can help to establish a wiring diagram and guide rigorous theoretical models. The ability to examine a complex sensorimotor integration center down to the level of individual synaptic connections is incredibly powerful.

In conclusion, the central complex is a fascinating sensorimotor hub that offers the tantalizing hope of fully understanding the neural workings of aspects of navigation that are relevant across species. It takes in sensory and motor input, tracks heading, possibly with an attractor network, and generates predictive motor outputs. Learning, memory, and context also help shape the activity in this network, adding further flexibility to the workings of this region. It is no wonder that this powerful set of neurons is conserved across insects and crustaceans, and it will be fascinating to learn how the structure has evolved to meet each species' specific needs.

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Dendrogramma is a siphonophore

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Dendrogramma was the iconic deep-sea animal of 2014, voted among the top-ten new species described that year [1]. The two species described are mushroom shaped animals, diploblastic, with an apparent gastrovascular system that extends from the base of the stalk to bifurcating canals that radiate through the flat disc [2]. The authors could not assign the new genus to any known animal group with certainty, leading to numerous media reports that it belonged to an entirely new phylum. Here we use phylogenomic data from newly collected specimens to show that *Dendrogramma* is a cnidarian, specifically a benthic siphonophore in the family Rhodaliidae. Although an entire *Dendrogramma* colony has not been found, we hypothesise that the mushroom-like bodies are bracts, possibly used to aid buoyancy or as defensive appendages to protect feeding gastrozooids or gonads.

In November 2015, an expedition by the Australian research vessel R/V Investigator to the continental slope off South Australia recovered 85 new specimens of *Dendrogramma* (Figure 1A,B). We preserved some specimens in RNALater and after the voyage successfully sequenced a partial transcriptome from extracted RNA. These are the first genetic data available for these species, as the original specimens were collected and preserved in formalin in 1986, which hindered extraction of DNA [2]. We targeted exons used in a recent metazoan phylogenomic study [3] as well as the ribosomal RNA genes (18S, 28S and 16S) used in older siphonophore-focused investigations [4,5]. Phylogenetic analyses of the exon data placed *Dendrogramma* as sister to two physonect siphonophores (*Agalma elegans* and *Nanomia bijuga*, 100% bootstrap support; Figure 1C, Supplemental information). The ribosomal BLAST and phylogenetic analyses identified the benthic siphonophore *Stephalia dilata* (family Rhodaliidae) as the nearest sequenced taxon to *Dendrogramma* (16S d_{xy} = 0.013; Supplemental information).

Siphonophores are bizarre pelagic colonial cnidarians in the class Hydrozoa. They are complex elongate or spherical organisms with specialised locomotive and feeding zooids, and a net of tentacles that can be extended to catch prey or attach to the seafloor [6]. There are 175 described species, living in a range of habitats from the sea surface (e.g., *Physalia physalis*, the Portuguese Man O'War) to the deep-sea [6]. Larger, more delicate species have been found mainly in the non-turbulent mesopelagic (300–1000 m) or bathypelagic zones (1000–3000 m).

A typical siphonophore has a pneumatophore for floatation, a short nectosome with nectophores (swimming bells) used for propulsion, and a siphosomal stem with repeating units called cormidia. Cormidial units have gastrozooids with long feeding tentacles, gonodendra for reproduction and bracts used for floatation or protection [6,7].

We hypothesise that the mushroom-shaped *Dendrogramma* is a cormidial bract. These can take various shapes, but notably rhodaliid genera such as *Tridensia*, *Arancialia* and *Archangelopsis* have detachable mushroom-like bracts with a central canal up the stalk that can branch through the disc on some species [7,8] (Supplemental information). *Dromalia* has quite complex branching, although the bracts are elongate [7]. While bract morphology is only available for ten of the fourteen species of the Rhodaliidae, bracts are typically small appendages that reach 2–6 mm in size. In contrast our largest specimen of *Dendrogramma* is 20 mm in diameter with bracteal canals that can branch at least five times, almost to the edge of the rounded disc. The canals are a pink or orange colour in life (Supplemental information). The 'mouth' of *Dendrogramma* is the attachment surface that articulates with a triangular bracteal lamella on the cormidial stem [8].

We also found an orange gas-filled object at two separate sites (Supplemental information), which is similar in appearance to a rhodaliid pneumatophore and the base of the siphosomal stem, denuded of all nectophores and cormidial units. Ribosomal DNA (16S, 28S) from one of these objects was identical to that found from the *Dendrogramma* bracts from the same site.

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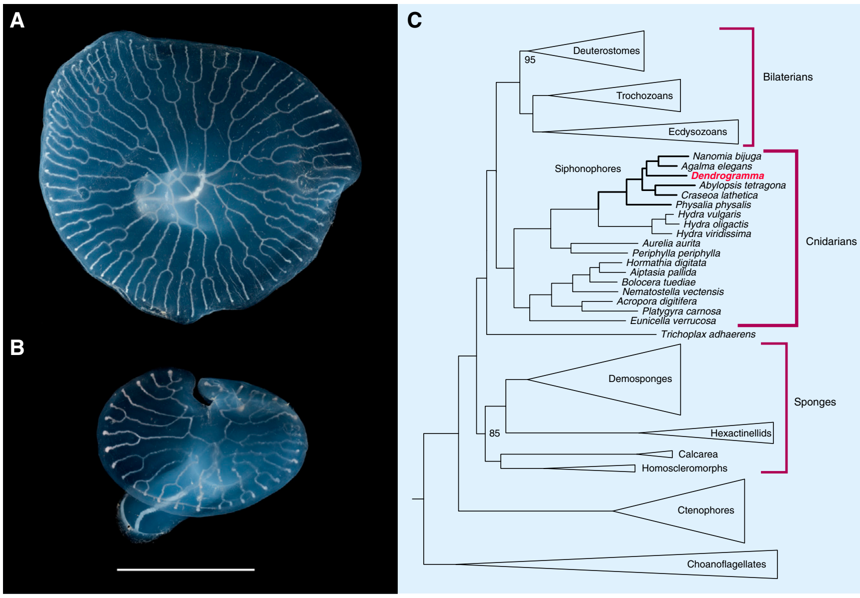

Figure 1. *Dendrogramma* in the tree of animal life.
Dendrogramma bracts showing the (A) 'discoides' and (B) 'enigmatica' morphologies (scale bar = 10 mm). (C) Simplified phylogenomic tree of the Metazoa, predominantly derived from Whelan *et al.* 2015 [3], showing the position of *Dendrogramma*. Bootstrap values are 100% unless otherwise indicated. The full tree is available in Supplemental Figure S1A.

Based on the phylogenetic analyses, available morphology, and the benthic environment from which specimens were collected, we conclude that *Dendrogramma* is a siphonophore in the family Rhodaliidae and that the Dendrogrammatidae is a junior synomym of that family. However, we have insufficient genetic or morphological evidence to identify *Dendrogramma* as a known rhodaliid genus or species. No described rhodaliid bracts are as large or with such complex canal branching patterns as *Dendrogramma*.

Additionally, we have evidence that there is only one, not two, species of *Dendrogramma*. Specimens with notched (*D. enigmatica*) or rounded (*D. discoides*) discs and long (*D. enigmatica*) or short (*D. discoides*) stalks (Figure 1A,B) were found in the same collection sample, with identical 16S sequences, and overall, collection site explains the low level of 16S variation ($\pi = 0.0015$) better than morpho-type (Figure S1C). Rhodaliid bract morphology is known to vary with ontology and location on the siphonosome. New bracts can replace older ones that become detached [7]. On this basis, we consider the two nominal species of *Dendrogramma* to be synonyms. The species *D. enigmatica* is the senior (and more appropriate) name as it was described first and nominated as the type species of the genus. *Dendrogramma enigmatica* is now known to occur around southern Australia from 34–42°S and 129–150°E at depths between 400 and 2900 m. All specimens have been collected with devices that sample surficial sediments and 0.5 m above the sediment, suggesting it lives attached to or just above the seafloor.

Genetic evidence has been used to shed light on many of the mysteries of evolution. Enigmatic deep-sea creatures such as vestimentiferans and pognophorans, at one point placed in their own phyla, have subsequently been found to be in the same family of polychaete worms [9]. On the other hand the simple bag-like *Xenoturbella* has been found to be a distinct bilaterian lineage [10]. Voyages of discovery continue to find new and engrossing animals in the deep-sea, including from the use of modern submersible technologies [4,10]. The description of life on our blue planet is far from complete.

SUPPLEMENTAL INFORMATION

Supplemental information includes two figures, experimental procedures and author contributions and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.04.051.

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