

Paper i

Invertebrates is an [umbrella term](#) describing [animals](#) that neither develop nor retain a [vertebral column](#) (commonly known as a *spine* or *backbone*), which evolved from the [notochord](#). It is a [paraphyletic](#) grouping including all animals excluding the [chordate subphylum Vertebrata](#), i.e. [vertebrates](#). Well-known [phyla](#) of invertebrates include [arthropods](#), [mollusks](#), [annelids](#), [echinoderms](#), [flatworms](#), [cnidarians](#), and [sponges](#).

The majority of animal species are invertebrates; one estimate puts the figure at 97%.^[1] Many invertebrate [taxa](#) have a greater number and diversity of species than the entire subphylum of Vertebrata.^[2] Invertebrates vary widely in size, from 10 [µm](#) (0.0004 in)^[3] [Myxozoans](#) to the 9–10 m (30–33 ft) [colossal squid](#).^[4]

Some so-called invertebrates, such as the [Tunicata](#) and [Cephalochordata](#), are actually sister chordate subphyla to Vertebrata, being more closely related to vertebrates than to other invertebrates. This makes the term "invertebrates" rather [polyphyletic](#), so the term has little meaning in [taxonomy](#).

Etymology

The word "invertebrate" comes from the Latin word *vertebra*, which means a joint in general, and sometimes specifically a joint from the spinal column of a vertebrate. The jointed aspect of *vertebra* is derived from the concept of turning, expressed in the root *verto* or *vorto*, to turn.^[5] The prefix *in-* means "not" or "without".^[6]






Taxonomic significance






The term *invertebrates* is not always precise among non-biologists since it does not accurately describe a [taxon](#) in the same way that [Arthropoda](#), [Vertebrata](#) or [Manidae](#) do. Each of these terms describes a valid taxon, [phylum](#), [subphylum](#) or [family](#). "Invertebrata" is a term of convenience, not a taxon; it has very little [circumscriptional](#) significance except within the [Chordata](#). The Vertebrata as a [subphylum](#) comprises such a small proportion of the [Metazoa](#) that to speak of the [kingdom Animalia](#) in terms of "Vertebrata" and "Invertebrata" has limited practicality. In the more formal taxonomy of Animalia other attributes that logically should precede the presence or absence of the vertebral column in constructing a [cladogram](#), for example, the presence of a [notochord](#). That would at least circumscribe the Chordata. However, even the notochord would be a less fundamental criterion than aspects of embryological development and symmetry^[7] or perhaps [bauplan](#).^[8]

Despite this, the concept of *invertebrates* as a taxon of animals has persisted for over a century among the [laity](#),^[9] and within the zoological community and in its literature it remains in use as a term of convenience for animals that are not members of the Vertebrata.^[10] The following text reflects earlier scientific understanding of the term and of those animals which have constituted it. According to this understanding, invertebrates do not possess a skeleton of bone, either internal or external. They include hugely varied [body plans](#). Many have fluid-filled, hydrostatic skeletons, like [jellyfish](#) or worms. Others have hard [exoskeletons](#), outer shells like those of [insects](#) and [crustaceans](#). The most familiar invertebrates include the [Protozoa](#), [Porifera](#), [Coelenterata](#), [Platyhelminthes](#), [Nematoda](#), [Annelida](#), [Echinodermata](#), [Mollusca](#) and [Arthropoda](#). Arthropoda include [insects](#), [crustaceans](#) and [arachnids](#).

Number of extant species

By far the largest number of described invertebrate species are insects. The following table lists the number of described [extant](#) species for major invertebrate groups as estimated in the [IUCN Red List of Threatened Species](#), 2014.3.^[11]

Invertebrate group	Phylum	Image	Estimated number of described species ^[11]
Insects	Arthropoda		1,000,000
Arachnids	Arthropoda		102,248
Snails	Mollusca		85,000
Crustaceans	Arthropoda		47,000
Clams	Mollusca		20,000

Invertebrate group	Phylum	Image	Estimated number of described species ^[11]
Corals	Cnidaria		2,175
Octopuses/Squid	Mollusca		900
Velvet worms	Onychophora		165
Nautilus	Mollusca		6
Horseshoe crabs	Arthropoda		4
Others jellyfish , echinoderms , sponges , other worms etc.	—	—	68,658
Total:			~1,300,000

The [UCN](#) estimates that 66,178 [extant vertebrate species](#) have been described,^[11] which means that over 95% of the described animal species in the world are invertebrates.

Characteristics

The trait that is common to all invertebrates is the absence of a [vertebral column](#) (backbone): this creates a distinction between invertebrates and vertebrates. The distinction is one of convenience only; it is not based on any clear biologically [homologous](#) trait, any more than the common trait of having wings functionally unites insects, bats, and birds, or than not having wings unites [tortoises](#), [snails](#) and [sponges](#). Being animals, invertebrates are heterotrophs, and require sustenance in the form of the consumption of other organisms. With a few exceptions, such as the [Porifera](#), invertebrates generally have bodies composed of differentiated tissues. There is also typically a digestive chamber with one or two openings to the exterior.

Morphology and symmetry

The [body plans](#) of most [multicellular organisms](#) exhibit some form of [symmetry](#), whether radial, bilateral, or spherical. A minority, however, exhibit no symmetry. One example of asymmetric invertebrates includes all [gastropod](#) species. This is easily seen in [snails](#) and [sea snails](#), which have helical shells. [Slugs](#) appear externally symmetrical, but their [pneumostome](#) (breathing hole) is located on the right side. Other gastropods develop external asymmetry, such as [Glaucus atlanticus](#) that develops asymmetrical [cerata](#) as they mature. The origin of gastropod asymmetry is a subject of scientific debate.^[12]

Other examples of asymmetry are found in [fiddler crabs](#) and [hermit crabs](#). They often have one claw much larger than the other. If a male fiddler loses its large claw, it will grow another on the opposite side after [moulting](#). [Sessile](#) animals such as [sponges](#) are asymmetrical^[13] alongside [coral colonies](#) (with the exception of the individual [polyps](#) that exhibit radial symmetry); [alpheidae](#) claws that lack pincers; and some [copepods](#), [polyopisthocotyleans](#), and [monogeneans](#) which parasitize by attachment or residency within the [gill](#) chamber of their [fish hosts](#)).

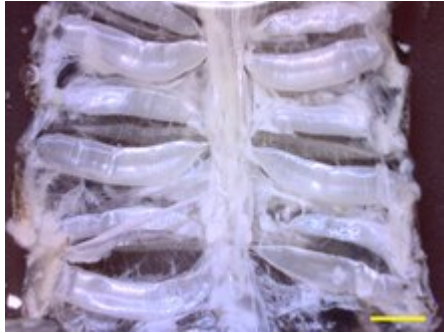
Nervous system

[Neurons](#) differ in invertebrates from mammalian cells. Invertebrates cells fire in response to similar stimuli as mammals, such as tissue trauma, high temperature, or changes in pH. The first invertebrate in which a neuron cell was identified was the medicinal [leech](#), [Hirudo medicinalis](#).^{[14][15]}

Learning and memory using nociceptors in the sea hare, [Aplysia](#) has been described.^{[16][17][18]} Mollusk neurons are able to detect increasing pressures and tissue trauma.^[19]

Neurons have been identified in a wide range of invertebrate species, including annelids, molluscs, [nematodes](#) and arthropods.^{[20][21]}

Respiratory system



Tracheal system of dissected [cockroach](#). The largest tracheae run across the width of the body of the cockroach and are horizontal in this image. Scale bar, 2



mm. The tracheal system branches into progressively smaller tubes, here supplying the [crop](#) of the cockroach. Scale bar, 2.0 mm.

One type of invertebrate respiratory system is the open [respiratory system](#) composed of [spiracles](#), tracheae, and [tracheoles](#) that [terrestrial](#) arthropods have to transport [metabolic](#) gases to and from tissues.^[22] The distribution of spiracles can vary greatly among the many [orders](#) of insects, but in general each segment of the body can have only one pair of spiracles, each of which connects to an atrium and has a relatively large tracheal tube behind it. The tracheae are invaginations of the cuticular [exoskeleton](#) that branch ([anastomose](#)) throughout the body with diameters from only a few micrometres up to 0.8 mm. The smallest tubes, tracheoles, penetrate cells and serve as sites of [diffusion](#) for [water](#), [oxygen](#), and [carbon dioxide](#). Gas may be conducted through the respiratory system by means of active [ventilation](#) or passive diffusion. Unlike vertebrates, insects do not generally carry oxygen in their [haemolymph](#).^[23]

A tracheal tube may contain ridge-like circumferential rings of [taenidia](#) in various [geometries](#) such as loops or [helices](#). In the [head](#), [thorax](#), or [abdomen](#), tracheae may also be connected to air sacs. Many insects, such as [grasshoppers](#) and [bees](#), which actively pump the air sacs in their abdomen, are able to control the flow of air through their body. In some aquatic insects, the tracheae exchange gas through the body wall directly, in the form of a [gill](#), or function essentially as normal, via a [plastron](#). Despite being internal, the tracheae of arthropods are shed during moulting ([ecdysis](#)).^[24]

Hearing

This section is an excerpt from [Ear § Invertebrates](#).^[edit]

Only vertebrate animals have ears, though many invertebrates detect sound using other kinds of sense organs. In insects, [tympanal organs](#) are used to hear distant sounds. They are located either on the head or elsewhere, depending on the insect [family](#).^[25] The tympanal organs of some insects are extremely sensitive, offering acute hearing beyond that of most other animals. The female cricket fly [Ormia ochracea](#) has tympanal organs on each side of her abdomen. They

are connected by a thin bridge of exoskeleton and they function like a tiny pair of eardrums, but, because they are linked, they provide acute directional information. The fly uses her "ears" to detect the call of her host, a male cricket. Depending on where the song of the cricket is coming from, the fly's hearing organs will reverberate at slightly different frequencies. This difference may be as little as 50 billionths of a second, but it is enough to allow the fly to home in directly on a singing male cricket and parasitise it.^[26]

Simpler structures allow other [arthropods](#) to detect [near-field](#) sounds. Spiders and cockroaches, for example, have hairs on their legs, which are used for detecting sound. Caterpillars may also have hairs on their body that perceive vibrations^[27] and allow them to respond to sound.

Reproduction

Like vertebrates, most invertebrates reproduce at least partly through [sexual reproduction](#). They produce specialized [reproductive cells](#) that undergo [meiosis](#) to produce smaller, motile [spermatozoa](#) or larger, non-motile [ova](#).^[28] These fuse to form [zygotes](#), which develop into new individuals.^[29] Others are capable of asexual reproduction, or sometimes, both methods of reproduction.

Extensive research with model invertebrate species such as [Drosophila melanogaster](#) and [Caenorhabditis elegans](#) has contributed much to our understanding of [meiosis](#) and reproduction. However, beyond the few model systems, the modes of reproduction found in invertebrates show incredible diversity.^[30] In one extreme example it is estimated that 10% of [oribatid mite](#) species have persisted without sexual reproduction and have reproduced asexually for more than 400 million years.^[30]

Reproductive systems

This section is an excerpt from [Reproductive system § Invertebrates](#).[\[edit\]](#)

Invertebrates have an extremely diverse array of reproductive systems, the only commonality may be that they all lay eggs. Also, aside from [cephalopods](#) and [arthropods](#), nearly all other invertebrates are [hermaphroditic](#) and exhibit [external fertilization](#).

Social interaction

Social behavior is widespread in invertebrates, including cockroaches, termites, aphids, [thrips](#), ants, bees, [Passalidae](#), [Acari](#), spiders, and more.^[31] Social interaction is particularly salient in [eusocial](#) species but applies to other invertebrates as well.

Insects recognize information transmitted by other insects.^{[32][33][34]}

Phyla



The fossil coral [Cladocora](#) from the [Pliocene](#) of [Cyprus](#)

The term invertebrates covers several phyla. One of these are the sponges ([Porifera](#)). They were long thought to have diverged from other animals early.^[35] They lack the complex organization found in most other phyla.^[36] Their cells are differentiated, but in most cases not organized into distinct tissues.^[37] Sponges typically feed by drawing in water through pores.^[38] Some speculate that sponges are not so primitive, but may instead be secondarily simplified.^[39] The [Ctenophora](#) and the [Cnidaria](#), which includes [sea anemones](#), [corals](#), and [jellyfish](#), are radially symmetric and have digestive chambers with a single opening, which serves as both the mouth and the anus.^[40] Both have distinct tissues, but they are not organized into [organs](#).^[41] There are only two main germ layers, the [ectoderm](#) and [endoderm](#), with only scattered cells between them. As such, they are sometimes called [diploblastic](#).^[42]

The [Echinodermata](#) are radially symmetric and exclusively marine, including [starfish](#) (Asteroidea), [sea urchins](#), (Echinoidea), [brittle stars](#) (Ophiuroidea), [sea cucumbers](#) (Holothuroidea) and [feather stars](#) (Crinoidea).^[43]

The largest animal phylum is also included within invertebrates: the Arthropoda, including insects, [spiders](#), [crabs](#), and their kin. All these organisms have a body divided into repeating segments, typically with paired appendages. In addition, they possess a hardened exoskeleton that is periodically shed during growth.^[44] Two smaller phyla, the [Onychophora](#) and [Tardigrada](#), are close relatives of the arthropods and share some traits with them, excluding the hardened exoskeleton. The [Nematoda](#) or roundworms, are perhaps the second largest animal phylum, and are also invertebrates. Roundworms are typically microscopic, and occur in nearly every environment where there is water.^[45] A number are important parasites.^[46] Smaller phyla related to them are the [Kinorhyncha](#), [Priapulida](#), and [Loricifera](#). These groups have a reduced coelom, called a pseudocoelom. Other invertebrates include the [Nemertea](#) or ribbon worms, and the [Sipuncula](#).

Another phylum is [Platyhelminthes](#), the flatworms.^[47] These were originally considered primitive, but it now appears they developed from more complex ancestors.^[48] Flatworms are [acoelomates](#), lacking a body cavity, as are their closest relatives, the microscopic [Gastrotricha](#).^[49] The [Rotifera](#) or rotifers, are common in aqueous environments. Invertebrates also include the [Acanthocephala](#) or spiny-headed worms, the [Gnathostomulida](#), [Micrognathozoa](#), and the [Cycliophora](#).^[50]

Also included are two of the most successful animal phyla, the Mollusca and Annelida.^{[51][52]} The former, which is the second-largest animal phylum by number of described species, includes animals such as [snails](#), [clams](#), and [squids](#), and the latter comprises the segmented worms, such as [earthworms](#) and [leeches](#). These two groups have long been considered close relatives

because of the common presence of [trochophore](#) larvae, but the annelids were considered closer to the arthropods because they are both segmented.^[53] Now, this is generally considered [convergent evolution](#), owing to many morphological and genetic differences between the two phyla.^[54]

Among lesser phyla of invertebrates are the [Hemichordata](#), or acorn worms,^[55] and the Chaetognatha, or arrow worms. Other phyla include [Acoelomorpha](#), [Brachiopoda](#), [Bryozoa](#), [Entoprocta](#), [Phoronida](#), and [Xenoturbellida](#).

Classification of invertebrates

Invertebrates can be classified into several main categories, some of which are [taxonomically](#) obsolescent or debatable, but still used as terms of convenience. Each however appears in its own article at the following links.^[56]

- [Sponges](#) (*Porifera*)
- [Comb jellies](#) (*Ctenophora*)
- [Medusozoans and corals](#) (*Cnidaria*)
- [Acoels](#) (*Xenacoelomorpha*)
- [Flatworms](#) (*Platyhelminthes*)
- [Bristleworms, earthworms and leeches](#) (*Annelida*)
- [Insects, springtails, crustaceans, myriapods, chelicerates](#) (*Arthropoda*)
- [Chitons, snails, slugs, bivalves, tusk shells, cephalopods](#) (*Mollusca*)
- [Roundworms or threadworms](#) (*Nematoda*)
- [Rotifers](#) (*Rotifera*)
- [Tardigrades](#) (*Tardigrada*)
- [Scalidophores](#) (*Scalidophora*)
- [Lophophorates](#) (*Lophophorata*)
- [Velvet worms](#) (*Onychophora*)
- [Arrow worms](#) (*Chaetognatha*)
- [Gordian worms or horsehair worms](#) (*Nematomorpha*)
- [Ribbon worms](#) (*Nemertea*)
- [Placozoa](#)
- [Loricifera](#)
- [Starfishes, sea urchins, sea cucumbers, sea lilies and brittle stars](#) (*Echinodermata*)
- [Acorn worms, cephalodiscids and graptolites](#) (*Hemichordata*)
- [Lancelets](#) (*Amphioxiformes*)
- [Salps, pyrosomes, doliolids, larvaceans and sea squirts](#) (*Tunicata*)
- [Cycliophora](#) (currently a monogeneric phylum)

History

The earliest animal fossils appear to be those of invertebrates. 665-million-year-old fossils in the Trezona Formation at Trezona Bore, West Central Flinders, South Australia have been interpreted as being early sponges.^[57] Some paleontologists suggest that animals appeared much earlier, possibly as early as 1 billion years ago^[58] though they probably became multicellular in the [Tonian](#). [Trace fossils](#) such as tracks and burrows found in the late [Neoproterozoic](#) era indicate the presence of [triploblastic](#) worms, roughly as large (about 5 mm wide) and complex as [earthworms](#).^[59]

Around 453 MYA, animals began diversifying, and many of the important groups of invertebrates diverged from one another. Fossils of invertebrates are found in various types of sediment from the [Phanerozoic](#).^[60] Fossils of invertebrates are commonly used in stratigraphy.^[61]

Classification

[Carl Linnaeus](#) divided these animals into only two groups, the Insecta and the now-obsolete [Vermes](#) (worms). [Jean-Baptiste Lamarck](#), who was appointed to the position of "Curator of Insecta and Vermes" at the [Muséum National d'Histoire Naturelle](#) in 1793, both coined the term "invertebrate" to describe such animals and divided the original two groups into ten, by splitting Arachnida and Crustacea from the Linnean Insecta, and Mollusca, Annelida, [Cirripedia](#), [Radiata](#), [Coelenterata](#) and [Infusoria](#) from the Linnean Vermes. They are now classified into over 30 [phyla](#), from simple organisms such as [sea sponges](#) and [flatworms](#) to complex animals such as arthropods and molluscs.

Significance of the group

Invertebrates are animals *without* a vertebral column. This has led to the conclusion that *invertebrates* are a group that deviates from the normal, vertebrates. This has been said to be because researchers in the past, such as Lamarck, viewed vertebrates as a "standard": in Lamarck's theory of evolution, he believed that characteristics acquired through the evolutionary process involved not only survival, but also progression toward a "higher form", to which humans and vertebrates were closer than invertebrates were. Although goal-directed evolution has been abandoned, the distinction of invertebrates and vertebrates persists to this day, even though the grouping has been noted to be "hardly natural or even very sharp." Another reason cited for this continued distinction is that Lamarck created a precedent through his classifications which is now difficult to escape from. It is also possible that some humans believe that, they themselves being vertebrates, the group deserves more attention than invertebrates.^[62] In any event, in the 1968 edition of *Invertebrate Zoology*, it is noted that "division of the Animal Kingdom into vertebrates and invertebrates is artificial and reflects human bias in favor of man's own relatives." The book also points out that the group lumps a vast number of species together, so that no one characteristic describes all invertebrates. In addition, some species included are only remotely related to one another, with some more related to vertebrates than other invertebrates (see [Paraphyly](#)).^[63]

In research

For many centuries, invertebrates were neglected by biologists, in favor of big vertebrates and "useful" or [charismatic species](#).^[64] Invertebrate biology was not a major field of study until the work of [Linnaeus](#) and [Lamarck](#) in the 18th century.^[64] During the 20th century, invertebrate zoology became one of the major fields of natural sciences, with prominent discoveries in the fields of medicine, genetics, palaeontology, and ecology.^[64] The study of invertebrates has also benefited law enforcement, as arthropods, and especially insects, were discovered to be a source of information for forensic investigators.^[44]

Two of the most commonly studied model organisms nowadays are invertebrates: the fruit fly [Drosophila melanogaster](#) and the nematode [Caenorhabditis elegans](#). They have long been the most intensively studied [model organisms](#), and were among the first life-forms to be genetically sequenced. This was facilitated by the severely reduced state of their [genomes](#), but many [genes](#), [introns](#), and [linkages](#) have been lost. Analysis of the [starlet sea anemone](#) genome has emphasised the importance of sponges, placozoans, and [choanoflagellates](#), also being sequenced, in explaining the arrival of 1500 ancestral genes unique to animals.^[65] Invertebrates

are also used by scientists in the field of [aquatic biomonitoring](#) to evaluate the effects of water pollution and climate change.^[66]