Quick guide

Upside-down jellyfish

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What are upside-down jellyfish? Upside-down jellyfish (*Cassiopea* spp.) are cnidarians, part of one of the earliest-diverging lineages in the animal kingdom. They take their name from their unusual posture: instead of drifting bell-up like most jellyfish, they rest on the seafloor with their bell downward and their frilly oral arms facing upward. They typically inhabit warm, shallow coastal waters across tropical and subtropical regions, from Caribbean mangrove lagoons to Indo-Pacific seagrass beds (Figure 1). Here, they often form dense carpets that can blanket large stretches of the seabed. Their diversity has long puzzled taxonomists — around two dozen species have been described, but molecular work suggests only about ten are valid. Like other true jellyfish (Scyphozoa), *Cassiopea* alternate between a sessile polyp stage and a free-swimming medusa stage. But unlike most jellyfish, the transition (*strobilation*) to medusa requires colonization of the animal by algal symbionts. Without these microscopic partners, *Cassiopea* cannot complete their life cycle. Once established, the algae enable the polyp to strobilate into medusae, which will grow into the upside-down adults that thrive in sunlit shallows.

Why upside-down? The upside-down posture of *Cassiopea* is all about harvesting sunlight, reflecting their symbiosis with photosynthetic dinoflagellates (Figure 2). Their upward-facing oral arms are packed with algae from the family Symbiodiniaceae, the same group that also lives in symbiosis with reef-building corals and that require light to produce energy. By lying bell-down and raising their arms toward the sun, the jellyfish maximize illumination for their algal symbionts. In return, the symbionts provide sugars and other nutrients — a mutualism closely resembling that of corals. However, like corals, *Cassiopea* are not entirely solar-powered. They retain the predatory habits of jellyfish, capturing zooplankton, fish larvae and other small prey with their oral arms and stinging cells. This dual strategy — autotrophy via photosynthesis and heterotrophy via predation — allows them to meet their energy demands while remaining largely sedentary, enabling them to thrive in habitats ranging from nutrient-poor lagoons to more turbid mangrove waters.

So they don't move? Upside-down jellyfish are far from passive carpets on the seafloor. They pulse rhythmically by contracting their flattened bells. Each pulse drives water upward through their oral arms, enhancing local fluid exchange and supporting gas and nutrient delivery to their algal symbionts while drawing plankton within reach. A single adult can move hundreds of liters of water per hour, and in dense populations, their combined activity can turn over the overlying water column within minutes.

These pulsations also shape the environment. By pumping water across the sediment–water interface, *Cassiopea* mobilize porewater (i.e. interstitial) nutrients such as ammonium, releasing them into the water where they fertilize seagrasses and algae, and support primary production in oligotrophic coral reefs. Their pulsing resuspends fine particles and enhances exchange between the seabed and the water column. In dense aggregations, this activity creates a continuous upward flow that can transform shallow parts of lagoons and mangroves into dynamic 'living pumps'. The effects vary with day–night cycles: at night, *Cassiopea* tend to increase sediment oxygen consumption and nutrient release, while in daylight photosynthesis by their symbionts shifts the balance toward oxygen production and nutrient uptake. In this way, *Cassiopea* promote benthic–pelagic coupling of nutrient cycles, with its pulsations tightly linking jellyfish physiology with broader ecological processes. Upside-down jellyfish may thus be viewed as ecosystem engineers in tropical coastal habitats.

Do they sting? Like all cnidarians, upside-down jellyfish use stinging cells (*cnidocytes*) to capture prey and deter predators. These are concentrated on their oral arms (Figure 2) and usually only cause mild irritation on contact. But unlike most jellyfish, *Cassiopea* can sting without being touched. When disturbed or feeding, they release mucus into the water containing tiny motile clusters called 'cassiosomes'. These structures, composed of cnidocytes, ciliated cells

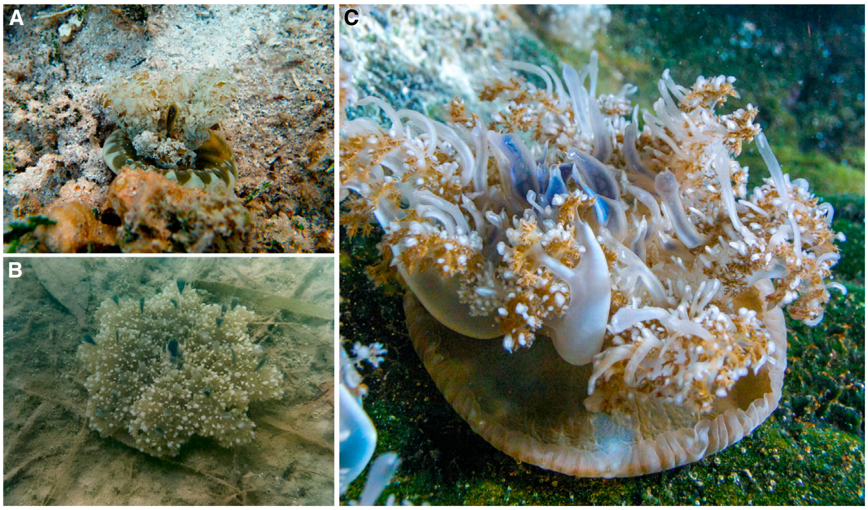

Figure 1. Upside-down jellyfish (*Cassiopea* spp.).
(A) Individual on a carbonate substrate in the Florida Keys. (B) Individual on a sandy-muddy bottom near mangroves in Tampa Bay (photos in (A,B) with permission by Frédéric Silvestre). (C) Close-up of an individual showing its characteristic upside-down posture, with the bell resting on the seafloor and oral arms extended upward (photo: © Oleg Kovtun/iStock.com).

Figure 2. Upside-down jellyfish in its natural habitat.
Close-up of the oral arms, containing algal symbionts and cnidocytes (photos used with permission by Frédéric Silvestre).

and sometimes also algal symbionts, are embedded in mucus and can move and discharge venom independently of the jellyfish. The result is 'stinging water', also known more colorfully as 'danger snot'. Reports from snorkelers, aquarists and researchers describe tingling, itching or burning sensations, sometimes escalating to hives or rashes that can persist for hours.

Why are they used in experimental biology? Upside-down jellyfish are relatively easy to culture, can reproduce clonally from polyp stages and provide genetically uniform lineages for controlled studies. With their comparatively simple body plan, decentralized nervous system and photosymbiotic lifestyle, *Cassiopea* offer a versatile system for studying regeneration, neural control of behavior, symbiosis and the evolution of traits. Their pulsation rate is a readily measurable behavioral metric and proxy for environmental and physiological health. At night, their pulsation frequency slows as they enter a reversible quiescent state that fulfills behavioral criteria for sleep, making *Cassiopea* one of the simplest known animals to display sleep-like behavior. In symbiosis research, *Cassiopea* serve as a practical alternative to reef-building corals. Both host photosynthetic Symbiodiniaceae, but *Cassiopea* tolerate heat stress more readily. This provides a useful contrast to study how symbioses are established and maintained, and how they may break down under environmental change. Their sedentary lifestyle also makes them excellent sentinels of environmental stress, as they accumulate pollutants such as heavy metals and microplastics. And their venom is of growing biomedical interest: extracts have shown diverse activities, from cytotoxicity and neurotoxicity to antiparasitic and anticancer effects. Although still exploratory, these findings suggest upside-down jellyfish could provide a source of new pharmacological insights, extending their role as a model organism from ecology and physiology into biomedicine.

What are the key open questions? Despite their growing popularity as a research model, much about *Cassiopea* remains puzzling. A central mystery is how they withstand environmental stresses that affect their algal symbionts. While the latter are highly sensitive to heat, the jellyfish host persists under conditions that lead to symbiont deterioration (bleaching) in corals. Which protective mechanisms allow the host to shield or buffer its symbionts? Their behavior also raises fundamental questions. Why does an animal without a brain or centralized nervous system enter sleep-like states, and what might this reveal about the origins and functions of rest across the animal kingdom?

Finally, as *Cassiopea* spreads beyond its native range, their invasive potential is a concern. How do these slow, sedentary jellyfish colonize new habitats, and what ecological impacts follow? And if they do affect local ecosystems, how should we monitor and manage their spread in the future?

Where can I find out more?

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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