ture by trypsinization of the tumor tissue. The resulting cultures exhibited colonial and cellular morphology identical with that of the original transformed, inoculated cells; they still produced T antigen.

Apparently, the adenovirus 12 genome, when interacting with a homogeneously fibroblastic BHK21 cell line, is capable of determining the morphology of the resulting transformed cells as well as the characteristic morphology of tumors induced by these cells. Of course, the extent to which one may generalize on the basis of these results is limited, without similar studies on pure strains of cells from a number of diverse tissues. Because the BHK21 cells used were clonally purified, we avoided the ambiguities of the malignant change in vivo or in mixed cell populations (for example, hamster embryo cultures). The demonstration of the virus-specific nature of the morphological alterations accompanying transformation by an adenovirus further defines the participation of this viral genome in oncogenesis.

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16. The uninfected BHK21 cells produced tumors more rapidly and with smaller inocula than did the transformed cells. This possibly results from a greater incompatibility of transplantation of the transformed cells due to additional adenovirus-12-specific antigens present in these cells.
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Homology of Retractile Filaments of Vampire Squid

Abstract. *The axial filament nerves of* Vampyroteuthis infernalis *are joined to two separate parts of the brain. One branch of the nerve, apparently efferent, arises from the anterior portion of the middle subesophageal mass, and the other, apparently afferent, enters the ventral magnocellular lobe. Since this innervation is entirely different from that of the arms, the filaments can no longer be considered homologous with the arms. The validity and primitive nature of the order Vampyromorpha, therefore, needs to be reexamined.*

Vampyroteuthis infernalis, a primitive, deep-sea cephalopod, was first described by Chun in 1903 (*1*) and placed in its own family, the Vampyroteuthidae, within the Octopoda. In 1929, Robson (*2*) elevated the group to subordinal ranking on the basis of increased knowledge of its peculiar anatomical features. Of particular importance was the discovery of a pair of retractile filaments situated between the first and second (dorsal) pairs of arms. Joubin (*3*) suspected that these filaments were related to the decapod tentacles, although they occupied a different position on the brachial crown (the two decapod tentacles represent the modified fourth pair of arms). Robson (*4*), however, who had been able to follow the axial filament nerve past the brachial lobe in a macerated specimen, was hesitant to accept the homology with the arms and suggested, ". . . it is not altogether impossible that they [the filaments] may be secondary pedal outgrowths."

Pickford, after preliminary anatomical investigations on *Vampyroteuthis* (*5, 6*), concluded that the filaments were homologous with the arms. Her evidence was based chiefly on the similarities of the venous drainage of the arms and filaments, and on the apparent origin of the axial filament nerves from the brachial lobe. She indicated, however, that the origin of the filament nerves was not definitely settled.

As a result of her investigations, Pickford erected a new order for *Vampyroteuthis* and, as a primary character for the establishment of the Vampyromorpha, stated (*6*), ". . . there are five pairs of arms, the second dorsal pair being modified to form retractile filaments." In addition, the structure of the pen, the attachment of the fins to the shell-sac, and the free position of the spermatophore glands within the mantle cavity led Pickford to conclude that the order had a primitive origin.

In 1964, Donovan (*7*), accepting Pickford's views that *Vampyroteuthis* has ten arms, found it necessary to assume that the order had separated, ". . . very early from the decapod stem before the fourth pair of arms had become specialized as tentacles in the ancestors of the squids and cuttlefish." Therefore, the arrangement of the brachial crown both confirmed and demanded a primitive position for the order.

The nature of the retractile filaments is clearly of primary importance in determining the phylogenetic position of this animal. During studies on the anatomy of *Vampyroteuthis*, it has become apparent that the filaments are not homologous with the arms. Evidence to support this view is derived primarily from the anatomical relationships of the axial nerves of the filaments.

Each filament nerve is situated between the axial nerves of the first and second arms. The arm nerves send most of their fibers into the anterior subesophageal mass (brachial lobe) (Fig. 1). Each filament nerve, consisting of two separate bundles of fibers, by-passes this lobe completely. The smaller bundle, probably consisting of efferent fibers, passes dorsal to or occasionally through the brachio-palliovisceral connective and enters the middle subesophageal mass. The fibers then plunge diagonally toward the anterior-median area of the lobe where the tract loses its identity. The larger bundle, apparently with afferent fibers, passes ventral to or sometimes through the brachio-palliovisceral connective and enters a lateral side of a large oval lobe which is situated on the ventral surface of the middle subesophageal mass. This lobe is a single median

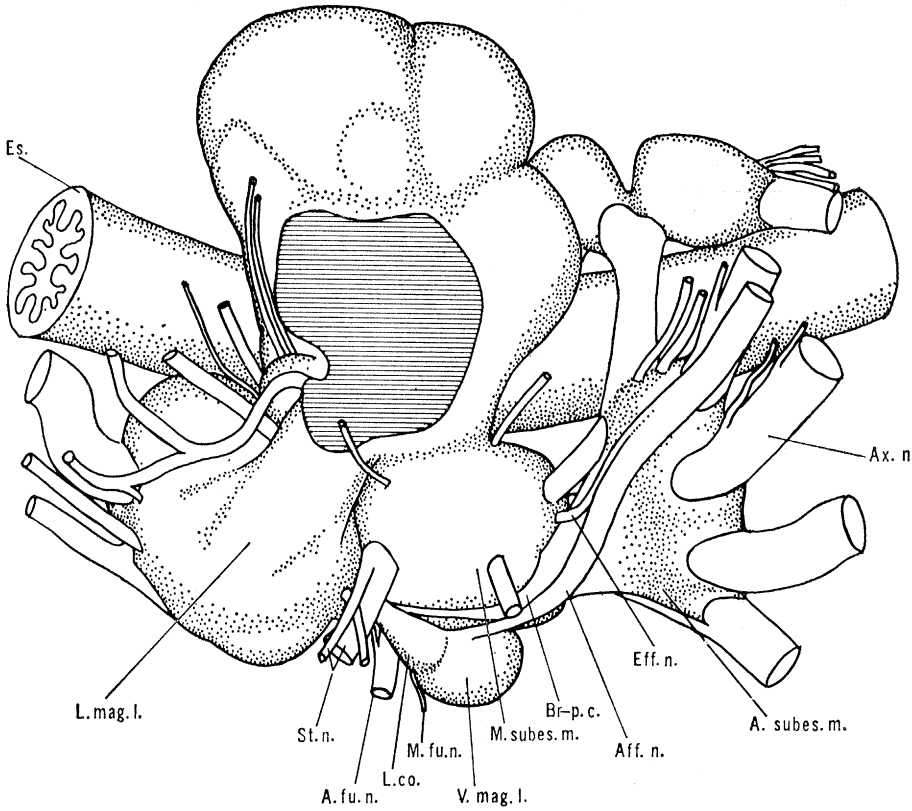

Fig. 1. Lateral view of the brain of *Vampyroteuthis infernalis*. *Aff. n.*, afferent nerve of right filament; *A. fu. n.*, anterior funnel nerve; *A. subes. m.*, anterior subesophageal mass; *Ax. n.*, axial nerve of second right arm; *Br.-p. c.*, brachio-palliovisceral connective; *Eff. n.*, efferent nerve of right filament; *Es.*, esophagus; *L. co.*, lateral cord of the ventral magnocellular lobe; *L. mag. 1.*, lateral magnocellular lobe; *M. fu. n.*, median funnel nerve; *M. subes. m.*, middle subesophageal mass; *St. n.*, nerves to the right statocyst; *V. mag. 1.*, ventral magnocellual lobe.

structure with a very highly organized neuropile and a rind consisting entirely of rather small cell bodies; the lobe is almost certainly homologous with the ventral magnocellular complex of decapods. This homology is indicated by the position of the lateral cords of the lobe and their association with the lateral magnocellular lobes; by the position of the lobe and lateral cords relative to the location of the anterior funnel nerves, the brachio-palliovisceral connectives, and the median funnel nerve; and finally by the presence of a strong commissure between the lateral cords.

The magnocellular lobes in octopods and decapods appear to be primarily concerned with defense and escape reactions (*8*). The ventral magnocellular lobe is absent in octopods (*9*), but in decapods it contains the first-order giant fibers which initiate rapid contraction of the mantle (*10*). Although unreported, *Vampyroteuthis* has an escape reaction. In addition, its retractile filaments are generally found coiled inside a pouch; however, they can extend farther than the arms and in almost any direction (*11*). These considerations suggest that the retractile filaments of *Vampyroteuthis* function in the detection of predators and in the initiation of the escape reaction.

The ventral magnocellular lobe in decapods receives a large nerve at a point which corresponds to the entry point of the filament nerve in *Vampyroteuthis*. This nerve, recorded by J. Z. Young (*10*) as the branchio-magnocellular connective, receives several branches, one of which passes through the cephalic cartilage along with the anterior occulomotor nerves and the others apparently with the antorbital and interbrachial nerves. It is doubtful that it receives any fibers from the anterior subesophageal mass or the axial arm nerves. The "brachio-magnocellular connective" possibly contains afferent fibers from the surface of the head.

The innervation of the filaments is, therefore, entirely different from the innervation of the arms. This finding in itself is enough for the conclusion to be drawn that the filaments and arms are not homologous. This conclusion indicates the need for a reevaluation of the ordinal status and of the primitive nature of the Vampyromorpha. It should be emphasized, however, that the relationships of the group are obscure and its inclusion, at the present time, in any other existing order, as recently suggested by Jeletzky (*12*), is premature. Similarly, although the character which Donovan used for determining the origin of the group is no longer valid, there remain many features of the order which must be considered very primitive.

Perhaps one of the major reasons for previously considering the filaments homologous with arms came from the belief that the filaments must be derived from something, and the arms seemed to offer the only possibility. J. Z. Young (*13*) has suggested another alternative: Perhaps the filaments are homologous with the preoccular tentacles of *Nautilus*. I have examined his slides of *Nautilus* with this idea in mind, but find that its brain is so far removed from that of recent coleoid cephalopods that only a few basic similarities can be recognized. The evidence, therefore, is not sufficient to confirm this idea; it remains, however, an intriguing possibility.

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