

Inarticulata

(*Nonarticulate lampshells*)

Phylum Brachiopoda

Class Inarticulata

Number of families 3

Thumbnail description

Exclusively marine group of lophophorate animals that are suspension feeders attached at the base to the ocean bottom; they are called “inarticulated” because their shells lack articulation

Photo: A brachiopod lampshell of the genus *Lingula*, showing its stalk and shelled body. (Photo by Biophoto Associates/Photo Researchers, Inc. Reproduced by permission.)



Evolution and systematics

Nonarticulate lampshells, also known as inarticulated brachiopods, have been known since the Lower Cambrian period, about 550–600 million years ago. The traditional placement of these animals is in the class Inarticulata, but a more recent classification divides them into two subphyla: the Linguliformea and the Craniiformea. The living representatives of the Linguliformea are divided into two families: the Lingulidae with two genera, *Lingula* and *Glottidia*; and the Discinidae with four extant genera, *Discina*, *Discinisca*, *Discradisca*, and *Pelagodiscus*. The Craniiformea have one family, the Craniidae, with four genera: *Craniscus*, *Neoancistrocrania*, *Neocrania*, and *Valdiviathyris*. The inarticulated brachiopods are related to the Phoronida (horseshoe worms).

Physical characteristics

The shells of organisms in this group may grow as large as 2.75 in (7 cm) in the lingulides and 0.78 in (2 cm) in the discinids and craniids. These shells have a ventral and a dorsal valve; the muscles that close the shell include single or paired posterior adductor muscles as well as paired anterior adductor muscles. The oblique musculature, generally three or four pairs of muscles, controls the rotations and sliding movements of the valves. The lateral muscles of the trunk wall control the hydraulic mechanism that opens the shell. This mechanism involves changes in the pressure inside the organism's coelom, or body cavity. The lophophore or feeding organ is spirolophous (has elongated and coiled lateral lobes), except in *Pelagodiscus*, which has a schizolophous (lobes with relatively few filaments along its edges) lophophore. The lophophore has no supportive skeleton. The digestive tract

ends in an anus. The ring of nerves around the animal's esophagus has either a single or paired dorsal and ventral ganglion (group or cluster of nerve cells).

Distribution

Lingulidae are exclusively infaunal (living in the sediment at the bottom of the ocean) in soft substrates from the intertidal zone to a depth of about 1,315 ft (400 m); they have a worldwide distribution within the 40° belt from temperate to equatorial areas. *Glottidia* occurs only in the Americas and *Lingula* in the waters of the other continents. The Discinidae are epifaunal (living on top of the bottom surface) on hard substrates and have a warm temperate to tropical distribution. They are found mainly on the continental shelf, except for the cosmopolitan deep-sea *Pelagodiscus*, which occurs from northern to southern high latitudes at depths between about 328 ft to about 18,044 ft (100 m to about 5500 m). The Craniidae are epifaunal on hard substrates and are widely distributed from northern to southern high latitudes, from shallow waters to a depth of about 7,546 ft (2,300 m) on the bathyal slope.

The life span of most animals in this group of brachiopods appears to be from 14 months to less than two years for *Glottidia*, to 6–10 years for *Lingula* and the discinids.

Habitat

The lingulides live in vertical burrows built within compact and stable sandy sediments under the influence of moderate water currents close to the bottom of the sea. The total length of the burrow is about ten times the length of the shell.

The distal bulb of the pedicle (footlike base of the organism) is firmly anchored into the substrate at the bottom of the burrow and is surrounded by a mass of sand and organic particles held together by sticky mucus.

The discinids live on hard substrates swept by currents under weak sedimentation. They occur singly or in clusters of many individuals attached to rocky surfaces or the shells of mollusks and brachiopods.

The craniids lack a pedicle; their ventral valves are cemented directly to hard substrates.

Behavior

Lingulides position their shells at the top of their burrows. The shell is held there by hydrostatic pressure exerted by the body cavity and the valves on the walls of the burrow; the pedicle plays no role in keeping the animal in this position. Lingulides cannot live in coarse or muddy substrata because the walls of the burrow do not support the shell in its normal filtering position. Rapid withdrawal into the burrow is an escape reflex or protective reaction that may be observed if the setae (bristles) on the front margin of the animal are touched or if there is a sudden change in light intensity.

The ventral valve of the discinids is always oriented towards the surface on which it lives. This positioning is related to the orientation of the larva when it settles on the substrate. Discinids are attached by a highly muscular pedicle to hard substrates.

The craniids are generally gregarious (living in groups), preferring to live on hard flat surfaces. They are cemented directly to the substrate by their ventral valves.

Feeding ecology and diet

Brachiopods are suspension feeders. The lophophore, which is suspended freely in the mantle cavity, functions as a feeding organ in capturing suspended particles. It also maintains the supply of oxygen to and removal of waste products from the mantle cavity by internal currents produced by the beating of its cilia.

Food items include plankton (mainly phytoplankton as diatoms); superficial meiobenthos (microscopic metazoans); colloidal (suspended) organic material; and dissolved organic

material. This group of brachiopods also derives nourishment from direct absorption of dissolved nutrients.

Reproductive biology

The onset of breeding and the length of the spawning season depend primarily on water temperature, together with latitudinal and seasonal effects. In temperate waters, the breeding period takes place in midsummer and lasts about a month and a half; in the tropics, however, breeding may take place throughout the year.

Inarticulated brachiopods are dioecious. The sex ratio, at least in lingulides, is one to one. There is a single continuous gonad mass on each side of the visceral cavity in lingulides. Discinids have two gonads in the posterior part of the visceral cavity; males sometimes possess an additional single U-shaped testis. In the craniids, the gonads are in six separate groups, two in the visceral cavity and two in each lobe of the mantle. Fertilization is external in the lingulides, with synchronization of spawning in the two sexes. Ova and sperm are discharged through the metanephridia (primitive excretory organs) acting as gonoducts into the current of water that leaves through the lophophore. The occurrence of fertilization is unknown in the discinids and craniids.

The larvae in lingulides and discinids have two parts: the lobe at the upper end or apex, which will form the future body; and the mantle lobe, which will develop into the future mantle lobes. The pedicle arises from the ventral mantle lobe during the larva's long planktotrophic stage. The larva grows in size and complexity as it feeds on phytoplankton. The duration of this stage ranges from 3–6 weeks. The lecithotrophic larva of *Neocrania* has a short larval stage of about 4–6 days after fertilization.

There is no true metamorphosis in the inarticulated brachiopods. The larval organs either atrophy (wither away) or are detached after the animal settles on the substrate.

Conservation status

No species are listed by the IUCN.

Significance to humans

Lingula species are eaten in the eastern Pacific islands, from Japan to New Caledonia. Specimens can be purchased at local markets.



1. *Glottidia pyramidata*; 2. *Neocrania anomala*. (Illustration by Bruce Worden)

Species accounts

No common name

Neocrania anomala

ORDER

Craniida

FAMILY

Craniidae

TAXONOMY

Neocrania anomala (Müller), 1776, North Atlantic Ocean.

OTHER COMMON NAMES

None known.

PHYSICAL CHARACTERISTICS

The shell is calcareous, punctuated, and rarely exceeds 0.78 in (20 mm) in width. The ventral valve is cemented directly to a hard substrate, the dorsal valve is smooth and conical. There is no pedicle. The lophophore is spirolophous with the spires directed upward; the main mantle canals (*vascula lateralia*) branch and radiate outward.

DISTRIBUTION

Subtidal to bathyal zone in the eastern North Atlantic Ocean and in the Mediterranean Sea. Known since the Pliocene period (1.8 million years ago).

HABITAT

This species lives on boulders and various hard substrates, cemented directly to them by its ventral valve. It is sometimes found in underwater caves and other cryptic (hidden) habitats. Its depth ranges from about 9.8 ft (3 m) to 4,920 ft (1,500 m).

BEHAVIOR

The ventral valve always faces toward the substrate and is directly cemented to it. *Neocrania* is generally gregarious and prefers rather flat hard surfaces.

FEEDING ECOLOGY AND DIET

Neocrania species are suspension feeders. The spirolophous lophophore collects food items—primarily phytoplankton, diatoms, superficial meiobenthos, suspended organic material, and dissolved organic material.

REPRODUCTIVE BIOLOGY

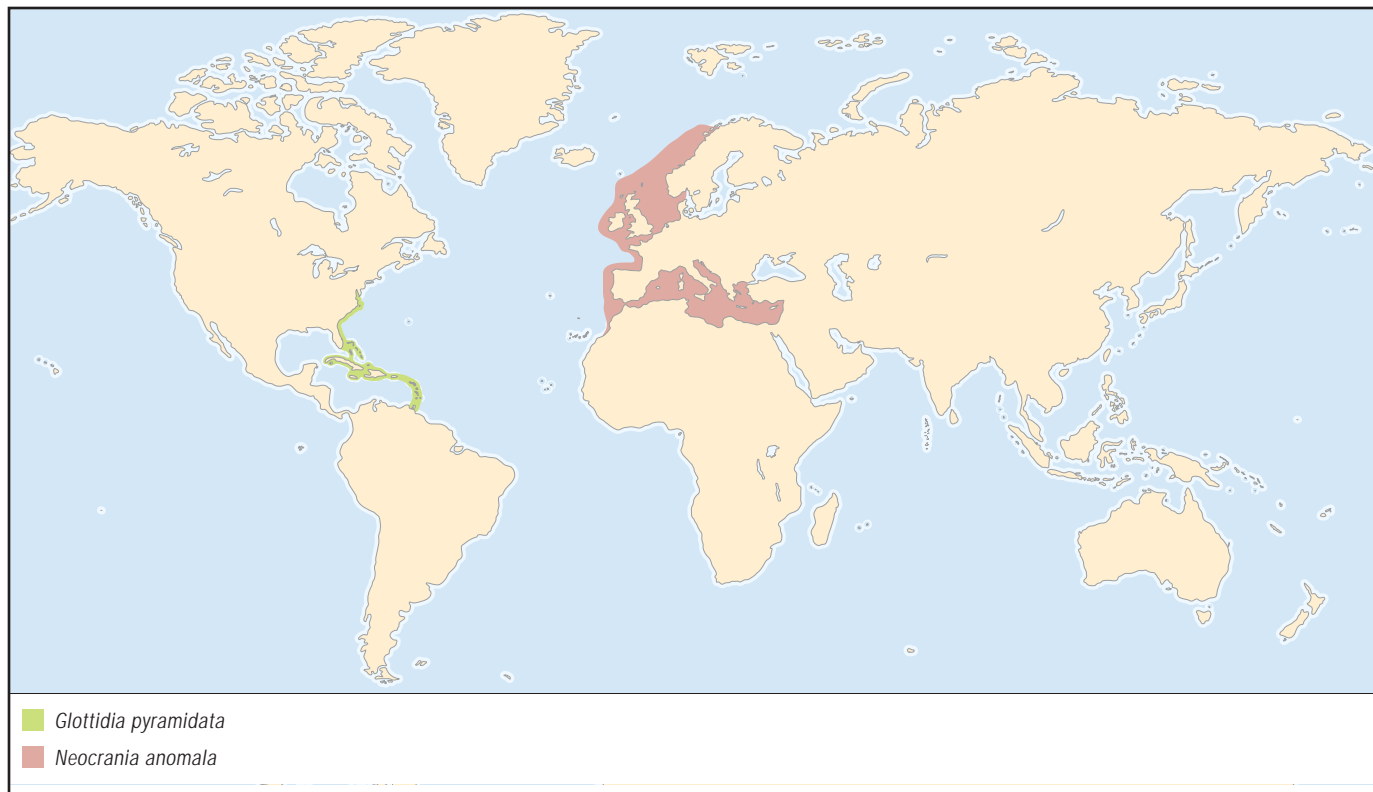
The eggs are freely spawned; they undergo radial cleavage and embolic gastrulation. The body cavity develops from a modification of the embryonic gut. The larvae are lecithotrophic (live on stored nutrients) and can settle immediately after complete embryogenesis in about a week.

CONSERVATION STATUS

Not listed by IUCN.

SIGNIFICANCE TO HUMANS

None known. ♦



No common name*Glottidia pyramidata***ORDER**

Lingulida

FAMILY

Lingulidae

TAXONOMY*Glottidia pyramidata* (Stimpson, 1860), Beaufort, South Carolina, United States.**OTHER COMMON NAMES**

None known.

PHYSICAL CHARACTERISTICS

The phosphatic shell is roughly circular, oblong, or oval in shape; it may grow as large as 1.2 in (3 cm). The single septum (dividing wall) in the dorsal valve reaches about 25–30% of the valve length and the two divergent septa in the ventral valve about 30–38%. The mantle papillae that are characteristic of this genus occur along the main mantle canals.

DISTRIBUTION

Littoral zone from the French West Indies to the eastern coast of Virginia.

HABITAT

Glottidia lives vertically in fine sand, sometimes covered by seagrass, in a burrow in which it is anchored by its pedicle. It is

found in shallow water from the intertidal zone to about 246 ft (75 m).

BEHAVIOR

The animal lives in the upper part of its burrow. Only the three aligned pseudosiphons formed by the setae of the anterior mantle edges are visible on the surface of the sediment: the two lateral openings take in water and the central opening discharges it. These setae are sensitive to touch; they trigger a protective closure of the shell accompanied by contractions of the pedicle, which draws the shell downwards into the burrow.

FEEDING ECOLOGY AND DIET

Food particles enter through the two intake currents and are filtered by the lophophore. These food particles consist of plant and animal matter, phytoplankton, and gastropod larvae. Waste products are discharged into the outgoing current of water.

REPRODUCTIVE BIOLOGY

The reproductive period extends over 7–9 months. *Glottidia* are dioecious, fertilization is external and eggs undergo equal and radial cleavage. Hatching occurs when the embryo has developed the first tentacles. The larva is planktotrophic for about 20 days, after which it settles to the bottom for a sedentary infaunal mode of life.

CONSERVATION STATUS

Not listed by IUCN.

SIGNIFICANCE TO HUMANS

None known. ♦

Resources**Books**

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