Correspondence

Neotenous origins for pelagic octopuses

Jan Strugnell[1], Mark Norman[2], Alexei J. Drummond[1] and Alan Cooper[1]

The ‘ctenoglossans’ are an enigmatic group of transparent, pelagic octopuses that spend their entire life without touching the seafloor. Molecular and morphological evidence shows that the ctenoglossans have arisen via neoteny, the persistence of larval attributes in the adult form. The ctenoglossans have evolved from the planktonic early-dispersal stages of familiar benthic octopuses. Extreme adaptations of this group to their midwater habitat have masked their origins. The general appearance of the ctenoglossans is strikingly similar to that of non-octopod midwater cephalopods, the Glass Squids (family Cranchiidae).

The Ctenoglossa include three families: the Glass Octopus (Family Vitreledonellidae, Figure 1A), Telescope Octopus (Family Amphitretidae, Figure 1B), and members of the family Bolitaenidae (Figures 1C,D). These octopuses live in tropical and temperate waters worldwide and possess many adaptations to their pelagic lifestyle, such as a transparent body, reduced organ size, modified eyes and in certain taxa large, simple chromatophores and light-producing organs. These adaptations have complicated morphological analyses and obscured the phylogenetic relationships of this group within the Octopoda [1,2]. Naef proposed that the Ctenoglossa diverged from all other octopods in the Upper Cretaceous [1]. Voight proposed that the Ctenoglossa were polyphyletic, with the Bolitaenidae placed as the sister group to all remaining incirrate octopuses, while the Amphitretidae and Vitreledonellidae were grouped with the shelled argonauts and their relatives (superfamily Argonautoidea) [3].

To investigate the origins of the ctenoglossan octopuses, we amplified a total of 3400 base pairs (bp) of DNA from the Vampire squid and 17 species of Octopoda, including three species from the ctenoglossan families Vitreledonellidae and Bolitaenidae. Sequences from three mitochondrial (12S rDNA, 16S rDNA, *cytochrome oxidase I*) and three nuclear (*rhodopsin*, *octopine dehydrogenase*, *pax-6*) genes were used in maximum likelihood (ML) and Bayesian analyses (Supplemental Data).

The phylogenetic tree for the concatenated dataset (Figure 1E) reveals that the ctenoglossans are more closely related to benthic octopuses than previously suspected. The closest sister taxa are members of the family Octopodidae, namely the Antarctic genus *Pareledone* (Figure 1F); the second nearest is the deep-water genus *Graneledone*. In contrast to the entirely pelagic ctenoglossans, members of both these genera have a wholly benthic lifestyle and large benthic hatchlings [4]. The distribution of the ctenoglossans in tropical and temperate waters contrasts with that of their closest relative, *Pareledone*, which is restricted to Antarctic waters. This geographic separation suggests that these groups diverged prior to the establishment of the Circum-Antarctic Current, about 33.5 million years ago (mya) [5]. To examine this hypothesis, molecular estimates of the divergence time of ctenoglossans and the *Pareledone/Graneledone* clade were obtained using the fossil calibration points of the vampire squid, *Vampyronassa rhodanica* (~162 mya), and the finned octopod, *Palaeoctopus newboldi* (~87 mya; Figure 1E). Penalised likelihood analyses estimated the divergence occurred in the mid Eocene, around 48.5 ± 7.5 mya (supplemental data). Examination of the morphology of adult ctenoglossan octopuses revealed that they share a number of characters with the planktonic juveniles (‘paralarvae’) of benthic octopuses [6]. These include a transparent body and limbs, size reduction of internal organs, simple large chromatophores (Figure 1G), groups of bristles embedded in the skin (‘Kölliker bristles’) [6], and a beak with teeth on the rostrum [7]. All of these characters are lost in adult benthic octopuses. The presence of juvenile (‘paralarval’) characters in adult ctenoglossans support the hypothesis that these pelagic octopuses evolved through neoteny of the juvenile planktonic dispersal larvae of the more familiar bottom-dwelling octopuses.

The dramatic divergence between adults of these related groups is likely to have occurred through selection for pelagic juveniles that remained increasingly longer in the plankton. If this was extended over geological time, a pelagic lifestyle would become necessary for survival. Possible selective scenarios include heavy predation of paralarvae settling on the seafloor or oceanic currents passing over limited or unsuitable habitats. The ‘super-paralarvae’ that occur in some benthic octopuses provide evidence of such selection [8,9]. These juveniles reach large sizes in the plankton (i.e. *Octopus rubescens*) [6], presumably due to an inability to settle. In contrast, the benthic hatchlings of *Pareledone* and *Graneledone* are likely to represent adaptations to polar and deep-water habitats. The critical step in the origins of the ctenoglossans would be attaining reproductive maturity and successfully mating within the plankton. Nothing is known of this process, although ctenoglossan octopuses have divorced themselves from the substrate by brooding their eggs within their arms [9].

The transformations seen in the ctenoglossan octopuses have parallels in some squid groups. Glass Squids occur in the same midwater habitats and show almost the identical morphological adaptations as the ctenoglossans:

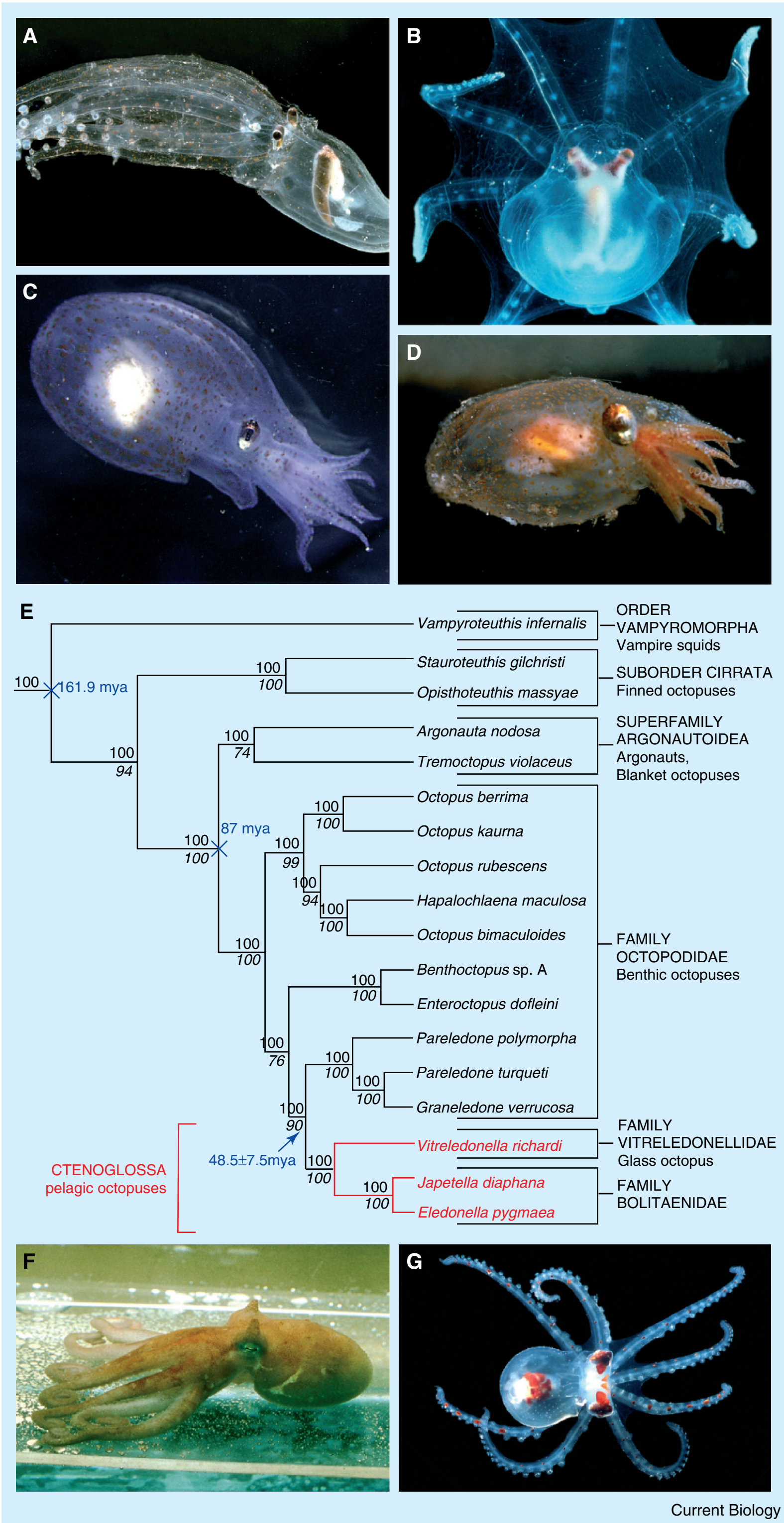

Figure 1.
(A–D) Ctenoglossan octopuses: (A) *Vitreledonella richardi*; (B) *Amphitretus pelagicus*; (C) *Bolitaena pygmaea*; (D) *Japetella diaphana*. (E) Maximum likelihood (ML) tree depicting the phylogenetic relationship of 17 species of Octopoda and *Vampyroteuthis infernalis*. The analysis employed 3 mitochondrial (12S rDNA, 16S rDNA, COI) and 3 nuclear genes (*octopine dehydrogenase, rhodopsin, pax-6*). Bayesian support values are indicated in bold, ML consensus values with 70% support in italics. 'X' indicates the known fossil calibration points of *V. rhodanica* (162 mya) and *P. newboldi* (87 mya). (F) *Pareledone framensis*; (G) *Octopus* sp. planktonic paralarva.

transparency, size reduction of organs, stalked or telescopic eyes, simple chromatophores and an elongate digestive gland that is always held in a vertical position to minimize silhouette as seen from below (as found in *Vitreledonella* and *Amphitretus*, Figure 1A,B) [9]. It may prove that both the ctenoglossans and the glass squids are two lineages of young planktonic cephalopods that both evolved through neoteny.

Supplemental Data

Supplemental Data are available at http://www.current-biology.com/supplemental

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[1]Molecular Evolution, Department of Zoology, South Parks Rd, Oxford OX1 3PS, UK. [2]Sciences, Museum Victoria GPO Box 666E Melbourne, Victoria 3001, Australia.