 cm of the surface. The burrows are ramifying tubes having an

◄ **Fig. 19.2** Selected arthropods and their lebensspuren. A, crayfish dwelling burrows and stacks, the latter being incidental to construction of burrows. B, theoretical crayfish tracks; single slashes made by 4th and 5th pereiopods and double ones by the 1st and 3rd pereiopods. C–E, crab burrows made in river banks (after Peters and Panning, 1933). F, trail of clam shrimp and burrow (lower right corner) (after Tasch, 1964). G–J, possible trails of tadpole shrimp: G, assuming very light contact of appendages and telson with substrate; H, interpretation assumes ploughing with appendages in the substrate; I–J, assume deep ploughing, the edge of the carapace and the telson leaving furrows. K, dorsal view of *Apus*, a tadpole shrimp. L, *Branchinecta paludosa*, a fairy shrimp. M, possible trail made by fairy shrimp. N, *Asellus communis*, an isopod. O, probable resting trace of aquatic isopod. P, cross section of ostracod burrow, enlarged. Q, cross section of ostracod burrow system. R, stonefly. S, claw and tarsal traces of a stonefly. T, mayfly larva. U, claw traces of mayfly larva. V, upper, cast of burrow of dragonfly naiad; lower, burrow of dragonfly naiad in substrate surface. W, dragonfly naiad. X, claw and tarsal traces of dragonfly naiad. Y, *Corydalus* larva. Z, resting trace of hellgrammite, showing claw and tarsal traces of appendages. AA, burrowing depth of different genera of dragonfly naiads (after Needham and Heywood, 1929).

oval cross-section only slightly larger than the burrower (Fig. 19.2P, Q). Systematic movement is not evident, and a boxwork of small burrows is quickly developed in suitable substrates.

Voigt and Hartmann (1970) described zigzag-like traces made by ostracods on the bottom of a desiccating pool in a limestone quarry in northern Germany. The ostracods moved forward with the dorsal rim inclined in the direction of movement.

Crustacea: Amphipoda (Scuds)

Amphipods are cosmopolitan in clear, unpolluted waters. They make a variety of lebensspuren, most of which have not been observed sufficiently to permit detailed descriptions. Kozhov (1963) reported that several forms burrow in Lake Baikal, Russia, both in shallow and deep water. He did not provide any further details. Amphipods make two types of crawling traces. Ones made when the body remains vertical consist of a criss-cross of slash marks, as the appendages scrape the substrate. The other form consists of irregular concave plough marks made when the scud chose to crawl across the substrate with its side resting on the substrate. The dwelling tubes described by Mills (1967) and the feeding burrows described by Howard and Elders (1970) from shallow marine environments may be considered as models for similar amphipod structures made in fresh water, until further studies are made. (See Fig. 22.11.)

Crustacea: Decapoda

Astacidae (Crayfish); Atyidae and Paleomonidae (Shrimp)

Crayfish (also called crawfish, crawdads, or "crabs") are common in temperate and tropical zones, and prefer shallow streams and lakes. Dwelling burrows are common (Figs. 19.2A, 19.7A). Some species habitually build burrows only when streams or ponds dry up or temperatures are lowered, whereas others build them only in wet pastures and marshy areas, and still others do not make burrows but remain in permanent waters (Pennak, 1953). The burrows differ widely in construction, depending on the species, substrate, and depth of the water table. Usually only one entrance exists, although as many as three have been observed. The tube leading from the entrance may proceed vertically, at an angle, or almost laterally in a sloping bank. In some the galleries are branched or irregular, but a chamber is always present at the lower end, where the crayfish remains during the hours of daylight. Certain burrows have a lateral chamber. The depth of a burrow ranges from a few centimeters to as much as 2 to 3 m, and is partially determined by the level of the water table; the chamber must contain water in order to keep the animal's gills wet. Burrows near the edge of a pond or stream are shallow; those farther away are deeper. Except during the animal's breeding season, each burrow houses a single crayfish. Burrows are constructed only at night, and the crayfish brings up pellets of mud and deposits them at the entrance to form a chimney. Such chimneys are approximately 15 cm high, but a few as high as 45 cm have been reported; they do not serve any particular purpose, but simply represent the safest and most convenient method of disposing of the mud pellets (Pennak, 1953, p. 456). [Also see Tack (1941) and Ortmann (1906).] The central tube in these burrows ranges from 1 to 5 cm, and the chimney from 4 to 15 cm, in diameter. The inside of the chimney is fairly smooth but the outside is very knobby, superficially resembling the burrows (*Ophiomorpha*) of *Callianassa major*, the marine ghost shrimp (cf. Fig. 2.2A).

Resting and walking traces have not been reported for crayfish or shrimp but can be inferred from the behavior and morphology of the animal, and would be comparable to those reported for fossil shrimp (Glaessner, 1969). Figure 19.2B is a speculative sketch of a walking trace for a shrimp or crayfish, the pereiopods placed as they might occur in a series.

Potamidae (Crabs)

Freshwater crabs are probably recently adapted to this habitat and have a limited distribution up-river, a few miles from the ocean. They build dwelling burrows several centimeters above water level, in the banks of rivers. The burrows are several centimeters in diameter and tens of centimeters deep (Fig. 19.2C–E). As in crayfish burrows, secondary galleries and large, open chambers are typical. The burrow may be completely filled with water, or only parts of the open chambers may be filled. [See Peters and Panning (1933) and Chace et al. (1959).]

Insecta

Plectoptera (Stoneflies)

Stonefly nymphs are abundant in well-oxygenated waters, particularly lotic environments. Stonefly nymphs generally remain on debris, aquatic plants, or under stones. Stonefly, dragonfly, dobsonfly, and mayfly nymphs or larvae are very similar, and make similar lebensspuren when they occasionally sprawl, creep, or scurry on clastic substrates (Fig. 19.2R–Z). Differentiation between mayfly traces and other lebensspuren is possible, based on preservation of markings made by a single claw on the tarsus of the mayfly leg. Dragonfly, dobsonfly, and stonefly larvae have paired claws (unguis) on the tip of the appendages.

Ephemeroptera (Mayflies)

The dwelling burrows made by some mayflies are much more significant than their sprawling, resting, or creeping traces (Fig. 19.2T, U). The dwelling burrows are horizontal or inclined U forms, and very regularly shaped (Figs. 19.3A, B; 19.6D, F; and 19.7G). [See Carpenter (1928), Ide (1935), Needham et al. (1935), Wesenberg-Lund (1943), Seilacher (1967, Fig. 1).] They occur in fine sand, silt, firm mud, and even in fine sediments between conglomerate clasts. Some are lined with a layer of finer particles. The Us range from 1 to 5 mm in tube diameter and are 1 to 2 cm across; they range from 5 to 15 cm in length. Although the animals occur worldwide in well-oxygenated shallow waters, particular species prefer particular environments. Almost all ephemerids burrow; baetids clamber, swim, and sprawl; and heptageniids are sprawlers in streams.

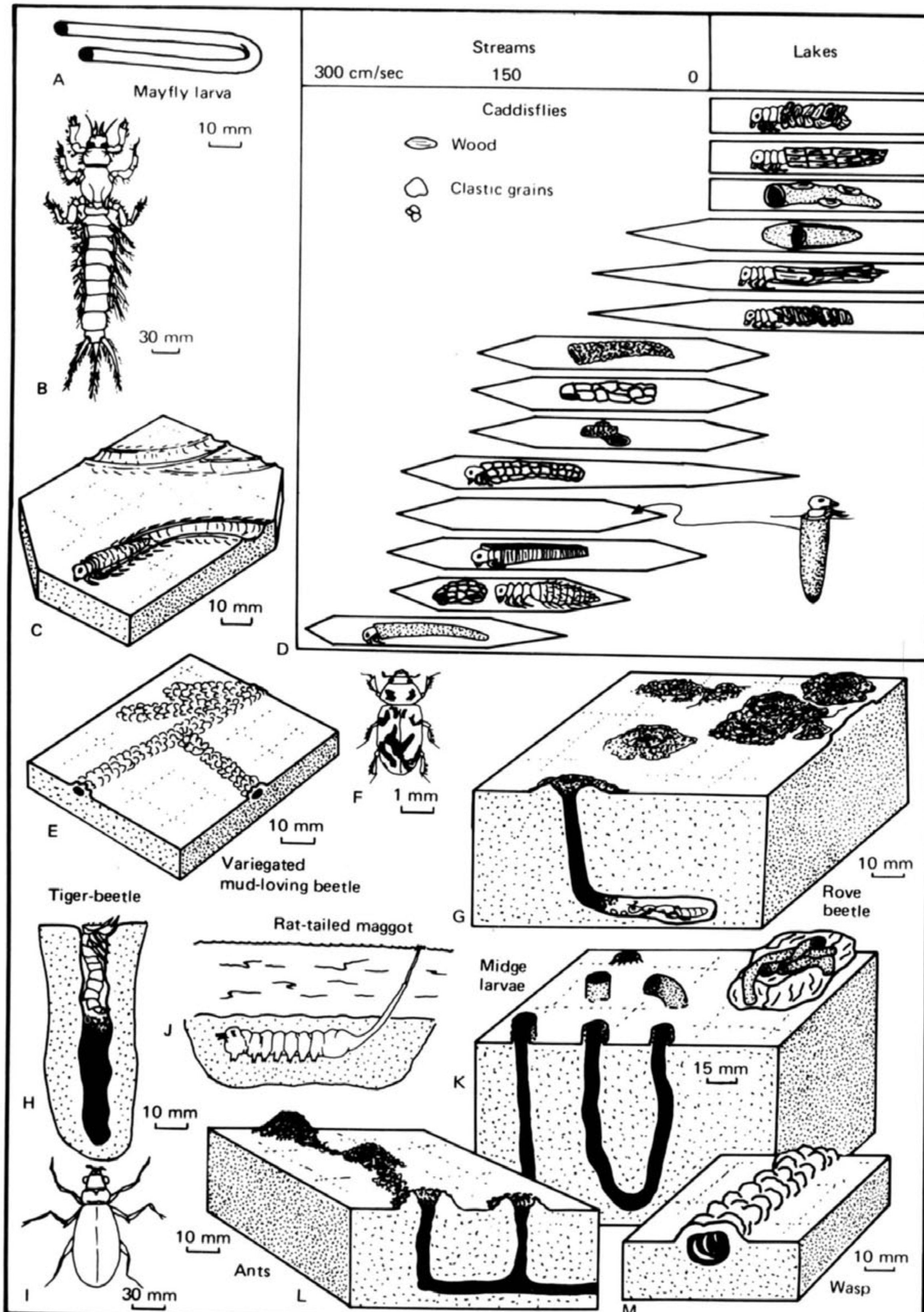
Odonata (Dragonflies)

In addition to sprawling and creeping traces (Fig. 19.2W, X), some dragonfly naiads burrow or plough shallowly in the substrate (Fig. 19.2V). Among the petalurids and gomphids, this burrowing is a search for aquatic insects, annelids, mollusks, and small crustaceans, on which they feed. The cordulegasterids construct a resting lebensspur, where the naiad awaits its prey. The traces range—with the size of the naiad—from 0.5 to 15 mm across and 10 mm to an indefinite length. The exact nature of the trace is not known, but in general it is a deep, irregular-bottomed furrow. Needham and Heywood (1929) compared the depth of burrowing of different genera, as shown here in Figure 19.2AA.

Dragonflies are widespread in all fresh waters, and are commonly found on the bottoms of ponds, streams, marshes, and shallows of lakes, in unpolluted waters. [See Wesenberg-Lund (1943), Pennak (1953), Smith and Pritchard (1956).]

Megaloptera (Hellgrammites)

The larvae of dobsonflies—called "hellgrammites"—are customarily found along the margins of ponds and lakes and under or between stones; but sometimes they lie buried, or crawl around on muddy substrates (Pennak, 1953). These crawling trails would be superficially similar to those of dragonfly and stonefly larvae (Fig. 19.2Y,


A
Mayfly larva
10 mm
30 mm
B
Streams
300 cm/sec
150
0
Lakes
Caddisflies
Wood
Clastic grains
10 mm
C
D
E
10 mm
Variegated
mud-loving beetle
F
1 mm
10 mm
G
Rove
beetle
Tiger-beetle
Rat-tailed maggot
Midge
larvae
H
10 mm
J
K
15 mm
I
10 mm
30 mm
Ants
L
10 mm
Wasp
M

Z). Resting traces might be distinguished by impressions of the abdominal spiracles, but speculation rather than observation is the basis for my remarks. Pupal chambers are constructed as much as 50 m landward from the water, and may be situated under various objects or 5 to 10 cm within the earth (Pennak, 1953).

Hemiptera: Salidadae (Shore-Bugs)

Comstock (1966) reported that shore-bugs burrow but did not provide details of their burrows. They abound along the shore of streams and lakes, especially in damp soils of marshes near coasts.

Trichoptera (Caddisflies)

Caddisfly larvae sometimes build dwelling cases very meticulously, choosing the materials and fashioning the exact form of the case. Some use only particular types of plants, mineral grains, small abandoned shells, or woody fragments. The animals may agglutinate these particles in (1) helical cases, (2) elongate, curving, or straight tapering tubes having round or square cross-sections, (3) "turtle shell" cases, or (4) structures agglutinated to rocks. Dobbs and Hisaw (1925) studied the relationship between case form and their distribution in lotic and lentic environments; that information is modified here as Figure 19.3D. The same forms may occur in lentic parts of both lakes or streams, and others in the lotic parts; but an intriguing zoogeography is nevertheless present. In general, heavy cases occur in swift lotic environments and plant cases in more lentic environments. Some forms build dwelling tubes by burrowing into the sand on the bottom of streams and cementing the walls of the burrow (Denning, 1956). Crawling trails occur very regularly when the larvae drag their dwelling cases across the substrate (Fig. 19.3C). This lebensspur may be distinguished from other rounded furrows where leg marks are preserved on both sides of the drag furrow.

Caddisfly larvae are widespread in almost all suitably oxygenated streams and lakes. They inhabit all types of substrates but are more prone to occupy those at shallower depths in lakes.

Coleoptera (Beetles)

Carabidae. Silvey (1936) studied the burrows of four species of *Dyschirius*, one of *Bembidion*, one of *Agonoderus*, and two of *Omophron*, all found on the shore of Douglas Lake, Cheboygan County, Michigan. The detailed description of those species are available in Silvey's paper. Some traces are simple inclined tubes; others are irregular or branched, and others are complex, having multiple branches.

Dytiscidae. The little predaceous diving beetle *Hydroporous mellitus* was described by Shelford (1937, p. 102) as burying itself in sand on the bottom of streams. Presumably it creates a resting trace, while it awaits prey; but details of the lebesspur were not given.

Georýssidae. The minute mud-loving beetle *Georýssus pusillus* is approximately 1.7 mm long. It is a shore species that dwells

◄ **Fig. 19.3** Selected arthropods and their lebensspuren. A, burrow of mayfly nymph. B, *Pentagenia*, mayfly nymph responsible for burrows found near Bryan, Texas. C, surface trails made by caddisfly larvae. D, environmental range of certain types of cases of caddisfly larvae, showing overlap from lakes to streams of larvae adapted to lotic or lentic conditions. Second example from bottom represents naked forms and turtle-shell forms; fourth from bottom represents tube-making form (modified after Dobbs and Hisaw, 1925). E, burrows made along damp shores by variegated mud-loving beetle, *Heterocerus*. F, adult *Heterocerus flexuosus*. G, rove beetle burrows and mounds (after Smith and Hein, 1971). H, larva of tiger-beetle in burrow, found in shore zone. I, adult tiger-beetle. J, *Tubifera*, rat-tailed maggot, in (?)burrow in mud. K, burrows and surface tubes of midge larvae. L, ant mounds and tunnels, found along river and lake shores. M, burrow of wasp, made in temporary pond.

in mud along banks of rivers and lakes (Borror and Delong, 1955). The nature of the lebensspur has not been reported. According to Comstock (1966), *Georÿssus* covers itself with a coating of mud or fine sand.

Heteroceridae. The variegated mud-loving beetle *Heterocerus* is a small insect, seldom longer than 2 mm. It makes distinctive burrows in mud and silt along the shores of streams and lakes (Figs. 19.3E, F; 19.5C–D; 19.7B). The burrow is largely superficial—just beneath the surface—and is made by pushing sediment upward bit-by-bit while forging forward. The result is a small tunnel, having striated walls and a hummocky ridge overhead, tracing its course. The animal seems to have no systematic plan in making this feeding burrow. Many perpendicular and angular branches are seen, and these may cross other burrows. In addition to the dwelling burrows, pupal chambers have also been reported. Williams and Hungerford (1911) illustrated urn-shaped mud cases of *Heterocerus* sp. that they thought were made by a larval stage. [See Claycomb (1919), Larsen (1936), Silvey (1936), and Wesenberg-Lund (1939).]

Hydraenidae. Leech and Chandler (1956) and Leech and Sanderson (1959) reported that some hydraeniids tunnel in damp sand near streams and that the larvae are predaceous, occurring also in the damp sand and mud at the edge of the body of water.

Hydrophilidae. Laccobius, a water scavenger beetle, crawls or dabbles for concealment in mud at the water's edge (Pennak, 1953).

Noteridae (or Noterinae). The burrowing water beetles have fossorial larvae that burrow and dig through mud around the roots of aquatic plants (Leech and Chandler, 1956).

Ptilodactylidae. Like the noteriids, some of the ptilodactylids burrow into the substrate in order to feed upon roots of water plants (Leech and Chandler, 1956).

Staphylinidae. Dwelling burrows of *Bledius,* one of the rove beetles, were described by Smith and Hein (1971) and mentioned by Leech and Chandler (1956). Smith and Hein observed the burrows in sandy areas after receding flood waters, along the Platte and Loup Rivers in eastern Nebraska. Small sandy mounds were heaped up by *Bledius* as spoil from the excavations. Smith and Hein showed the galleries to be first inclined, in shallow parts, and then horizontal, in deeper parts, but did not provide any further details. If continued burrowing was to be maintained in search for food, then the burrows would probably be more complex than that shown in Figure 19.3G.

Cicindelidae. Larvae of *Cicindela hirticollis,* the beach tiger-beetle, have been observed to build simple vertical dwelling tubes in moist areas on the shore of streams and lakes (Shelford, 1937). The tubes are as much as 15 cm deep and a few millimeters across (Fig. 19.3H, I). Wallis (1961) reported that *C. hirticollis* prefers dry sand. *C. repanda* and *C. duodecimgutta* burrow in heavy, moist soil along river banks—especially mud flats and sandy bars—as much as 30 cm or so from the water's edge. *C. oregona* prefers margins of lakes and streams, in clay or sandy soil. *C. nevadica* was found on wet mud along the margins of saline or alkaline lakes and streams. Wallis did not describe the burrows, except to write that *C. repanda* burrows are approximately 15 cm long.

Adults make shallow burrows at night or in the heat of day. The aestivation burrows of adults and larvae are about equally deep. When building hibernation chambers, the adult initially burrows several centimeters, throwing the soil out behind; then the soil is packed in the burrow behind the beetle as it burrows deeper. The burrow is kept large enough for the animal to turn around. In the chamber at the bottom, enough room remains both for turning and for backfilling when the beetle ends its hibernation. (See also Fig. 2.1.)

Diptera (Flies)

Syrphidae. Rat-tailed maggots are the larvae of flower or hover flies. *Tubifera* burrows into mud or silt, but details of the burrow are not known. They are limited to shallow water (a few centimeters) because they extend their elongate caudal respiratory tube to the surface (Fig. 19.3J) [see Wigglesworth (1964, Fig. 21)].

Tabanidae. Horsefly larvae burrow in the substrate in order to feed on organic matter or on snails, oligochaetes, and insect larvae. Details of the burrow are not known, but it probably reflects a random search pattern. The larvae are cosmopolitan, some even occupying swift waters; but most are found in shallow muddy waters of ponds and swamps (Pennak, 1953).

Chironomidae. Blood worms, or midge larvae, are widely distributed in sluggish streams, ponds, and lakes, and even in fine sediments dispursed among gravels in swift streams. They construct dwelling tubes 0.5 to 3 mm across and as much as 15 cm deep (see Figs. 19.3K—left side, 19.5F, 19.7I). Most tubes are irregular U forms having two entrances, but some seem to be blind ends or juxtaposed, vertical tubes lacking another outlet. Tubes are extended above or onto the surface by the agglutination of organic detritus, algae, or fine-sand and silt grains. Under certain conditions (e.g., low water or oxygen-poor habitats) the tubes are constructed irregularly for several centimeters across the substrate surface. Many tubes are fixed to stones or plant debris (Fig. 19.3K—right side).

Curry (1954) studied midge larvae in Hunt Creek, Michigan, and observed definite substrate preferences exhibited by different genera. Three made tunnel-like chambers in sand masses fixed to mossy stones, in lentic waters, and twelve genera preferred lotic waters. Larvae in lotic waters built tubes in mud and sand substrates.

Hymenoptera: Formicidae (Ants) and Sphecidae (Wasps)

Ants occur down to the saturated edge of many streams and lakes, where they build small mounds, shafts, and shallow galleries (Figs. 19.3L, 19.7E). These galleries are irregular, extend indefinitely, and range to depths of 5 to 10 cm. They are linked to the surface mounds by irregular vertical shafts spaced 3 to 10 cm apart. The galleries average approximately 3 mm across. Although some food is probably encountered during construction of the galleries, extensive above-ground foraging is probably the main means of food gathering, and the galleries are mainly for dwelling.

In an ephemeral puddle, I observed an unidentified wasp tunneling into the cohesive mud, by scraping the mud and removing it, apparently to build pupal chambers (Fig. 19.3M). During the process, the tunnel was constructed more than 60 cm long; it had scrape marks on the inside and a hummocky ridge tracing its course on the surface. The structure was almost identical to that made by mole crickets, discussed below.

Orthoptera (Crickets)

Gryllotalpinae. The mole crickets (Fig. 19.4D) are widespread and build dwelling tunnels in moist sand or mud, particularly along moist margins of streams and ponds (although many gardeners will declare that they are most common elsewhere). Comstock (1966) stated that their burrows extend 20 to 30 cm below the surface, but those observed by me near waterways generally have galleries just beneath the surface. Some do dip down several centimeters under obstacles, or to terminate in a resting chamber. Near the water's edge, they have been observed to branch repeatedly—the animal apparently processing the sediment adjacent to water level (Figs. 19.4A, B; 19.6B). The gallery is constructed by pushing the sediment forward and lift-

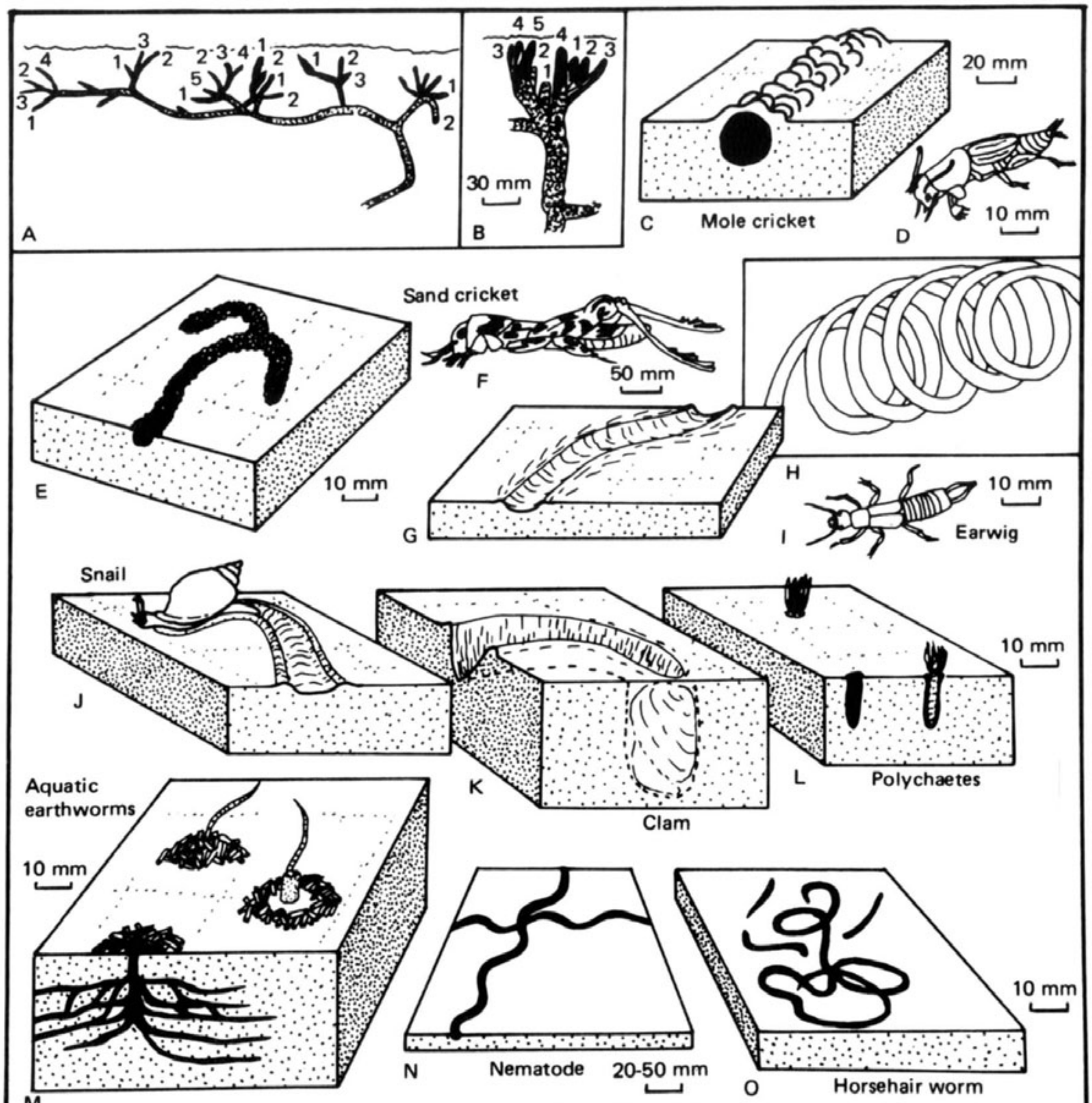


Fig. 19.4 Selected worms, arthropods, and mollusks, and their lebensspuren. A, mole cricket burrows (plan view) along a bayou near Houston, Texas; numbers indicate order of uncovered burrows at edge of stream. B, mole cricket burrows, as in A. C, mole cricket burrow. D, mole cricket *Gryllotalpa*. E, burrows of sand cricket *Tridactylis*, as found in lakes, stream shores, and wet gardens. F, *Tridactylis apicalis*, the sand cricket (or pygmy mole cricket). G, H, trails of earwigs in ephemeral puddles, after a storm; H, a pattern made by an injured earwig. I, adult earwig (Dermaptera). J, snail trail, as in rivers and lakes, showing only simple surface expression. K, trail of bivalve, typical of large rivers and lakes. L, small agglutinated tubes of polychaetes found in lakes or streams. M, *Tubifex*, an aquatic earthworm, extending from small agglutinated surface tube (on right) and surrounded by circular ridge of clastic fecal rods. N, nematode trails. O, possible bottom traces left by horsehair worm (Nematomorpha).

ing it bit-by-bit, so that a hummocky ridge traces the course of the burrow (Figs. 19.4C, 19.6B). The galleries range from approximately 0.5 to 1 cm across and may comprise a continuous system traceable for a few meters. Burrows shown by Hanley et al. (1971) from Seminoe Reservoir, Wyoming, and those by Frey and Howard (1969, Pl. 4, fig. 4) are mole cricket burrows.

Tridactylidae. The sand or pygmy mole cricket *Tridactylus* (Fig. 19.4F) builds distinctive dwelling burrows in moist sand or mud, particularly on shores or bars of streams and lakes. The burrows described by Blatchley (1920) occurred in sandy margins of ponds; the upper parts were vertical, and lower parts ran horizontally —not more than 3 cm below the substrate surface. The latter were approximately 1 mm in diameter.

Urquhart (1937) observed *Tridactylis apicalis* in northeastern Toronto throughout the year. Hibernation chambers were found 45 to 60 cm below the surface, in a soft sand underlying a sandy clay. Brood chambers were observed at another time; a tunnel extended to depths of 2 to 4 cm below the surface, and widened out into a small chamber at the far end. Solitary females were found inside, guarding 10 to 27 eggs in each batch.

In Texas, the lebensspuren of sand crickets seldom went below the surface when I observed them in July and August. Sand crickets there built a superficial burrow by working a few grains of sand into small clusters, using their maxillary palpi, and adeptly sticking the balls together in an arch over the excavation (Figs. 19.4E, 19.5A, B). The burrows were laid out irregularly, branching perpendicularly or angularly, and curving or looping. Most of them were less than 10 cm long, and the width of an individual tunnel was less than 5 mm. I have seen regions adjacent to the Brazos River, Texas, that were extensively worked in a zone a meter or more wide paralleling the shore. In wet muds, sand crickets observed along the Brazos and the Hocking River of Ohio built wider burrows —as much as a centimeter across and ramifying through an area of several centimeters. The surface was hummocky, suggesting that it had been lifted bit-by-bit rather than being built by piecing separate mud balls together.

Dermaptera (Earwigs)

Among the fortuitous trails made in ephemeral rills and puddles are those of earwigs (Fig. 19.4G–I). After a severe storm, I observed several crawling trails that consisted of a round furrow approximately 4 mm across, having appendage marks along the side. Another, more intriguing pattern was made by injured earwigs; they made erratic circular traces that were superficially reminiscent of many of the complex grazing patterns of marine animals noted in the geologic record [e.g., *Cruziana semiplicata* (Seilacher, 1970, Pl. 1)].

Mollusca

Gastropoda (Snails)

Snails are cosmopolitan and abundant in almost all freshwater environments. Most of their trails seem to be simple furrows corresponding to the width of the foot of the animal (Figs. 19.4J, 19.8B—left). Details of their burrows and trails are not known. Based on the complex structure of the trace fossil *Scolicia*, attributed mainly to snails, a great deal of variability is probably present in freshwater trails. Commonly, the trace involves more than a ploughing of the substrate as the foot moves peristaltically across it. Often, layers of sediment are indiscriminately pushed aside or behind the foot. In some forms, the shell may be carried in such a way that it also makes a print in the substrate; in others, a continuous fecal string may be part of the trail. Whether the snail is on top of the substrate, or partially or totally concealed within it, also makes a difference. Obviously, a great deal of study is needed in order to determine the exact nature of the burrows and trails. Aestivation and hibernation chambers several centimeters deep are made by some forms; again, the characteristics

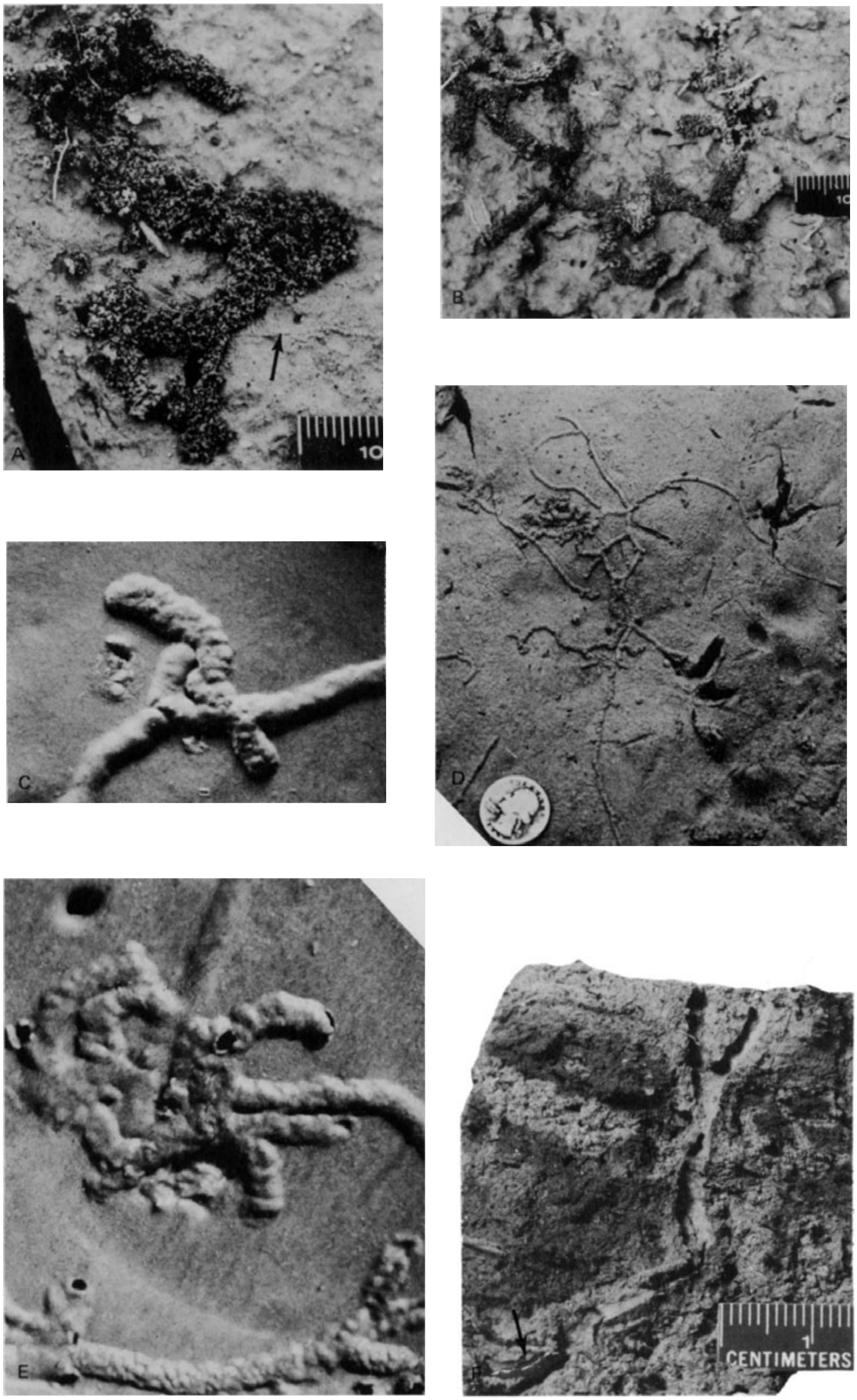


Fig. 19.5 Arthropod lebensspuren. A, B, burrows of *Tridactylis* in shore of bayou, near Houston, Texas. Small rod-like burrow at arrow, in A. Many such burrows present in wet and dry sediments along the stream have survived several rains. (10 mm scales.) C–E, burrows of *Heterocerus*, the variegated mud-loving beetle. D, from shore of Brazos River, Bryan, Texas; bird tracks also present. (Quarter-dollar coin for scale.) C, E, from bayou: Houston, Texas. F, midge larvae tubes from Dow Lake, Athens, Ohio; larva in lower left, at arrow.

and variability of these structures are unknown.

Bivalvia (Clams and Mussels)

Clams and mussels are widespread in unpolluted fresh water. They prefer stable gravel, sand, and mixed sand-silt substrates in the shallows of large rivers. The lebensspuren are essentially grooves ranging from a few millimeters to several centimeters in width, depending on the age and species of the clam (Figs. 19.4K, 19.6E, 19.7H, 19.8B).

Pryor (1967) studied clam burrows on point bars in the Whitewater River of western Ohio and Wabash River in western Indiana, and found distinctive patterns. His observations are summarized in a subsequent part of this chapter.

ASSEMBLAGES OF NONMARINE AQUATIC LEBENSSPUREN

Information available on the zoogeography of freshwater trace-making animals is both limited and widely dispersed in texts and journals. No general synthesis has been made (cf. Chapter 2, Table 2.1), and consequently, only a few generalizations and speculations can presently be made about these assemblages. Northern Hemisphere, temperate lakes and streams were selected —mainly because of availability of data at the time of writing—and great limitations are inherent in the particular selections.

Ephemeral Ponds and Lakes

Branchiopods are highly selective as to the ponds they inhabit, and seldom occur where carnivorous animals persist. Consequently, one or only a few species seem to characterize particular ephemeral, saline or alkaline, muddy ponds, puddles, or lakes. A distinctive and easily described assemblage of freshwater lebensspuren should occur in such lakes, and should include the scrape, crawl, or plough marks of tadpole shrimp, clam shrimp, and (or) fairy shrimp. The trace fossil assemblage described by Savage (1971) from a late Paleozoic varvite in Natal is not too different from those both known and to be expected in similar Holocene lakes and ponds.

Shores

River and lake shores seem to be dominated by a beetle-trace assemblage that includes larval tubes of the tiger-beetle *Cicindela,* dwelling burrows of the variegated mud-loving beetle *Heterocerus,* and dwelling or feeding burrows of species of the rove beetle *Bledius.* The orthopterid mole crickets and sand crickets seem to be almost equally common, and locally the crayfish burrows may form a significant part of the stream-shore assemblage of lebensspuren.

Shelford (1937) recorded the occurrence of beach tiger-beetle larvae (*Cicindela hirticollis*) in moist parts of the shore of Lake Michigan. The tubes were simple vertical forms. No other burrows were mentioned. Wallis (1961) reported *C. hirticollis* from dry sands, and *C. rapanda, C. duodecimguttata, C. oregona,* and *C. nevadi* from wet shores of lakes or streams.

The rove beetles *Bledius pallipennis* and *B. bellicosus* were found by Smith and Hein (1971) burrowing in sandy bars and anabranches along the Platte and Loup Rivers of Nebraska, following recession of high waters.

Silvey (1936) found eight species of carab beetles, one species of heterocerid, and one rove beetle along lake shores. Both adults and larvae were found to make distinctive burrows in the inner beach—from the water's edge up to the dry-sand line.

Along the shore of the Brazos River, west of Bryan and at Richmond, Texas, and along the shore of various bayous in and around Houston, I observed a distinctive freshwater lebensspuren assemblage that contains the burrows of *Heterocerus,* mole crickets, sand crickets, and ants.

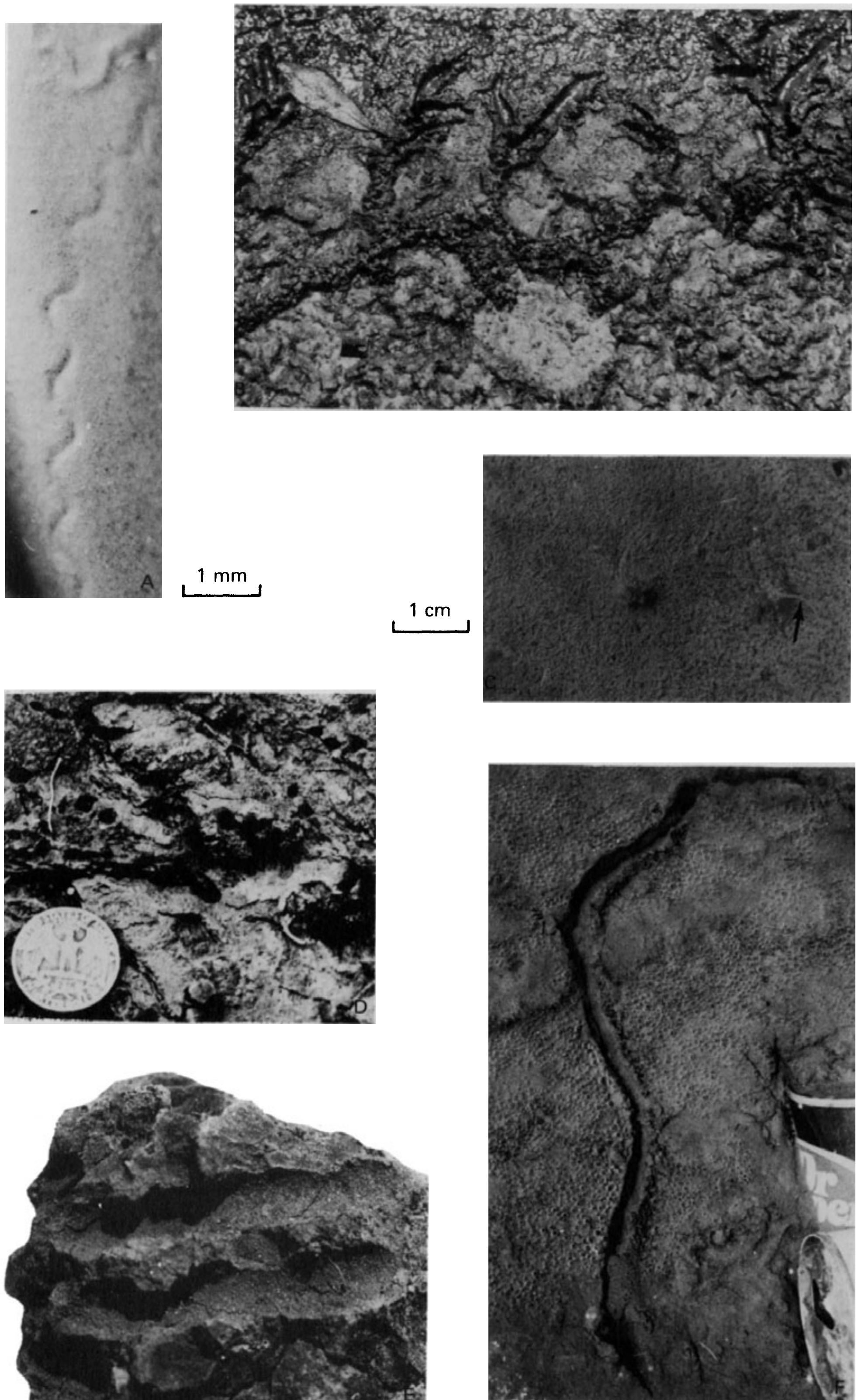


Fig. 19.6 Worm, arthropod, and mollusk lebensspuren. A, nematode trail from bayou near Houston, Texas. B, mole cricket burrows from shore of bayou near Houston, Texas; water edge at top. C, *Tubifex* in tubes; worm at arrow, and fecal rods around tubes. Small dark holes are ostracod burrows, and larger one at upper right is midge larva burrow. D, F, burrows of mayfly larva, *Pentagenia*, from near Bryan, Texas. Burrows are Holocene, made in Tertiary shales. D, paired tube openings; quarter-dollar coin for scale. F, plan view of paired tubes (horizontal), the basal U missing. E, burrow of clam *Anodontoides*, from Richmond, Texas, along Brazos River; refuse for scale.

Classical U-shaped burrows of mayfly nymphs are very abundant west of Bryan. Although burrows are made below water level, they can be collected above the water line where Holocene burrows in Tertiary shales are exposed at low water. Bivalves burrowing near the shore and just below the water line also may be considered as part of this shore assemblage. Various birds and mammal tracks are present, and along the smaller, less permanent waterways, numerous crayfish burrows are found. The traces made by crayfish, ants, mayfly nymphs, and bivalves are essentially dwelling burrows whereas the coleopteran and orthopteran traces are horizontal feeding burrows. I observed a distinct zonation within this overall shore assemblage (Fig. 19.7). Sand crickets are most abundant in the algae-rich, water-saturated muds and silts (but do not range exactly to the waters edge), sparse in the transition zone to damp sediments, and abundant again in the damp shore zone. Mole crickets are abundant in the saturated muds and silts all the way to the water's edge, and sparse in the damp shore. Variegated mud-loving beetles and ants occur more or less evenly through the saturated and damp shore, but not down to the water's edge.

Streams

Lateral zonations related to bathymetry may be established in lakes relatively easily; but in streams, few definitive criteria seem to be available for describing assemblages. The work by Dobbs and Hisaw (1925) is an exception, and suggests the kind of results that might be possible with proper study. Through high- and low-energy streams and in lotic and lentic parts of lakes, they observed a distinctive distribution of caddisfly larvae (Fig. 19.3D).

The assemblage of freshwater molluskan lebensspuren described by Pryor (1967) occurred in the bar-foreshores and back-bar sloughs of the Wabash River in western Indiana and the Whitewater River of western Ohio. The larger species and individuals were found on the upstream parts of the bars, where the sediment size is coarser and the flow regime higher. The size of individual mollusks gradually de-

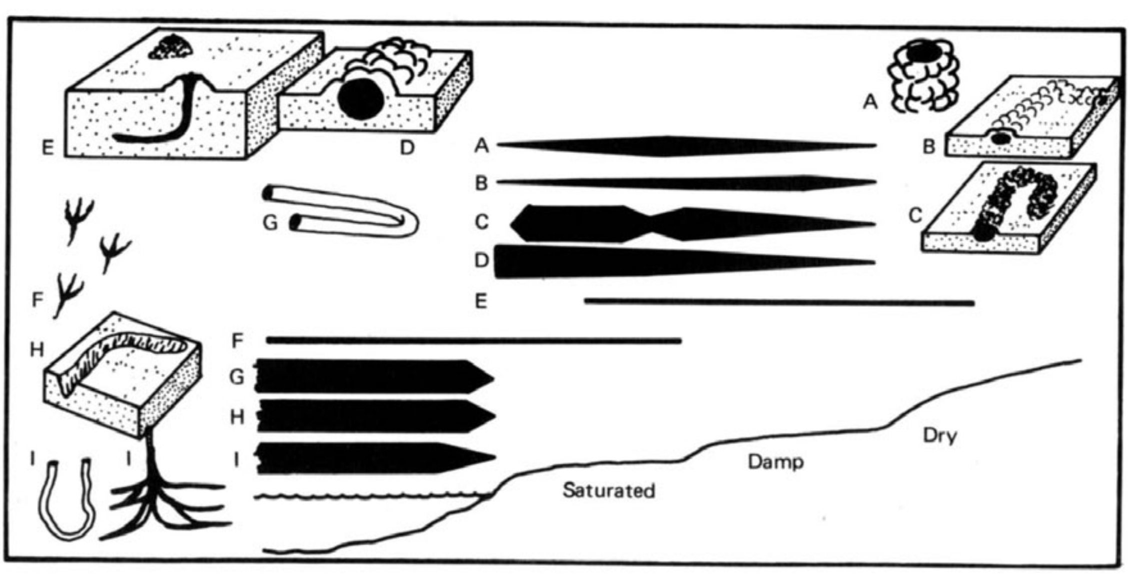


Fig. 19.7 Composite illustration of shore and nearshore range of lebensspuren from Brazos River, near Bryan and Richmond, Texas, and a bayou near Houston, Texas. A, crayfish. B, *Heterocerus*, the variegated mud-loving beetle. C, *Tridactylis*, a sand cricket. D, mole cricket. E, ants. F, vertebrates. G, mayfly larvae. H, bivalves. I, midge larvae (U tube) and aquatic earthworms (dichotomous burrow).

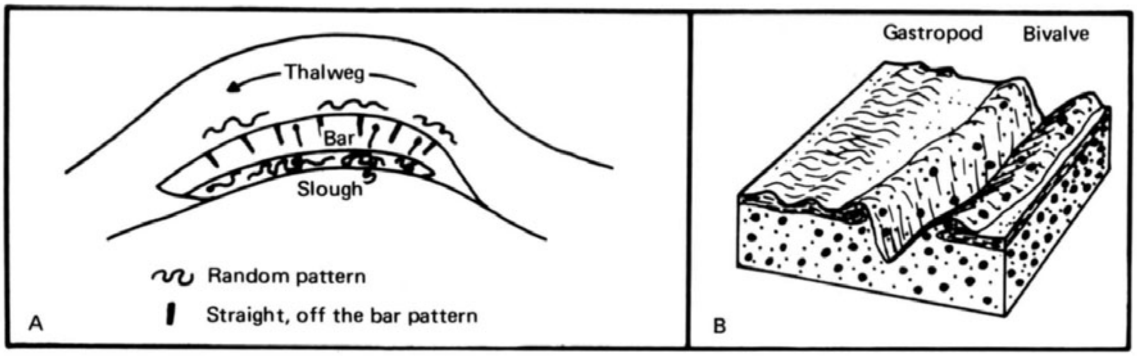


Fig. 19.8 Distribution of mollusk lebensspuren on point bars of the Wabash River, Indiana, and Whitewater River, Ohio. A, straight, off-the-bar traces made as flood waters recede. Irregular and crisscross patterns in the slough occur after water recedes and slough begins to dry. Random patterns nearshore, along the bar, are normal, daily patterns. B, plough-depth patterns observed: snails disturbed top, muddy layer; clams ploughed up coarse material. (After Pryor, 1967.)

creases downstream, toward the quieter parts of the bars. During periods of stable water level, the mollusks burrow randomly below water level (Fig. 19.8A). When the water rises, they climb higher in order to attain their optimum water depth. As the water level drops, the clams plough directly down the length of the bar, toward the water. If they are left behind by the receding water, they burrow. Mollusks caught in a back-bar slough initially burrow randomly, without much crisscrossing of trails; but as the water level drops farther, they make numerous meandering, crisscrossing trails. As the water level drops below the substrate surface, the bivalves burrow in and the snails die. Bivalves in the back-bar slough ploughed deep enough to bring coarser sediment up, in lateral ridges, whereas snails ploughed through only the finer, muddy sediment, leaving a central furrow and two lateral ridges (Fig. 19.8B—left).

Along lentic and lotic parts of the Hocking River of Ohio, Ludwig (1932) observed the distribution of freshwater animals. In the lentic areas, midge larvae and aquatic earthworms were abundant. Snails and bivalves were also present, but less abundantly. In the lotic parts, caddisfly larvae, isopods, and amphipods were more abundant. In a small, abandoned part of the Hocking River—where the stream is approximately 2 m across and normally 20 cm deep—aquatic earthworms are common along the edges, where mud is trapped by cattails and grasses. Snail burrows course randomly through mud, sand, or fine gravel on the bottom. Dragonfly naiads plough randomly through the mud, remaining just below the substrate surface.

Lakes

The distribution of animals that might, or do, make lebensspuren in lakes is similar in Lake Simcoe, Canada; Esrom Lake, Denmark; and Lake Baikal, Russia (Fig. 19.9). Most forms are restricted to shallow depths (a few tens of meters), and include leeches, flatworms, ostracods, isopods, mayfly nymphs, caddisfly larvae, and gastropods. Bivalves and midges extend into intermediate depths (several tens of meters). Amphipods and oligochaetes occur at all depths—from the shore to hundreds of meters (where they are the dominant benthic forms).

As in marine environments, many deposit feeders live in the deeper waters of lakes. Resting, dwelling, crawling, and suspension-feeding behaviors are typical of the animals in shallower waters.

Esrom Lake in Denmark is 8 km long, 2 to 3 km wide, and 22 m deep. It is situated in glaciated terrain, amid forests and farms. At depths greater than 14 m, the substrate is mud; at shallower depths, the substrate

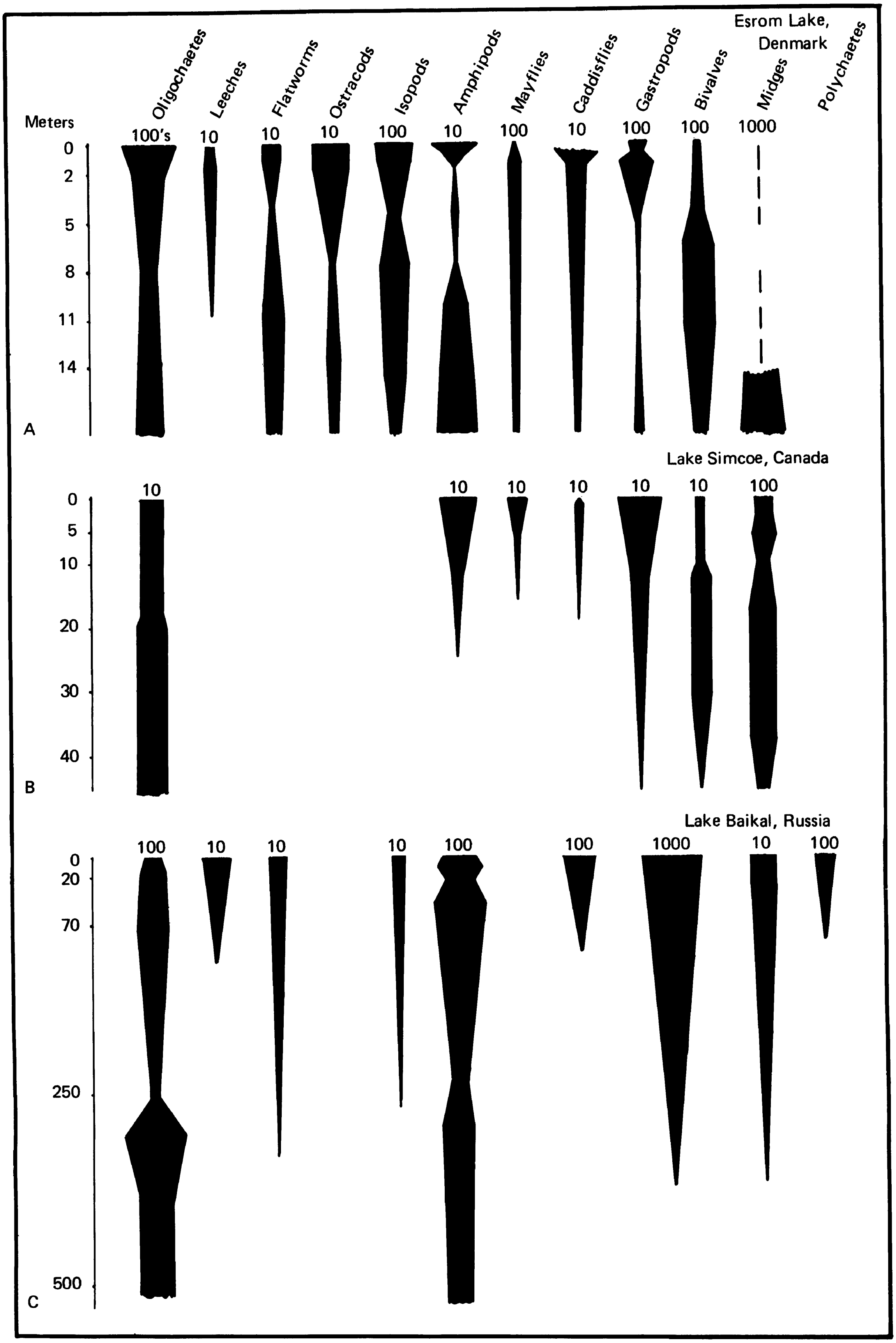


Fig. 19.9 Bathymetric distribution of some possible trace-making invertebrates of certain shallow (A), intermediate (B), and deep-water (C) lakes of northern temperate zones. Available data sketchy, and expressed in units not easily standardized; distributions expressed in relative numbers of specimens.

is sand or sand and gravel. Berg studied the fauna extensively, and the data from his 1938 book, as summarized by Macan (1966), are the basis for Figure 19.9A.

Rawson (1930) studied Simcoe Lake and provided rather good data on this glacial lake, situated just northwest of Lake Ontario. Lake Simcoe is more or less of equal dimensions and covers approximately 200 km^2. Figure 19.9B summarizes Rawson's data, but only includes those forms that might have left traces.

Lake Baikal is the world's deepest lake, and one of the oldest. It is located in central Siberia; thus, like Lake Simcoe and Esrom Lake, it is in the northern temperate zone. The data in Figure 19.9C are taken from Kozhov (1963).

FRESHWATER VERTEBRATE LEBENSSPUREN

Insufficient information and limited space allow only a cursory report on vertebrate lebensspuren in nonmarine aquatic environments. Consequently, the purpose of this section is to provide—in the context of overall assemblages—at least some idea of the types of tracks, trails, burrows, or other structures made by fish, amphibians, reptiles, birds, and mammals. This topic is covered further in Chapters 14 and 15.

Dwelling structures, feeding traces, hibernation burrows, and nesting structures are made by aquatic or semiaquatic freshwater vertebrates, but shore tracks and trails are probably the most common traces.

Dwelling Structures

The sea lamprey is an extant representative of the first vertebrates, the jawless fish (Agnatha). The young individuals mature inside dwelling burrows in the bottom of streams (Fig. 19.10A; see Applegate and Moffett, 1971). Most dwelling burrows made by other vertebrates are dug into the banks of rivers or lakes. The duck-billed platypus (*Ornithorhynchus*)—a monotreme mammal —makes a long burrow in the bank, just above water line; the structure has a leaf-lined chamber at the end, and other auxillary galleries branching off (Fig. 19.10B; see Bergaminii, 1967). The water opossum (*Chironectes minimus*) of Central and South America is a marsupial mammal that makes burrows similar to those of the platypus; it is the only marsupial adapted to an aquatic life, having webbed hind feet. Walker et al. (1968) reported at least eight insectivores that are either fully aquatic or semiaquatic, most of which maintain dwelling burrows in the banks of streams or lakes: for example, the rice tenrec (*Oryzorictes hova*) of Madagascar, the otter shrew (giant African water shrew, *Potamogale velox*), the web-footed water shrew (Tibetan water shrew, *Nectogale elegans*), and the Russian desmans (*Desmana moschata*). Beaver, muskrats, and nutria are some of the more familiar aquatic rodents. Beaver and muskrats build lodges, using sticks and mud, and burrow extensively into river banks (Fig. 19.10C). Muskrats use smaller material than do beavers. Nutria burrows, built in banks, consist of a main tunnel having a slightly enlarged chamber at the back (Collins, 1959). The flat-tailed otter (*Pteronura brasiliensis*) is not only a carnivore that is adapted to an aquatic life style, but it also maintains a den in the bank of the river (Walker et al., 1968).

Tracks and Trails

Tracks and trails made on the shores of lakes and rivers are very extensive and diverse, and certainly are not limited to the strictly aquatic or semiaquatic vertebrates; included are the fortuitous tracks of vertebrates merely passing through the area, or more commonly those made on the shore while animals are drinking. Such tracks, mainly mammal, are treated in several texts, such as those by Mason (1943), Collins (1959), Carrington (1963, p. 186–187), and Ormond (1965). Some of the characteristic tracks of aquatic or semiaquatic vertebrates

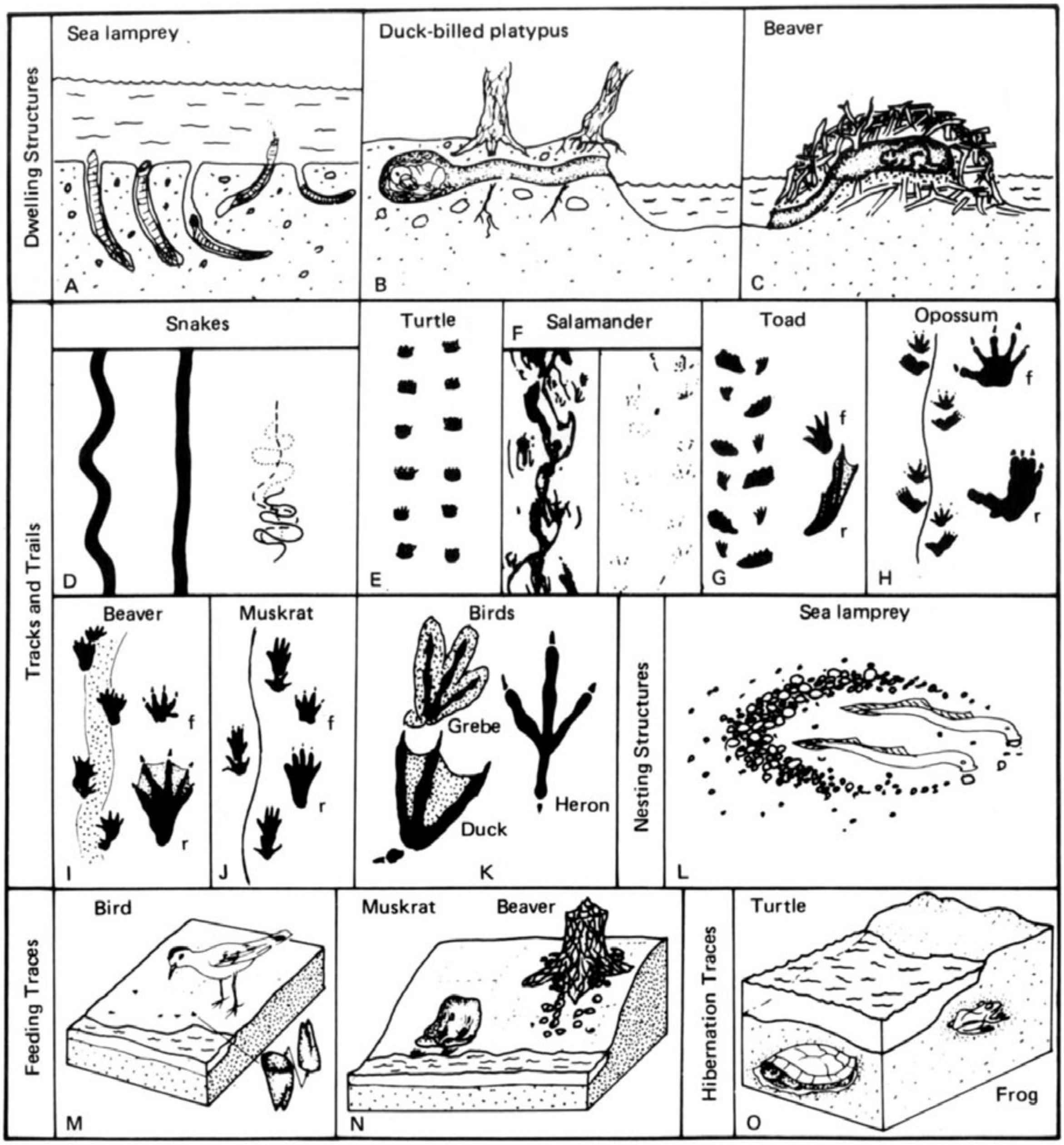


Fig. 19.10 Selected vertebrates and their lebensspuren. A, sea lamprey larvae living in dwelling burrows in bottom of stream, as they mature (after Applegate and Moffett, 1971). B, duck-billed platypus in dwelling burrow, in bank of stream (after Bergaminii, 1967). C, beaver lodge made of sticks and mud, in pond. Muskrats also construct such dwellings, using smaller sticks, mud, and pieces of water plants. D, snake crawling traces, as found along lake or river shores, might include the classic serpentine pattern (left), inchworm crawl (middle), or concertina (right)—solid line= initial state, dashed=forward advance of head, and dotted=forward advance of tail. E, turtle trail through a bayou near Houston, Texas. F, copy of salamander locomotion traces, made on a carbon drum (Evans, 1946). Left trace shows rapid movement, the body on the ground; right trace shows slow movement, the body raised. G, toad walking trace.* H, opossum tracks and trail, commonly found near streams.* I, beaver tracks and trail.* J, muskrat tracks and trail.* K, tracks of aquatic and semiaquatic birds. L, nesting trace of sea lampreys; similar structures are made by sunfish. M, bird feeding traces, made on shores of lakes and streams, consist of conical pits that may be bifurcated. N, muskrat feeding traces, in the form of small burrows or scraped-out areas, and beaver-gnawed stumps and limbs, and wood chips. O, turtle and frogs hibernating, as in substrate of stream or pond. (* f=front, r=rear foot.)

include those of walking catfish; amphibians such as toads, frogs, or salamanders (Fig. 19.10F, G); reptiles such as certain turtles (Fig. 19.10E), alligators and crocodiles, and certain snakes (Fig. 19.10D); numerous birds (Figs. 19.5D, 19.10K); and mammals such as opossums (Fig. 19.10H), beavers (Fig. 19.10I), muskrats (Fig. 19.10J), hippopotamuses, and probably the Baikal seals. Alligators, crocodiles, and hippopotamuses all make extensive wallow holes.

Resting Traces

Hiding or resting traces made within the substrate are probably most characteristic of the lower vertebrates; the traces conform partly to body morphology but mostly to animal movements within the sediment. Frogs, fish, and turtles are commonly seen darting into soft substrates in order to evade predators; some species conceal themselves while awaiting prey.

Feeding Traces

Feeding structures comparable to those made by invertebrates are lacking for vertebrates. Birds commonly make peck marks in the beach as they seek infaunal invertebrates (Fig. 19.10M). Many aquatic animals are herbivores, and while feeding or during construction of lairs, may leave gnaw marks on pieces of wood or plant material (e.g., beaver; Fig. 19.10N); others, such as the muskrat, make irregular burrows in shores and banks as they gather small plants (Fig. 19.10N).

Nesting and Hibernation Structures

Several fish, such as the sea lamprey (Fig. 19.10L), sunfish, tilapia, pumpkinseed, and port, make nesting structures by (1) gathering pebbles into a circle or hemicircle, and scouping out a central depression or (2) by merely brushing out a depression. The stickleback constructs a tubular nest by agglutinating plant material together; some structures include a little sand around the base (Ommanney, 1964).

Excluding the more or less permanent dwellings of the mammals, hibernation or aestivation structures are made mainly by turtles, frogs (Fig. 19.10O), and lungfish.

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