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XIPHOSURIDA

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Xiphosurida

A subclass of the class Merostomata. These "sword-tailed" arthropods have three distinct body divisions: a prominent horseshoe-shaped, fused head and thorax, the prosoma; a segmented "abdomen," or opisthosoma; and a spikelike terminal segment, the telson (Fig. 1). The Xiphosurida includes three major subgroups, the Aglaspida, Synxiphosurida, and Limulida, which span over

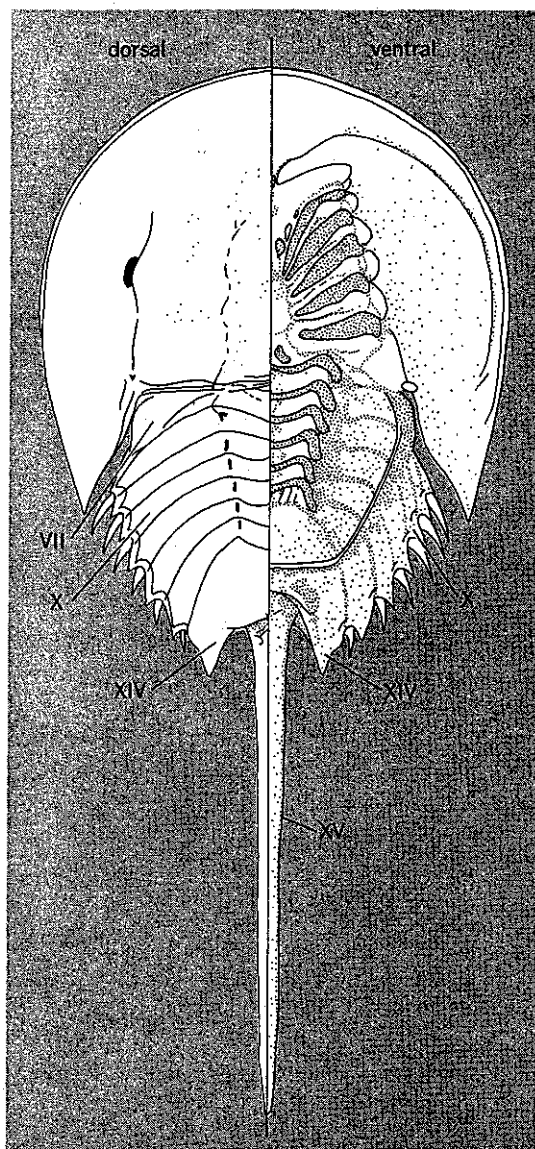


Fig. 1. Segmentation of *Limulus polyphemus*. Inconclusive evidence indicates that there are 15 segments (6 in the prosoma, 9 in the opisthosoma). The telson (XV) may be a terminal spine that has become articulated and has incorporated the anus into its base.

500,000,000 years of evolution (Fig. 2). All are, or were, inhabitants of shallow brackish water areas and tolerant of wide ranges of salinity.

The Aglaspida were elongate Xiphosurida with prominent compound eyes and free segments in the opisthosoma; they had a broad-based telson. The Synxiphosurida usually lacked compound eyes. Some species had a distinct axial, or cardiac, region, free segments in the opisthosoma, and a broad, short telson. The Limulida include the species constituting a clearly recognizable horseshoe "crab" group: Belinuracea, Euproopacea, and Limulacea (Fig. 3).

Distribution. The Mesozoic waters of Europe were the probable center of dispersal of the ancestors of present species. The geographical distribution of the Limulacea along the coasts of the United States is heaviest, and the size of the adult

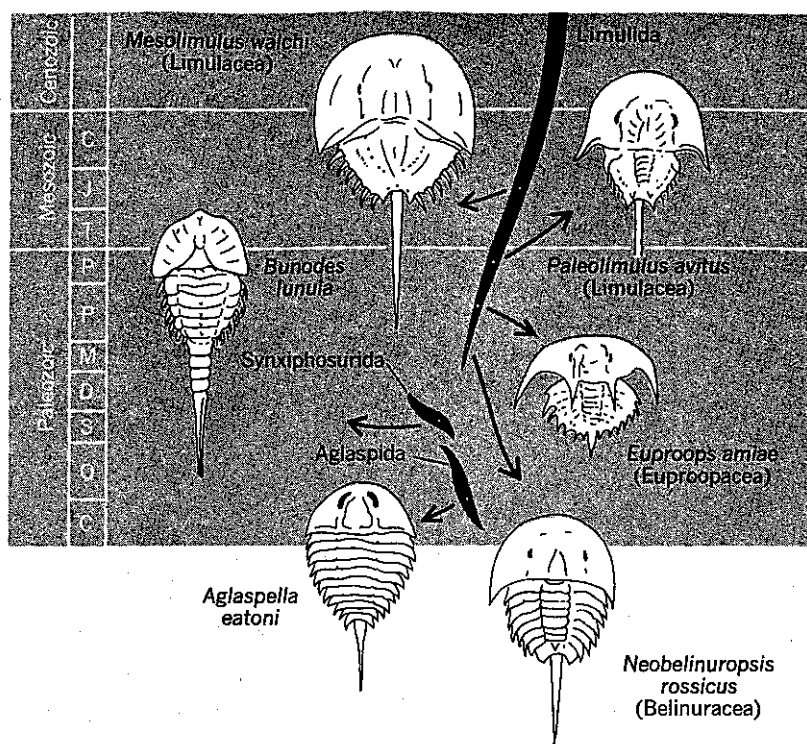


Fig. 2. Phylogeny and representative species of the three major subgroups of Xiphosurida.

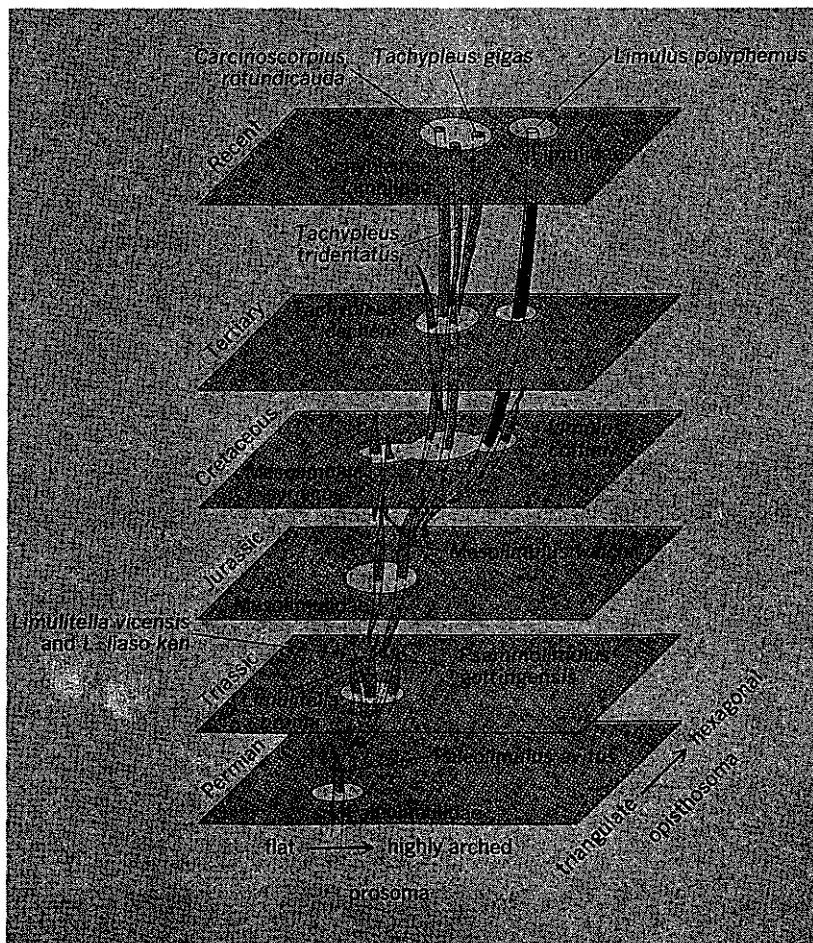


Fig. 3. Limulacea family tree.

Limulus is useful in research. It is relatively simple in structure, tenacious of life, and easy to obtain. It is of interest as a living fossil.

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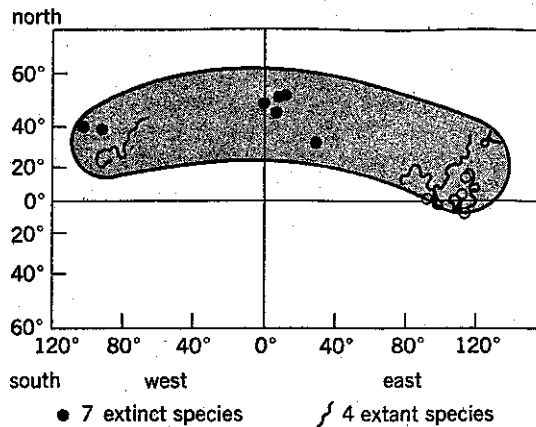


Fig. 4. The restricted geographical distribution of Limulacea, lower Permian to Recent.

Limulus is largest in the midportion of its range, which extends from Georgia through Delaware Bay. It is smaller to north and south; this indicates the Limulacea always have been tropicotemperate water species (Fig. 4).

The four living species of Limulacea have a restricted geographic range (Fig. 5). *Limulus polyphemus* (L.) is found along the Atlantic coast of North America from Nova Scotia to Yucatan. *Carcinoscorpius rotundicauda* (Latr.), *Tachypleus tridentatus* (Leach), and *Tachypleus gigas* (Müller) are endemic to the Indo-Pacific region.

L. polyphemus is the most studied species. Its common names include horsefoot or horseshoe "crab" (preferred), horsefeet, pan "crab," piggy-back "crab," and, unfortunately, "king crab," an erroneous name because *Paralithodes camtschatica* is a true king crab.

Life history. The life history of *Limulus* in Delaware Bay, where the largest population abounds, is characteristic of the species. Adults spend the colder months in 20- to 60-ft depths both within and outside the bay. Warming waters and increasing daylight stimulate the adults to migrate toward the sandy bay beaches to spawn. Most follow the path of least resistance and follow the strong flood tide currents into the eastern side of Delaware Bay. Fewer horseshoe "crabs" gather along the western shore, except when rough waves strike Cape May beaches during prevailing northwesterlies and drive the animals back into the deeper water. Then they may venture westward toward the wind-protected shore.

On new moon, and especially full moon, high tides in May and June, thousands of the adults congregate on the beaches to spawn. Males "patrolling" along the shore grasp the females heading for the beach. In an excavation dug beneath her body, each female lays several thousand eggs which are fertilized when the spermatozoa are washed into the nests by the waves. After making one or more nests, the animals leave the beach when the tide ebbs. Limuli that do not beat the receding tide are stranded upon the tidal flats where they dig in to await the next high water.

Minnows swarm along the beaches at night and feed upon the eggs washed out of the nests by wave action. During the day sharp-eyed shore birds, mostly migrants such as plovers and sandpi-

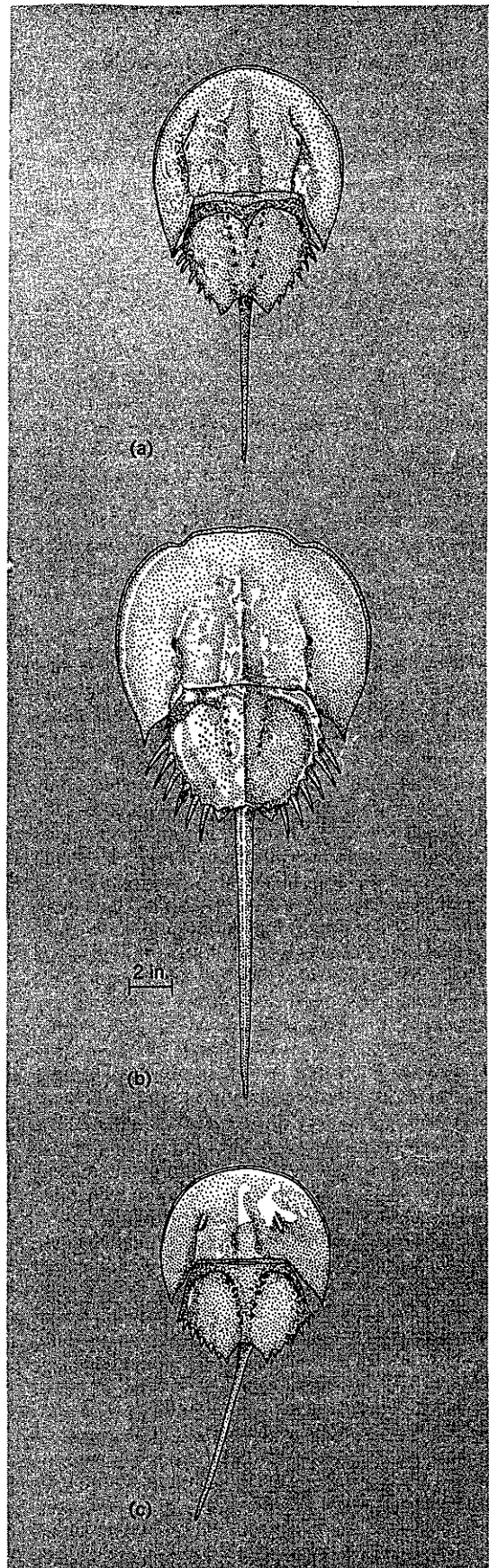


Fig. 5. Limulacea carapaces (tests or shells). (a) *Limulus polyphemus*. (b) *Tachypleus tridentatus*. (c) *Carcinoscorpius rotundicauda*.

pers, dig into the nests and gorge themselves.

Horseshoe "crab" embryos begin to develop within the opaque, tough-coated eggs. In a few days each egg cover ruptures and a thin, transparent sphere, formed during embryonic development, balloons out to assume a diameter larger than the original egg (Fig. 6a). In this transparent showcase, growth of the legs, their first feeble attempts to move, and then their almost incessant movement are clearly visible (Fig. 6b).

Within 2 weeks some of the tiny animals reach the larval stage and are ready to hatch, although development and hatching may be delayed for several weeks. If the waves churn up a nest, the moving sand grains rupture the enclosing membrane and liberate the larvae (Fig. 6c). From then on, until they reach maturity in some 9–11 years and 15 or more stages later, their life is essentially that of seeking food and growing. Food consists mainly of marine worms, such as *Nereis*, and soft-shelled mollusks, such as *Mya arenaria*. The larger the immature animal, the more it moves toward the deeper bay water, from which, as an adult, it begins the spawning migration to create the life cycle anew.

The newly hatched larva, the "trilobite" or Euproops stage, is in many respects still an embryo. Its incompletely formed digestive tract and nervous and circulatory systems develop further during early subsequent stages. The yolk-filled midgut serves as food for the larvae while they "learn" to right themselves from the upside-down position in which gravity held them during development in the egg (Fig. 6c). All ages of limuli swim on their backs, however, and usually at the water surface.

Molting. Molting occurs several times during the first 2 or 3 years of life, but rarely more than once thereafter until adult size is reached. It is preceded by the formation of the new skin, recognizable externally in the larger animals by a deeper olive-green coloration with yellow margins of the shell. The new skin forms pleats which unfold as the animal expands with the uptake of water during emergence. These pleats in the premolt skin give the hardened exoskeleton its dark-lined, mosaic appearance. A circumferential splitting, just within the ventral margin of the prosoma, is the first outward evidence of molting. Exuviation then proceeds slowly until the animal emerges one-third of the way and is loosened from the old shell. Emergence then proceeds more rapidly. The first-tailed stage emerges within an hour but an animal 100 mm wide may require over 24 hr. Young specimens molt earlier than older ones, with cast shells appearing in sequence during July and August on tidal flats and in beach wrack. Instinctively, the larger, annually molting animals seek the areas along the edges of tidal flats and dig in prior to molting. Burying protects them from their enemies, birds, fishes, and crabs. The moist substratum supplies water at all times.

Nutrition. In feeding, the pincer-tipped legs grasp and bring prey to the heavy bases of the "pushers," the fifth pair of legs, where shells of mollusks are crushed. A pair of paddlelike appendages and spines on the leg bases then push and "knead" the prey forward toward the mouth, which is surrounded by the leg bases. Chelipeds in front of upper lip push food backward. Chitinous

ridges of the muscular gizzard, with the aid of ingested sand and shell, grind up prey into pulp which is squeezed into the midgut where it is partially digested. The resulting chyle is forced into the many-branched digestive gland where digestion within the cells completes the process. Large pieces of shell and pebbles are regurgitated from the gizzard, but fine sand and smaller shell fragments may be passed with undigested residues in soft, slime-enveloped, fecal cylinders.

Anatomy. The carapace (test or shell) is composed of chitin, strengthened internally in the adults by bridgelike struts within the shell margins (Fig. 7). Sensory structures on the carapace include chemoreceptors for taste on the bases of the legs and a pair of simple eyes, or ocelli. The multi-lensed compound eyes form mosaic images and are sensitive to polarized light.

Adult males are easily distinguished from the larger females by the higher anterior arch of the prosoma, the pair of "fist-and-thumb" claspers used in mating, and by the hard, conical projections bearing the genital pores on the back of the operculum (eighth appendage). The female apertures are larger, soft, and oval.

The organ systems, except the peripheral blood vessels and nerves, digestive, and reproductive glands, which branch extensively into the lateral portions of the prosoma, are mainly within the prominent axial region (Fig. 7c). This region con-

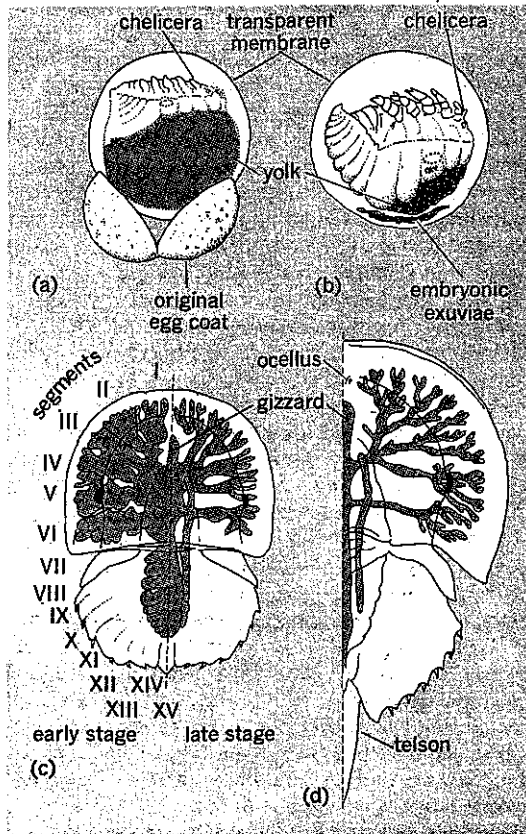


Fig. 6. Embryonic and larval development of *Limulus polyphemus*. (a) Early embryo, side view. (b) Late embryo. (c) Yolk-filled digestive tract of larva. Note the segmentation of yolk in newly hatched stage and the six lobes of digestive gland. (d) First tailed stage.

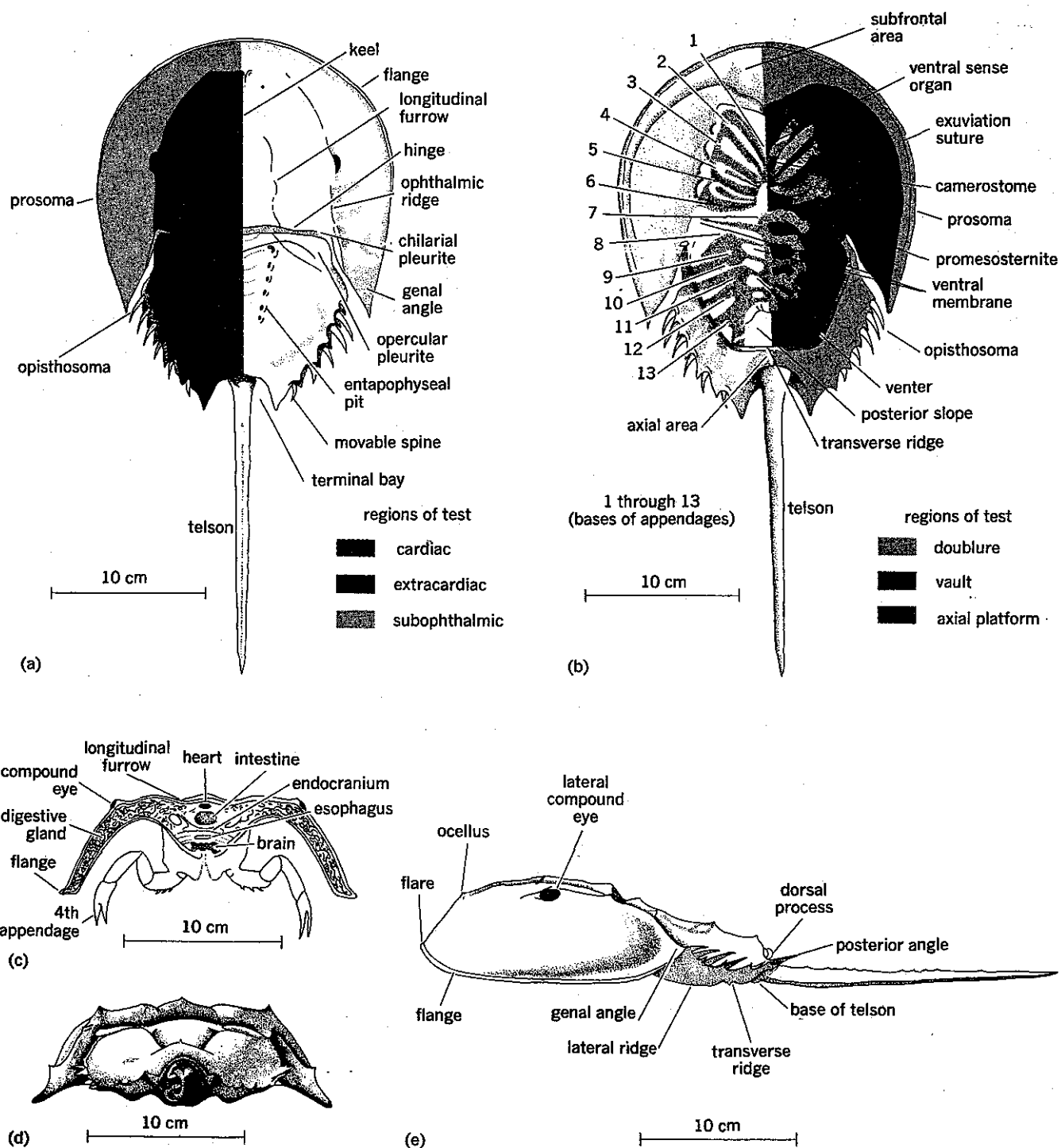


Fig. 7. External morphology of *Limulus polyphemus*, the horseshoe "crab." (a) Dorsal view. (b) Ventral view.

(c) Cross section through the prosoma. (d) Posterior aspect. (e) Lateral view.

tains the musculature of the paired appendages, hinge, and telson, the digestive tube, the coxal (excretory) gland, and the respiratory, central circulatory, and nervous structures. The dorsally situated tubular heart lies within a sinus which receives venous blood, the hemolymph, from the book gills, the respiratory structures, and the body. The central nervous system and the major nerve branches are sheathed by arteries. A plate of "cartilaginous" chitin, the endocranium, forms a roof over the brain. Flat, elliptical, primitive white blood cells,

the amebocytes, circulate in the hemolymph. When exposed to air, the amebocytes send out pseudopods and fragment to form a clot. The blood pigment is hemocyanin. See RESPIRATORY PIGMENTS (INVERTEBRATE).

Importance. Horseshoe "crab" meal, which has a protein content of 46%, is used in fertilizers. Quartered animals are good eel bait and food for poultry and hogs. The roe reportedly increase growth of broilers and egg laying, although a fishy flavor is imparted to both flesh and eggs.