

## **A new dinoflagellate from the Indian Ocean: a link between the genera *Amphisolenia* and *Triposolenia* (Dinophyceae)?**

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An interesting dinoflagellate belonging to the Order Dinophysiales was found in a phytoplankton sample collected by net from the Indian Ocean (13°35.8'N, 70°50.0'E) on the cruise IOE 'Meteor'. The specimen was isolated and studied by light and scanning electron microscopy. The species has a large cell size (340 µm length and 55 µm width) with some characters typical of the genus *Amphisolenia* Stein: compressed head, short neck, and an elongated, wide midbody. However, it lacks a posterior narrowing and develops two nearly straight and symmetrical posterior processes, each with two spines at the end, which are features of the genus *Triposolenia* Kofoid. Therefore, we are dealing with a new species, *Triposolenia fallax* Hernández-Becerril et Meave, which has unique characteristics. We consider this species to be a link between the two genera of the Family Amphisoleniaceae. The adaptive morphology of the species and possible evolutionary trends of the genera are discussed.

### **INTRODUCTION**

The family Amphisoleniaceae Lindemann belongs to the subclass Dinophysiphycidae Möhn *ex* Fensome *et al.* and order Dinophysiales Kofoid and contains unicellular (solitary) dinoflagellates that are usually extremely elongated with a sagittal suture that extends along the cell length, dividing the cell into two valves (left and right). They have an anterior cingulum and a reduced episome, the hyposome may divide into two or more prongs, and the flagella are inserted ventrally and emerge from a single flagellar pore. Thecal plates are relatively few, cingular and sulcal lists are weakly developed, and there is a relatively broad middle part known as 'midbody' (Taylor 1987a; Balech 1988; Fensome *et al.* 1993; Steidinger & Tangen 1997).

The Amphisoleniaceae includes only two genera: *Amphisolenia* Stein (Stein 1883) and *Triposolenia* Kofoid (Kofoid 1906a), with approximately 44 extant species, 35 species of *Amphisolenia* following Sournia (1973, 1978, 1986), and nine species of *Triposolenia*, according to Schiller (1933) and Sournia (1986); no fossil species are known (Fensome *et al.* 1993). Most of the species, probably all of them, are heterotrophic [nonphotosynthetic, according to Hallegraeff & Jeffrey (1984), although Kofoid (1906a) and Steidinger & Tangen (1997) mentioned that chloroplasts are probably present], but some forms (especially some *Amphisolenia* species) harbor intracellular blue-green algae (Cyanophyta) (Taylor 1982; Hallegraeff & Jeffrey 1984; Gaines & Elbrächter 1987; Lucas 1991). Additionally, Lucas (1991) found in *Amphisolenia bidentata* Schröder and *A. thrinax* Schütt endosymbiotic phototrophic eukaryotic cells and groups of bacteria.

Members of this family are truly planktonic and are found

in tropical (warm-water) areas (Taylor 1987b; Balech 1988). Most species are considered oceanic (Balech 1988) and are regarded as shade forms (Sournia 1967; Balech 1988). In particular, *Triposolenia* species (*T. truncata* Kofoid, following Sournia 1982) are generally encountered in deep waters (Kofoid 1906a, 1906b; Léger 1971; Sournia 1982) and have low population densities.

Some species of this family have been studied in detail by Kofoid (1906b), dealing with *Triposolenia* species, and Kofoid & Skogsberg (1928). However, many others remain practically unknown, our knowledge of their morphological variability is poor, and we have little information about their biology (Sournia 1967; Balech 1988). This is because most species are extremely rare.

There are few recent studies on the morphology of members of *Amphisolenia* or *Triposolenia*. Abé (1967) analyzed the morphology of five species of *Amphisolenia*, including one newly described species (*A. microcephalus* Abé) and *Triposolenia bicornis* Kofoid. Saifullah & Hassan (1973) described and illustrated seven species of *Amphisolenia*, including two new species. Balech (1977) studied the plate pattern of *A. bidentata* in detail (this species is one of the most abundant of the genus). Taylor (1976) illustrated the 'antapex' of *A. schauinslandii* Lemmermann by SEM, and later (Taylor 1987a) he illustrated a complete cell of *T. truncata* Kofoid, also by SEM. Hernández-Becerril (1988a) described *A. bidentata* based on SEM observations. The nature of the pigmented phaeosomes of three species of *Amphisolenia* was studied using TEM by Lucas (1991).

In the present paper, we discuss a new species of the genus *Triposolenia* that is distinctive because it shares general features of species of both genera of the Amphisoleniaceae and may be considered a link between these genera. The possible evolutionary trends of these genera are discussed.

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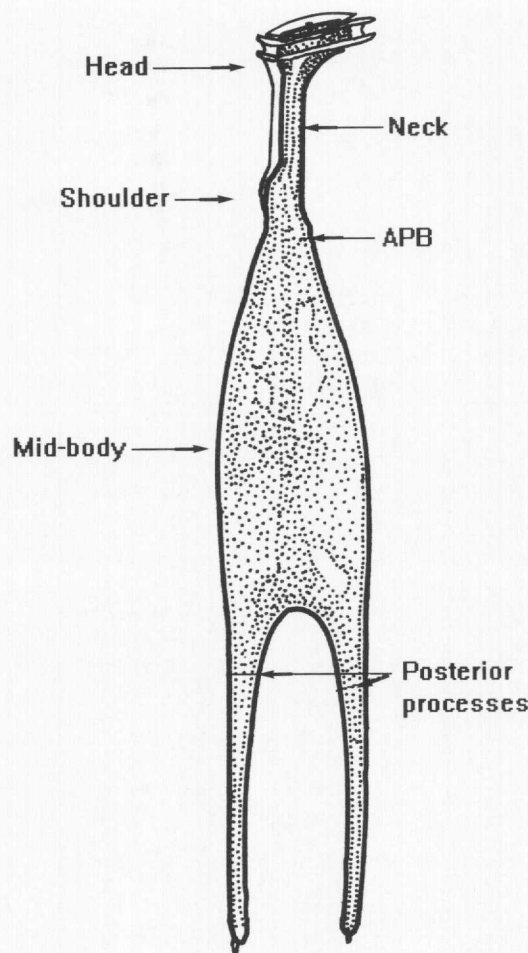
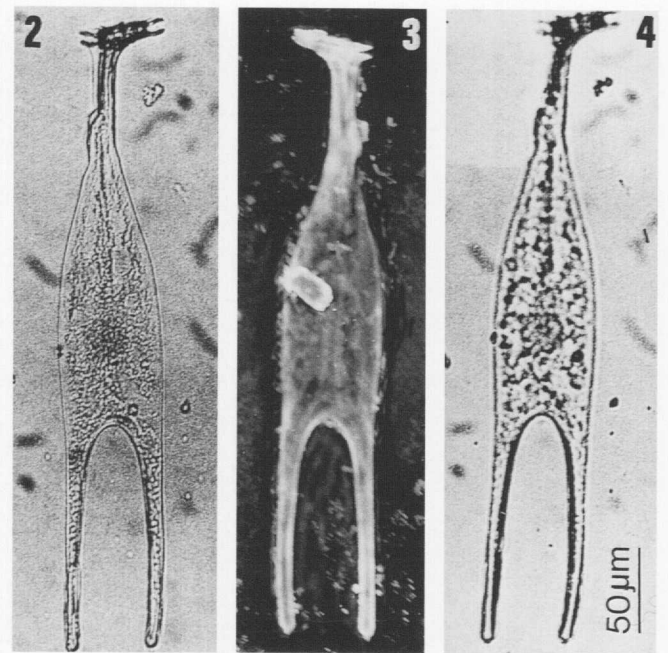


Fig. 1. *Triposolenia fallax* sp. nov. Diagram of the morphology of the species with the prominent features labeled. APB, anterior part of the body.

## MATERIAL AND METHODS

We studied a preserved net (54  $\mu\text{m}$  mesh) phytoplankton sample collected on 18 February 1965 from the Indian Ocean (13°35.8'N, 70°50.0'E) in a vertical net haul (180 m to surface) during a cruise of the 'Meteor'. The material was preserved in 4% Formalin. For examination, material was rinsed with distilled water and analyzed by light microscopy (Reichert Diastar, phase contrast and Nomarski contrast). When the specimen of the new entity was discovered, it was measured and photographs were taken. The cell was isolated with a micropipette, placed on a coverslip, air-dried, and coated with gold for subsequent observation by scanning electron microscopy (JEOL-JMS 35).

The terminology adopted here borrows from several authors, particularly Kofoid (1906a), Balech (1988), Fensome *et al.* (1993), and Steidinger & Tangen (1997). Cells of members of the Amphisoleniaceae may be divided into the following parts: head, neck, anterior part of the body (APB), midbody, and posterior (caudal) processes ('antapical horns' in Kofoid 1906a) (Fig. 1). The head is formed by the episome and the cingulum. The neck is the thin and elongated part that supports the head and corresponds to the sulcal region. The APB is a region wider than the neck but thinner than the midbody.



Figs 2–4. *Triposolenia fallax* sp. nov., light (LM) and scanning electron microscopy (SEM).

Fig. 2. Left lateral view of the species, LM (Nomarski contrast).

Fig. 3. Right lateral view of the same specimen, SEM.

Fig. 4. Same specimen in LM (bright field). The scale bar (50  $\mu\text{m}$ ) is the same for all figures.

The midbody begins from a rounded part, the 'shoulder' (or 'nipple'), in the region of the flagellar pore; the midbody is the widest region of the cell where the nucleus and other organelles are located. The posterior (or caudal) processes are antapical extensions that arise from the midbody and may be simple or forked.

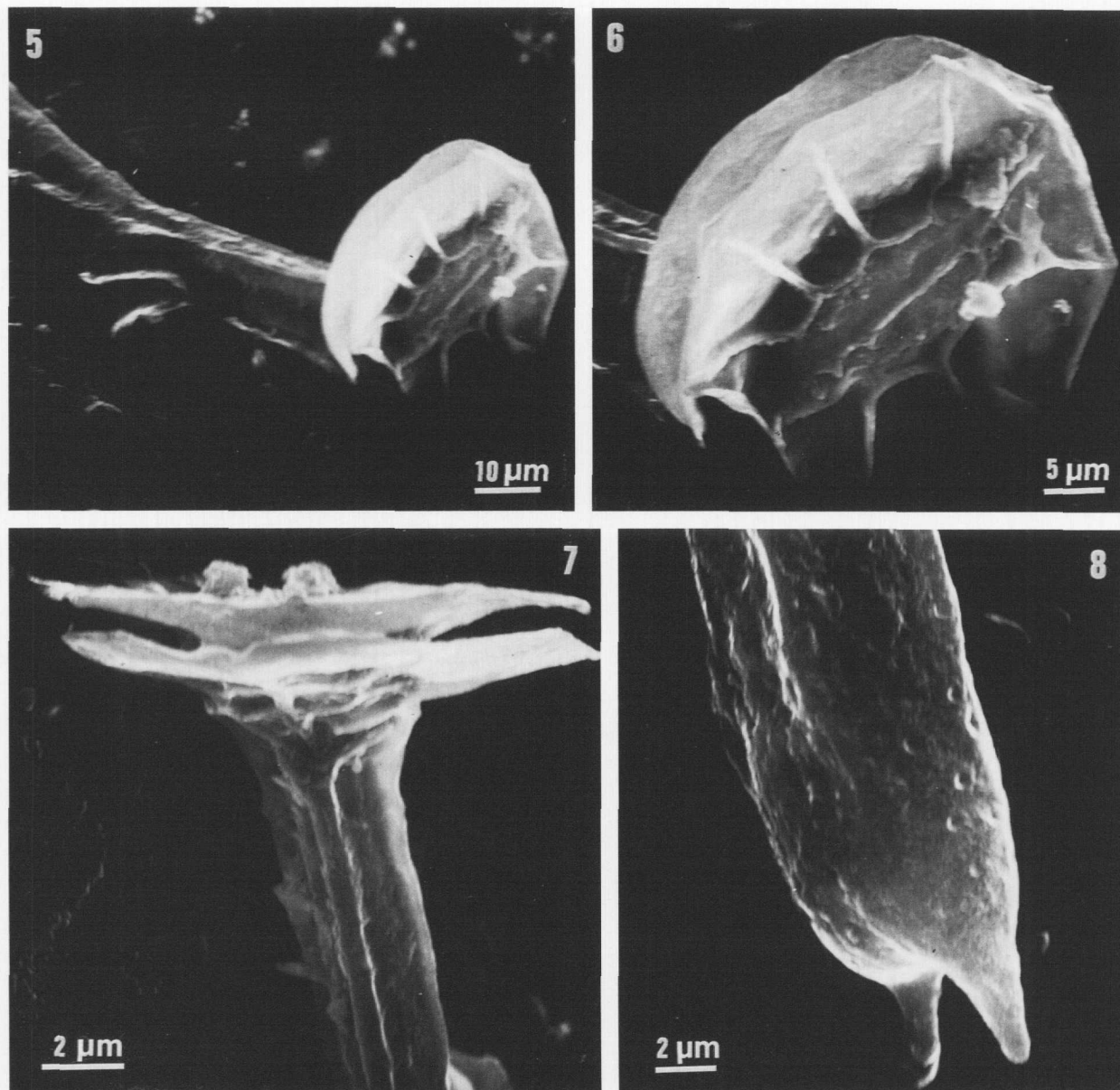
## OBSERVATIONS

### *Triposolenia fallax* Hernández-Becerril et Meave sp. nov.

Figs 1–8

DIAGNOSIS: Cellula solitaria, crassa, depressa aspectu ventrali, habens character tripartita. Testa crassa, episoma plana. Ala cingulari anterior a 9 costas. Alae sulcales parvae. Collum rectus, umerus conspicuus. Corpo medio elongato. Duo processus posteriores, subaequales, rectus ortus ex corpo medio. Dua spinae in processus postice terminans. Theca hyalina, pori in collum et processus posteriores. Ratio longitudo/latitudo = 6.3.

The species is solitary and has a tripartite character (Figs 1–4). It is ventrally compressed and robust (Figs 2–4) and is 340  $\mu\text{m}$  long and 55  $\mu\text{m}$  wide in lateral view. It has two posterior processes that are equivalent and subequal (Figs 2–4). The head is large with a flat, elliptical episome (42  $\mu\text{m}$  long, including lists, and 12.5  $\mu\text{m}$  wide) (Fig. 5). The sagittal suture is conspicuous in the neck, bearing small spines (Fig. 5). The anterior cingular list is about the same size as the posterior cingular list and is supported by nine ribs (Fig. 6). The cingulum is oblique to the main axis (Fig. 7). The sulcal lists are reduced, but become wider and triangular in the APB. The neck (42  $\mu\text{m}$  long and 12.5  $\mu\text{m}$  wide) is straight and



Figs 5–8. *Triposolenia fallax* sp. nov., SEM.

Fig. 5. Head and neck, also showing the sulcal lists.

Fig. 6. Detail of the head, with its cingular lists, the anterior with nine ribs.

Fig. 7. Dorsal view of the head and neck, with the sagittal suture.

Fig. 8. Tip of one posterior process showing its two spines and some scattered pores.

cylindrical, with no displacement from the main axis, and the shoulder is conspicuous (Figs 2–4).

The APB is not prominent (19 µm wide), with a very slight dorsal displacement. The midbody is elongate (fusiform), with the anteroventral and anterodorsal margins nearly straight, whereas the posterior margin is concave (Figs 2–4). The posterior processes (8 µm wide) are straight, arising from the posterior ends of the midbody. The dorsal process is slightly shorter and more curved than the ventral process (about 3 µm difference) (Figs 2–4). The tips of the processes have two sagittal spines 0.4 µm long (Fig. 8). Hyaline thecae with small pores are mainly on the neck and posterior processes. Length/width ratio = 6.3.

**HOLOTYPE:** The holotype will be deposited in the Herbario Nacional de México (Instituto de Biología, UNAM): MEXU Colección Ficológica (Phycological Collection), No. 1492.

**ETYMOLOGY:** The epithet *fallax* means 'false'.

**TYPE LOCALITY:** Indian Ocean (13°35.8'N, 70°50.0'E).

#### DISCUSSION

The new species described here has some morphological characteristics that fit well into the circumscription of the genus *Amphisolenia*, and others that fit well with *Triposolenia*. Therefore, we suggest that this species is a link between these

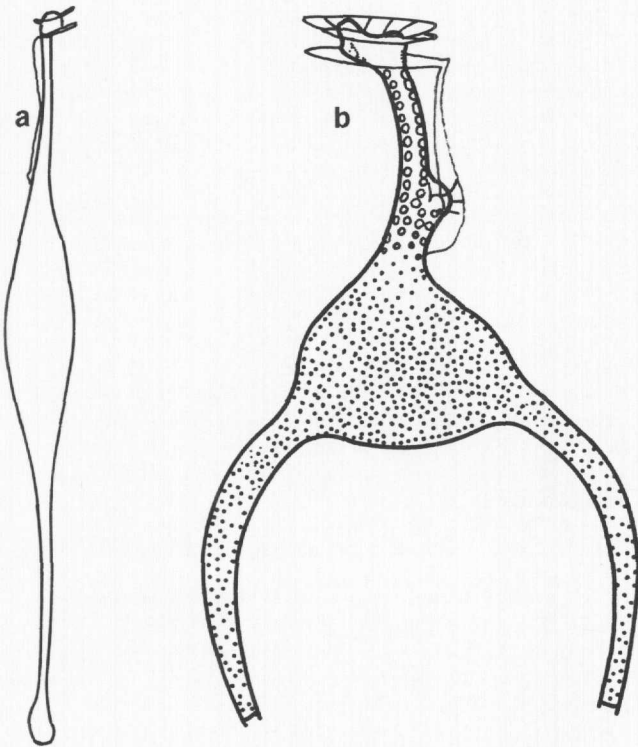


Fig. 9. Drawings of the type species of the two genera of the Amphisoleniaceae. Figures are not drawn to scale. a. *Amphisolenia globifera*. b. *Triposolenia truncata*.

genera, as envisioned by Kofoid (1906b, p. 117), "As yet no species have been found which will afford a transition between *Triposolenia* and the most nearly related genus *Amphisolenia* which has a fusiform midbody and a single simple or branched antapical horn."

Species of *Amphisolenia* have only one posterior process, which is generally straight, either simple or forked, and always arising from the terminal part of the midbody, not from the center of the midbody. The tip of the posterior process may be truncated or globose, smooth or with two to four minute spines or teeth. The midbody is elongate (fusiform); the APB is generally poorly developed, and the thecae have small pores (the type species, *Amphisolenia globifera* Stein, is illustrated in Fig. 9a). By contrast, the anterior portion of *Triposolenia* cells is similar to that of *Amphisolenia*, with a well-developed shoulder and a wide central body that is triangular, rounded, or bursiform, from which arises two posterior processes, usually subequal and curved outwardly and with small spines or projections on the external margin; the tips of these processes may be smooth or with minute spines.

*Triposolenia* has a particularly tripartite character due to the presence of the two posterior processes and the neck and head of the organisms. Another important characteristic is the marked asymmetry in both dorsoventral and lateral views. The APB leans toward the dorsal part ( $10\text{--}20^\circ$  in relation to the main axis) and the neck is displaced  $10^\circ$  to  $35^\circ$  dorsally. The cingulum is usually perpendicular to the main axis (the type species, *Triposolenia truncata* Kofoid, is illustrated in Fig. 9b).

The characteristics of *Triposolenia fallax* that agree with

those of *Amphisolenia* are the symmetry of the body, the APB and neck with no clear displacement, the elongate, fusiform midbody, and no prominent APB, whereas the presence of two posterior processes and the equilibrated relationship between the length of the neck and the posterior processes clearly differ from *Amphisolenia*.

*Triposolenia fallax* also shows characteristics typical of the genus *Triposolenia*: tripartite character (i.e. neck, head, and two posterior processes of equivalent dimensions), posterior processes arising from the midbody, asymmetry of the posterior processes, shoulder conspicuous, and neck short in relation to the length of the midbody. However, some characters do not fit (e.g. symmetry in lateral and dorsoventral views, the midbody is elongate and fusiform, the posterior processes are straight and near each other, and the neck and APB exhibit no displacement from the main axis). The presence of two posterior processes arising from the midbody, which produces the tripartite character, is considered a very important taxonomic character for inclusions of this species in *Triposolenia*. This species is, however, larger than all those previously described for the genus (Kofoid 1906b).

Describing new species on the basis of just one specimen is risky and may lead to future confusion, but we are persuaded by distinctive characteristics of the new species: shape, dimensions, number and form of the posterior processes, and symmetry of the body. Another specimen of this species has been collected from the Indian Ocean (M.C. Carbonell-Moore, personal communication).

Most species of *Amphisolenia* and *Triposolenia* are extremely rare, and some species have been described from a single cell [e.g. *Triposolenia exilis* Kofoid (Kofoid 1906a), *Amphisolenia curvata* Kofoid and *A. asymmetrica* Kofoid (Kofoid 1907), and *Amphisolenia sigma* Halim (Halim 1965)]. It is common to find records of a single specimen of certain species placed in both genera [e.g. *Amphisolenia curvata* (Wood 1954), *Amphisolenia truncata* Kofoid et Michener (Silva 1955; Halim 1960), *Triposolenia depressa* Kofoid (Silva 1957; Balech 1988), *T. truncata* Kofoid (Silva 1957), *Amphisolenia palaeotheroides* Kofoid (Balech 1962), *Amphisolenia brevicauda* Kofoid (Rampi 1969), *Amphisolenia complanata* Kofoid et Skogsberg (Léger 1973), *Amphisolenia asymmetrica* Taylor (1976), *Amphisolenia lemmermanni* Kofoid (Hernández-Becerril 1988b)]. Sournia (1967) pointed out that specimens of *Triposolenia* species are even more rare than those of *Amphisolenia*.

We do not believe that the species described here is a morphological variant of a described species of *Amphisolenia* or *Triposolenia*. There are no observations of sexual reproduction in the family, but an origin of this morphological form by hybridization cannot be excluded. However, this suggestion requires intergeneric hybridization.

We suggest the following possible evolutionary trends: (1) *Amphisolenia* is an older genus than *Triposolenia*; (2) originally the posterior processes of *Triposolenia* were straight and close to each other but separated when the body became wider; and (3) separation of the posterior processes and the increasing asymmetry of these (dorsal and ventral processes) may have caused the leaning of the neck and the APB to balance the equilibrium point of the organism, necessary for locomotion (swimming), orientation, or flotation (see Kofoid 1906a, 1906c; Taylor 1987a).

A variety of other evolutionary speculations could be proposed, with differing taxonomic consequences: (1) the new species retains primitive characteristics of *Tripsolema*; (2) the new species links the species of the Amphisoleniaceae such that there is a gradient of morphological forms and all species can be viewed as belonging to the type genus, *Amphisolenia*; and (3) the posterior processes of this species are analogous to those of *Tripsolema*; therefore, we are dealing with a new genus. Still another view (voiced by an anonymous referee) is that *Tripsolema* may have evolved from species of the genus *Dinophysis* Ehrenberg (particularly *D. miles* Cleve), and *Amphisolenia* derived from either *Tripsolema* or other species of *Dinophysis*. These are interesting possibilities that could be resolved by molecular systematics of these taxa.

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