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# Marine planktonic dinoflagellates of the order Dinophysiales (Dinophyta) from coasts of the tropical Mexican Pacific, including two new species of the genus *Amphisolenia*

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*Despite a recent revision of the dinoflagellates of the order Dinophysiales on Mexican coasts and a checklist of dinoflagellates from the Mexican Pacific, many records still need to be confirmed, for there are very few reliable illustrations and/or descriptions. In this paper, species composition and distribution of dinoflagellates belonging to the Dinophysiales, the product of the analysis of net phytoplankton material collected from coasts of the tropical Mexican Pacific (Jalisco to Chiapas) are presented. The material has been studied using light microscopy, although a few species were also studied by scanning electron microscopy (SEM). Forty-one species from five genera were identified, with two new records annotated for the Mexican Pacific:* Amphisolenia thrinax *and* Metaphalacroma skogsbergii*, and two new species of the genus* Amphisolenia*,* Amphisolenia fusiformis *sp. nov. and* Amphisolenia michoacana *sp. nov. Illustrations, dimensions and distribution data are provided for each species, and descriptions of the new species are also given.* Amphisolenia palmata*,* A. rectangulata*,* A. truncata*,* Dinophysis apicata*,* D. hindmarchii*,* Histioneis biremis*,* H. crateriformis*,* H. pulchra*,* Ornithocercus cristatus*,* O. heteroporoides *and* O. orbiculatus *are illustrated for the first time in the waters of the Mexican Pacific. The number of species found in this study is relatively low. The species* Dinophysis norvegica *and* D. sacculus*, reported in previous papers, do not seem to occur in Mexican waters, as their distribution is rather limited to the Mediterranean Sea and the North Atlantic, respectively. Finally, the identity of certain species of* Dinophysis *and the nature of the new species described here are discussed.*

**Keywords:** dinoflagellates, Dinophysiales, Mexican Pacific, new species, phytoplankton

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## INTRODUCTION

Marine dinoflagellates of the order Dinophysiales Kofoid are a group of thecate and motile forms that are laterally depressed with a sagittal serrate suture extended throughout the body, and show cingular and sulcal lists of variable development. In general the epitheca is reduced whereas the hypotheca is elongated (species of the genus *Amphisolenia* Stein are extremely elongated forms, reaching more than 1 mm). The thecae have two valves, left and right, and a number of plates, usually 18 with certain exceptions: 6–7 in the epitheca (2 apical and 4 epithecal), four cingular, four sulcal and four hypothecal (Sournia, 1986; Fensome *et al.*, 1993). The number of recognized species within the order varies from 240 to 382 (Sournia, 1995), with the highest diversity found in tropical waters and certain forms are limited to oligotrophic waters (Sournia, 1986), and yet other forms have umbrophylic preferences (Sournia, 1982). Most forms are truly planktonic, but species of *Synophysis* Nie & Wang have benthic habits (Hernández-Becerril, 1988a; Faust, 1993; Hoppenrath, 2000). One of the most diverse genera is *Dinophysis* Ehrenberg, with more than 200 species recognized (Sournia, 1986), due in part to the transfer of species of the genus *Phalacroma* Stein (Abé, 1967a; Balech, 1967). Several species of *Dinophysis* are considered to be toxic for they produce okadaic acid or dinophysistoxin, which cause diarrhoetic shellfish poisoning (DSP) (Lee *et al.*, 1989; Godhe *et al.*, 2002; Taylor *et al.*, 2003).

Many species of this order are not photosynthetic, but species that are photosynthetic, especially belonging to *Dinophysis*, contain pigments and chloroplasts of endosymbiotic origin, related to Cryptophyta (Schnepf & Elbrächter,

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1988, 1999), Chrysophyceae or Haptophyceae (Hallegraeff & Lucas, 1988), and Prasinophyceae (Berland *et al.*, 1995a); furthermore, Schnepf & Elbrächter (1999) have mentioned that chloroplasts in Dinophysiales are not typical of the dinoflagellates. In addition, kleptochloroplasts have been recently reported for the species *Dinophysis mitra* (Schütt) Abé (Koike *et al.*, 2005). Various species of *Dinophysis* are mixotrophs or even heterotrophs, and may develop 'peduncular' structures or organic tubes as strategies to feed (Hansen, 1991; Jacobson & Andersen, 1994; Hansen & Calado, 1999; Jacobson, 1999). Cyanobacteria symbionts are relatively commonly found in species of the genera *Amphisolenia*, *Citharistes* Stein, *Histioneis* Stein, *Ornithocercus* Stein and *Triposolenia* Kofoid; in *Ornithocercus*, *Histioneis* and *Citharistes* species these associations are called 'phaeosomes' and are located in special chamber-like structures or 'phaeosomal chambers' (Taylor, 1982; Hallegraeff & Jeffrey, 1984; Gaines & Elbrächter, 1987; Lucas, 1991; Janson *et al.*, 1995; Schnepf & Elbrächter, 1999). More recently, picoplanktonic cells have been found attached to the cellular surface in species of *Dinophysis*, and this fact has been thought to provide food in this genus (Imai & Nishitani, 2000; Nishitani *et al.*, 2002).

No species of the order has been successfully cultured (Nishitani *et al.*, 2003), although incubation of cells up to 30 days have been achieved (Koike at al., 2006), and thus details on the biology of most species within the order are unknown, in general, for instance sexual reproduction. Some sexual processes in *Dinophysis* have been recently suggested from live and preserved field samples (MacKenzie, 1992; Berland *et al.*, 1995b; Subba Rao, 1995; Giacobbe & Gangemi, 1997); presence of possible 'gametes' and cysts in *Dinophysis* may be part of complex life cycles, including smaller forms that have been considered as true species, but now they should be regarded as part of those cycles (Bardouil *et al.*, 1991; Reguera *et al.*, 1995; Reguera & González-Gil, 2001; Dodge, 2003; Taylor *et al.*, 2003). Some patterns of the cellular cycle have been approached in field samples, through the postmitotic index (Reguera *et al.*, 2003). Evidence for engulfment of 'small cells', as part of the sexual life cycle of *Dinophysis fortii* Pavillard, was recently found by Koike *et al.* (2006).

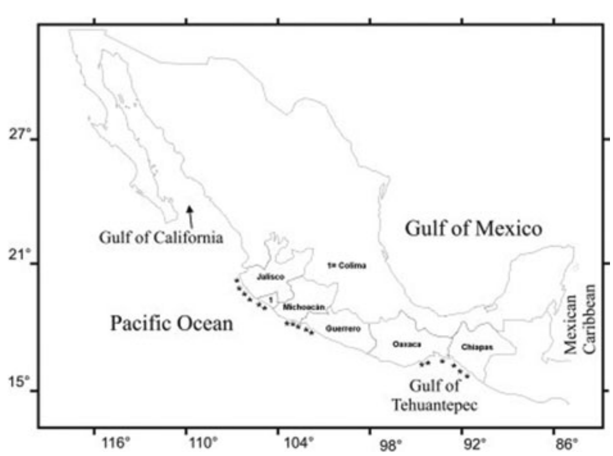


**Fig. 1.** Map showing the sampling locations in the tropical Mexican Pacific for this study.

Most species of the genera *Amphisolenia*, *Histioneis* and *Triposolenia* show very low density populations, thus many forms of these genera are considered rare: many species have been described on the basis of one single specimen (Kofoid, 1907; Wood, 1954; Taylor, 1976; Hernández-Becerril & Meave, 1999), and they have not been reported since then.

The classification into families is based on morphological characters: shape of thecae, position of flagellar and ventral pores, development of cingular and sulcal lists and the presence of spines (Fensome *et al.*, 1993). Sournia (1986) proposed Dinophysiaceae Stein, Oxyphysaceae Sournia and Citharistaceae Kofoid & Skoksberg, whereas Fensome *et al.* (1993) and Steidinger & Tangen (1997) mentioned Dinophysiaceae Stein, Amphisoleniaceae Lindemann and Oxyphysaceae Sournia. Hernández-Becerril *et al.* (2003) also included the family Citharistaceae, considering that the genus *Citharistes* has particular characteristics: the location of the 'phaeosomal chamber' in the hypotheca (not the cingulum) and the largest hypothecal plates which join two other smaller intercalary plates (six hypothecal) (Balech, 1971, 1988). Sournia (1986) recognized only 11 genera within the order, whereas Fensome *et al.* (1993) considered 14 genera. More recently, Gómez (2005a) included three families: Citharistaceae, Dinophysiaceae and Oxyphysaceae, with 12 genera. A revision of the order in Mexican waters was recently done by Hernández-Becerril *et al.* (2003), including historical, taxonomic and distribution information of the group, with a list of 90 taxa (species and varieties) in 11 genera and no illustrations; various records need to be confirmed. Finally, a recent report of a species of the genus *Dinofurcula* Kofoid & Skogsberg, *Dinofurcula* cf. *ultima* (Kofoid) Kofoid & Skogsberg, was made from the Gulf of Tehuantepec (Hernández-Becerril & Bravo-Sierrra, 2004). In this work we attempt to give contemporary information on species of the order Dinophysiales in the central and southern, tropical Mexican Pacific to produce a general guide to the group.

## MATERIALS AND METHODS

This work is based on analysis of preserved net samples collected during the period 1980–2006 on coasts of the central and southern, tropical Mexican Pacific (states of Jalisco, Colima, Micoacán, Guerrero, Oaxaca and Chiapas). Figure 1 shows sampling points. Phytoplankton net (47, 54, 60, 64 and 66 μm mesh) hauls (either horizontal or vertical, up to 80 m) were done to collect samples, which were preserved in formalin 4%. Parts of the material are deposited in: (1) the Instituto de Ciencias del Mar y Limnología, UNAM; (2) the Phycological collection, Laboratorio de Biología Acuática, Facultad de Biología, UMSNH; (3) the Department of Ecology (CUCBA, U de G); and (4) the Section of Algae, Herbarium of the Faculty of Sciences (FCME, UNAM).

Species were identified and measured in a light microscope (Carl Zeiss Axiolab and Olympus), in bright field, using fresh or rinsed material. Occasional observations were done by SEM (JEOL JMS) following conventional protocols (e.g. rinsing, drying and coating material). The terminology used was according to Fensome *et al.* (1993), Steidinger & Tangen (1997) and Hernández-Becerril & Meave (1999). References, dimensions and distribution information are provided for each species.

## RESULTS AND OBSERVATIONS

Forty-one species from five genera were identified. The systematic account, and references, measurements and distribution data are given for each species.

Division DINOFLAGELLATA (Bütschli) Fensome *et al.*
Class DINOPHYCEAE Pascher
Subclass DINOPHYSIPHYCIDAE Möhn ex Fensome *et al.*
Order DINOPHYSIALES Kofoid
Family DINOPHYSIACEAE Stein
Genus *Dinophysis* Ehrenberg
*Dinophysis acuminata* Claparède & Lachmann
(Figure 2)

*References*: Tai & Skogsberg, 1934, p. 433, figure 4; Balech, 1988, p. 39, pl. 5, figures 5–8; Hernández-Becerril, 1992, p. 102, figures 1–6; Larsen & Moestrup, 1992, p. 3, figure 1a–d; Steidinger & Tangen, 1997, p. 429, pl. 11; Balech, 2002, p. 130, figures 9–12.

*Conspicuous synonyms*: *Dinophysis borealis* Paulsen, *Dinophysis lachmanii* Paulsen, *Dinophysis boehmii* Paulsen (others in Gómez, 2005a).

Schiller, 1933, p. 120, Gómez, 2005a, p. 141.

*Remarks*: this species shows a high morphological variability, hence the difficulty to positively identify it and the number of synonyms. Balech (2002) considered at least two varieties, *Dinophysis acuminata* var. *acuminata*, and *D. acuminata* var. *lachmanii* Paulsen.

*Dimensions*: 59–65 μm (62 μm) length (L), 38–41 μm (40 μm) width (W).

*Local distribution*: localities in Jalisco, Colima, Michoacán and Oaxaca.

*General distribution*: temperate to tropical waters.

*Dinophysis amandula* Sournia
(Figure 3)

*References*: Sournia, 1973, p. 18; Balech, 1988, p. 50, pl. 10, figures 16 &17.

*Conspicuous synonyms*: *Phalacroma ovum* Schütt, *Dinophysis amygdala* Balech.

Schiller, 1933, p. 81, figures 73a–c.

*Dimensions*: 65–75 μm (71 μm) L, 54–58 μm (56 μm) W.

*Local distribution*: localities in Jalisco.

*General distribution*: warm waters (tropical to subtropical).

*Dinophysis apicata* (Kofoid & Skogsberg) Abé
(Figure 4)

*References*: Abé, 1967a, p. 73, figure 23c–g; Taylor, 1976, p. 33, figure 36.

*Basynonym*: *Phalacroma apicatum* Kofoid & Skogsberg

Kofoid & Skogsberg, 1928, p. 111, figure 10; Schiller, 1933, p. 76, figure 68a–c.

*Dimensions*: 92–100 μm (95 μm) L, 76–80 μm (78 μm) W.

*Local distribution*: one locality in Jalisco.

*General distribution*: tropical to subtropical.

*Remarks*: this species is closely related to *Dinophysis argus* (Stein) Abé, from which it can be distinguished for its 'more sharply conical epitheca', and its more developed left sulcal list (according to Abé, 1967a; Taylor, 1976).

*Dinophysis argus* (Stein) Abé
(Figure 5)

*References*: Abé, 1967a, p. 71, figure 23a,b; Taylor, 1976, p. 33, pl. 4, figure 35; Balech, 1988, p. 51, pl. 11, figures 7–10; Hernández-Becerril, 1988b, p. 426, figure 6.

*Basynonym*: *Phalacroma argus* Stein

Schiller, 1933, p. 74, figure 67a; Steidinger & Tangen, 1997, p. 437, pl. 14.

*Dimensions*: 90 μm L, 80 μm W.

*Local distribution*: localities in Jalisco, Michoacán and Guerrero.

*General distribution*: temperate, subtropical and tropical.

*Dinophysis caudata* Saville-Kent
(Figures 6 & 7)

*References*: Taylor, 1976, p. 34, pl. 6, figure 59; Balech, 1988, p. 45, pl. 8, figures 2 & 3; Hernández-Becerril, 1992, p. 106, figure 21; Larsen & Moestrup, 1992, p. 6, figure 3a,b; Steidinger & Tangen, 1997, p. 431, pl. 12; Balech, 2002, p. 132, figure 22.

*Synonym*: *Dinophysis homunculus* Stein

Stein, 1883, pl. 21, figures 1, 2 & 5–7.

*Dimensions*: 68–90 μm (75 μm) L, 62–72 μm (68 μm) W.

*Local distribution*: widely distributed from Jalisco to Chiapas.

*General distribution*: cosmopolitan in temperate to tropical waters.

*Dinophysis cuneus* (Schütt) Abé
(Figure 8)

*References*: Abé, 1967a, p. 68, figure 21a–h; Taylor, 1976, p. 35, pl. 5, figures 46 & 47; Dodge, 1985, p. 19; Balech, 1988, p. 51, pl. 11, figures 4–6; Rivera Tenenbaum *et al.*, 2006, p. 118.

*Phalacroma cuneus* Schütt

Jörgensen, 1923, p. 11, figure 11; Steidinger & Tangen, 1997, p. 439, pl. 14.

*Dimensions*: 87–92 μm (90 μm) L, 92–95 μm (93 μm) W.

*Local distribution*: localities in Jalisco and Michoacán.

*General distribution*: warm waters (tropical to subtropical).

*Dinophysis diegensis* Kofoid
(Figures 9 & 10)

*References*: Kofoid, 1907, p. 313, pl. 33, figures 57, 59–61; Balech, 1988, p. 185, pl. 7, figure 9; Hernández-Becerril, 1992, p. 106, figures 7–12.

*Dimensions*: 59–65 μm (62 μm) L, 34–38 μm (36 μm) W.

*Local distribution*: localities in Jalisco and Michoacán.

*General distribution*: temperate to tropical waters.

*Remarks*: This species is also considered more recently as a 'small cell' of *D. caudata* (Reguera & González-Gil, 2001; Dodge, 2003). Our Figure 10 shows a 'mature' cell, with own morphological characteristics, different from *D. caudata*.

*Dinophysis doryphora* (Stein) Abé
(Figure 11)

*References*: Norris & Berner, 1970, p. 161, figures 23–45; Taylor 1976, p. 35, pl. 4, figures 41 & 42; Balech, 1988,

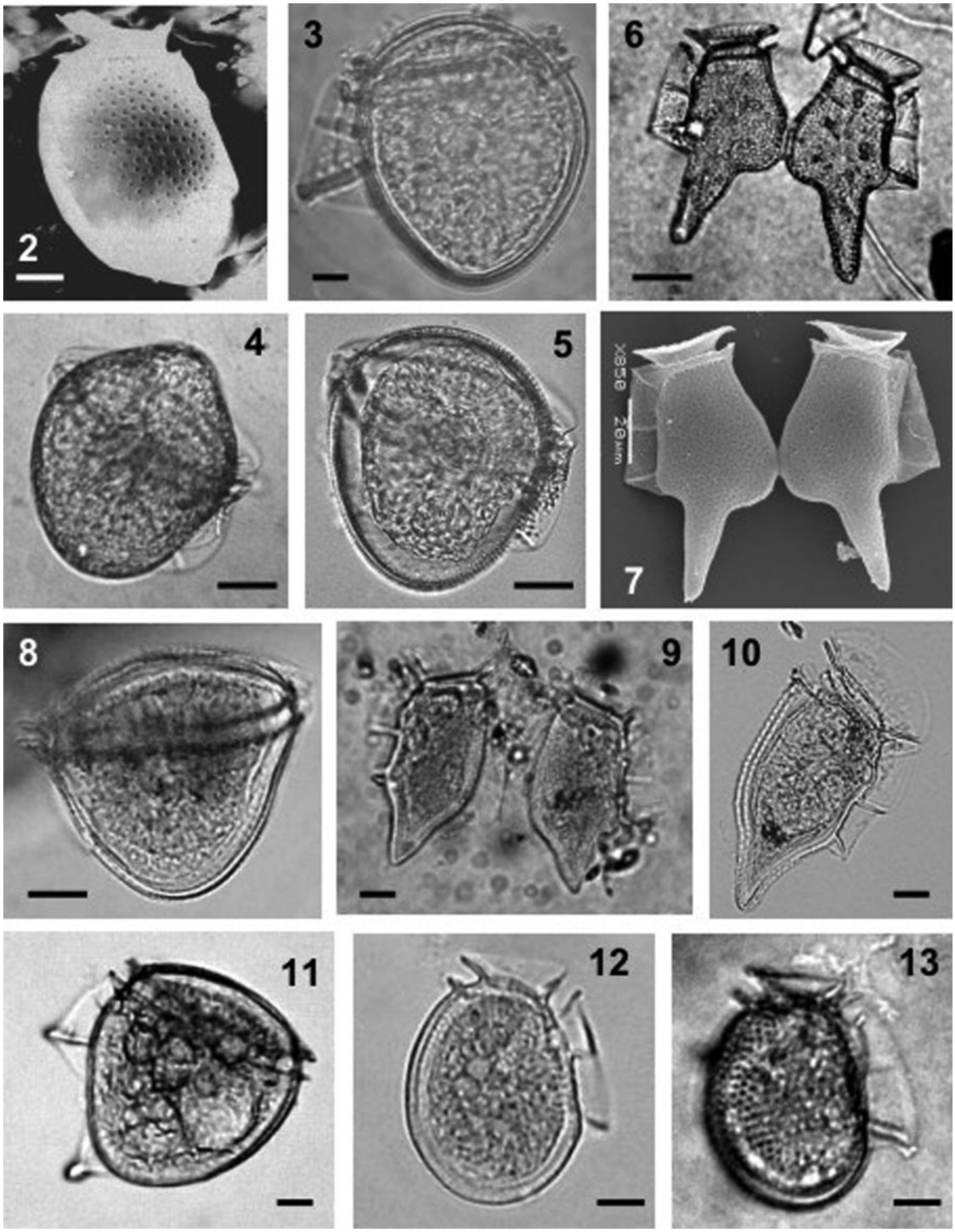


**Fig. 2–13.** Light microscopy (LM) and scanning electron microscopy (SEM). Figure 2. *Dinophysis acuminata*, SEM. Figure 3. *Dinophysis amandula*, LM. Figure 4. *Dinophysis apicata*, LM. Figure 5. *Dinophysis argus*, LM. Figures 6 & 7. *Dinophysis caudata*, LM and SEM, respectively. Figure 8. *Dinophysis cuneus*, LM. Figures 9 & 10. *Dinophysis diegensis*, a pair of cells and a single cell, LM. Figure 11. *Dinophysis doryphora*, LM. Figures 12 &13. *Dinophysis fortii*, LM. Scale bars: Figures 4–8, 20 μm; Figures 2,3,9–13, 10 μm.

p. 55, pl. 13, figures 11–13; Hernández-Becerril, 1988b, p. 426, figure 7; Licea *et al*., 1995, p. 19, pl. 6, figure 5.

*Basynonym*: *Phalacroma doryphorum* Stein

Jörgensen, 1923, p. 16, figure 17.

*Dimensions*: 69–79 μm (75 μm) L, 67–69 μm (68 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: tropical to subtropical form.

*Dinophysis favus* (Kofoid & Michener) Balech
(Figures 16 & 17)

*References*: Taylor, 1976, p. 36, pl. 5, figures 50 & 51.

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*Basynonym*: *Phalacroma favus* Kofoid & Michener

Jörgensen, 1923, p. 15, figure 16; Steidinger & Tangen, 1997, p. 439, pl. 14.

*Dimensions*: 64–71 μm (67 μm) L, 53–55 μm (54 μm) W.

*Local distribution*: Jalisco, Colima and Michoacán.

*General distribution*: distributed from temperate to tropical waters.

*Remarks*: this species resembles *Dinophysis hindmarchii* (Murray & Whitting) Balech, but whereas *D. favus* has its dorsal margin straight and is less rounded than *D. hindmarchii*, the posterior process of the latter is more rounded and short, and has its left sulcal list shorter, with a robust and large R3.

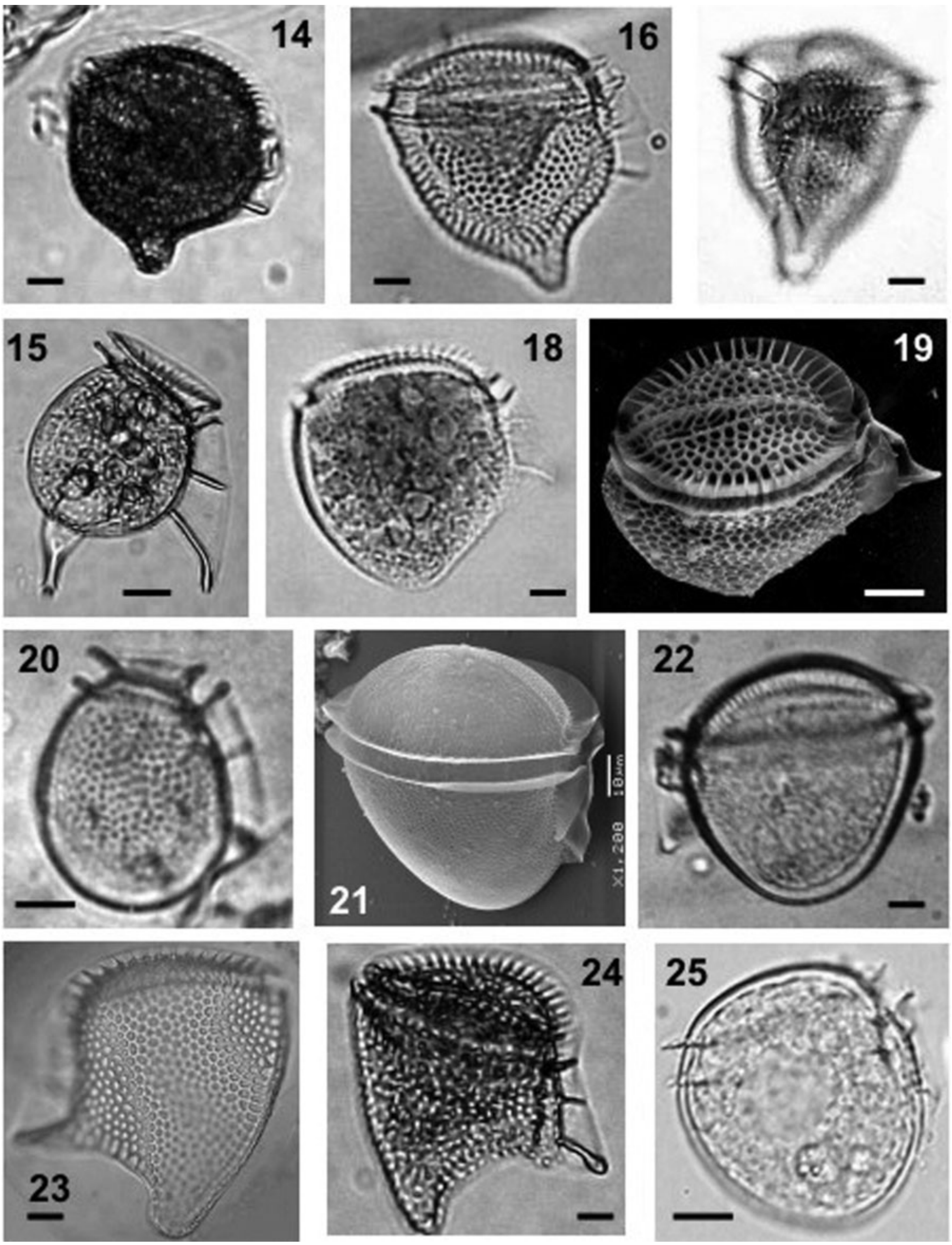


**Fig. 14–25.** Light microscopy (LM) and scanning electron microscopy (SEM). Figure 14. *Dinophysis hindmarchii*, LM. Figure 15. *Dinophysis hastata*, LM. Figures 16 & 17. *Dinophysis favus*, lateral and ventral views, respectively, LM. Figures 18 & 19. *Dinophysis mitra*, LM and SEM. Figure 20. *Dinophysis ovum*, LM. Figures 21 & 22. *Dinophysis porodictyum*, SEM and LM. Figures 23 & 24. *Dinophysis rapa*, LM. Figure 25. *Dinophysis rotundata*, LM. Scale bars: 10 μm.

*Dinophysis fortii* Pavillard
(Figures 12 & 13)

*References*: Tai & Skogsberg, 1934, p. 439, figure 5, pls. 11 & 12; Balech 1988, p. 43, pl. 6, figures 18 & 19; Hernández-Becerril, 1988b, p. 426, figures 4 & 35; Larsen & Moestrup, 1992, p. 6, figure 4a–c; Steidinger & Tangen, 1997, p. 431, pl. 11; Balech, 2002, p. 131, figure 15.

*Dimensions*: 59–62 μm (61 μm) L, 44–48 μm (46 μm) W.

*Local distribution*: from Jalisco to Guerrero.

*General distribution*: widely distributed in warm and temperate waters.

*Dinophysis hastata* Stein
(Figure 15)

*References*: Norris & Berner, 1970, p. 165, figures 45–59; Taylor, 1976, p. 37, pl. 5, figures 52–55; Dodge, 1985, p. 21; Balech, 1988, p. 54, pl. 13, figures 1–3; Larsen & Moestrup, 1992, p. 7, figure 5a,b; Steidinger & Tangen, 1997, p. 433, pl. 12.

*Dimensions*: 56–78 μm (67 μm) L, 53–64 μm (58 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: tropical to subtropical.

*Dinophysis hindmarchii* (Murray & Whitting) Balech
(Figure 14)

*References*: Balech 1988, p. 52, pl. 12, figure 4; Rivera Tenenbaum *et al.*, 2006, p. 148.

*Basynonym*: *Phalacroma hindmarchii* Murray & Whitting
Murray & Whitting, 1899, p. 330, pl. 5, figure 15.

*Dimensions*: 70 μm L, 65 μm W.

*Local distribution*: localities in Jalisco and Michoacán.

*General distribution*: distributed in tropical to subtropical waters.

*Dinophysis mitra* (Schütt) Abé
(Figures 18 & 19)

*References*: Taylor, 1976, p. 39, pl. 5, figure 49; Balech, 1988, p. 45, pl. 8, figures 9–11; Balech, 2002, p. 132, figures 20 & 21.

*Basynonym*: *Phalacroma mitra* Schütt
Steidinger & Tangen, 1997, p. 439, pl. 14.

*Dimensions*: 72–82 μm (77 μm) L, 63–65 μm (64.55 μm) W.

*Local distribution*: from Jalisco to Oaxaca.

*General distribution*: distributed from temperate to tropical waters.

*Dinophysis ovum* Schütt
(Figure 20)

*References*: Jörgensen, 1923, p. 22, figure 26; Schiller, 1933, p. 116, figure 109; Dodge, 1982, p. 53, figure 3J; Konovalova, 1998, p. 68, pl. 4, figure 13.

*Dimensions*: 42–51 μm (47 μm) L, 36–40 μm (38 μm) W.

*Local distribution*: localities in Jalisco, Colima and Michoacán.

*General distribution*: temperate to tropical waters.

*Dinophysis porodictyum* (Stein) Abé
(Figures 21 & 22)

*References*: Abé, 1967a, p. 61, figure 17a–f; Taylor, 1976, p. 40, pl. 4, figure 45; Dodge, 1985, p. 25; Balech, 1988, p. 50, pl. 10, figures 18–20.

*Basynonym*: *Phalacroma porodictyum* Stein
Jörgensen, 1923, p. 9, figure 6.

*Dimensions*: 70–78 μm (74 μm) L, 65–69 μm (67 μm) W.

*Local distribution*: from Jalisco to Oaxaca.

*General distribution*: temperate to tropical.

*Dinophysis rapa* (Stein) Abé
(Figures 23 & 24)

*References*: Taylor, 1976, p. 40, pl. 5, figure 48a,b, pl. 41, figure 48; Balech, 1988, p. 44, pl. 8, figures 6–8; Licea *et al.*, 1995, p. 21, pl. 6, figure 6.

*Basynonym*: *Phalacroma rapa* Stein
Jörgensen, 1923, p. 14, figure 14; Steidinger & Tangen, 1997, p. 439, pl. 14.

*Dimensions*: 87 μm L, 85 μm W.

*Local distribution*: localities in Jalisco, Colima and Michoacán.

*General distribution*: distributed from temperate to tropical waters.

*Dinophysis rotundata* Claparède & Lachmann
(Figure 25)

*References*: Tai & Skogsberg, 1934, p. 426, figure 2A–L; Balech, 1976, p. 91, figure 4O–T; Larsen & Moestrup, 1992, p. 9, figure 8a–d; Balech, 2002, p. 131, figures 16–19.

*Basynonym*: *Phalacroma rotundatum* (Claparède & Lachmann) Kofoid & Michener
Jörgensen, 1923, p. 5, figure 2; Steidinger & Tangen, 1997, p. 439, pl. 14.

*Synonym*: *Dinophysis whittingae* Balech
Balech, 2002, p. 131.

*Dimensions*: 42–50 μm (46 μm) L, 42–51 μm (47 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: widely distributed in temperate and warm waters.

*Dinophysis schuettii* Murray & Whitting
(Figure 26)

*References*: Norris & Berner, 1970, p. 179, figures 92–112; Taylor, 1976, p. 41, pl. 6, figures 65 & 66; Balech, 1988, p. 53, pl. 12, figures 7–9; Hernández-Becerril, 1992, p. 107, figures 13–18; Steidinger & Tangen, 1997, p. 433, pl. 12.

*Dimensions*: 41–47 μm (44 μm) L, 36–39 μm (37 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: tropical to subtropical.

Genus *Histioneis* Stein
*Histioneis biremis* Stein
(Figure 61)

*References*: Stein, 1883, pl. 22, figure 13; Schiller, 1933, p. 254, figure 250; Taylor, 1976, p. 44, pl. 9, figure 89.

*Dimensions*: 84 μm L, 50 μm W.

*Local distribution*: localities in Michoacán.

*General distribution*: tropical to subtropical.

*Histioneis crateriformis* Stein
(Figure 63)

*References*: Stein, 1883, pl. 22, figures 5 & 6; Balech, 1971, p. 15, pl. 3, figures 40–46; Balech, 1988, p. 63, pl. 15, figure 8; Rivera Tenenbaum *et al.*, 2006, p. 126.

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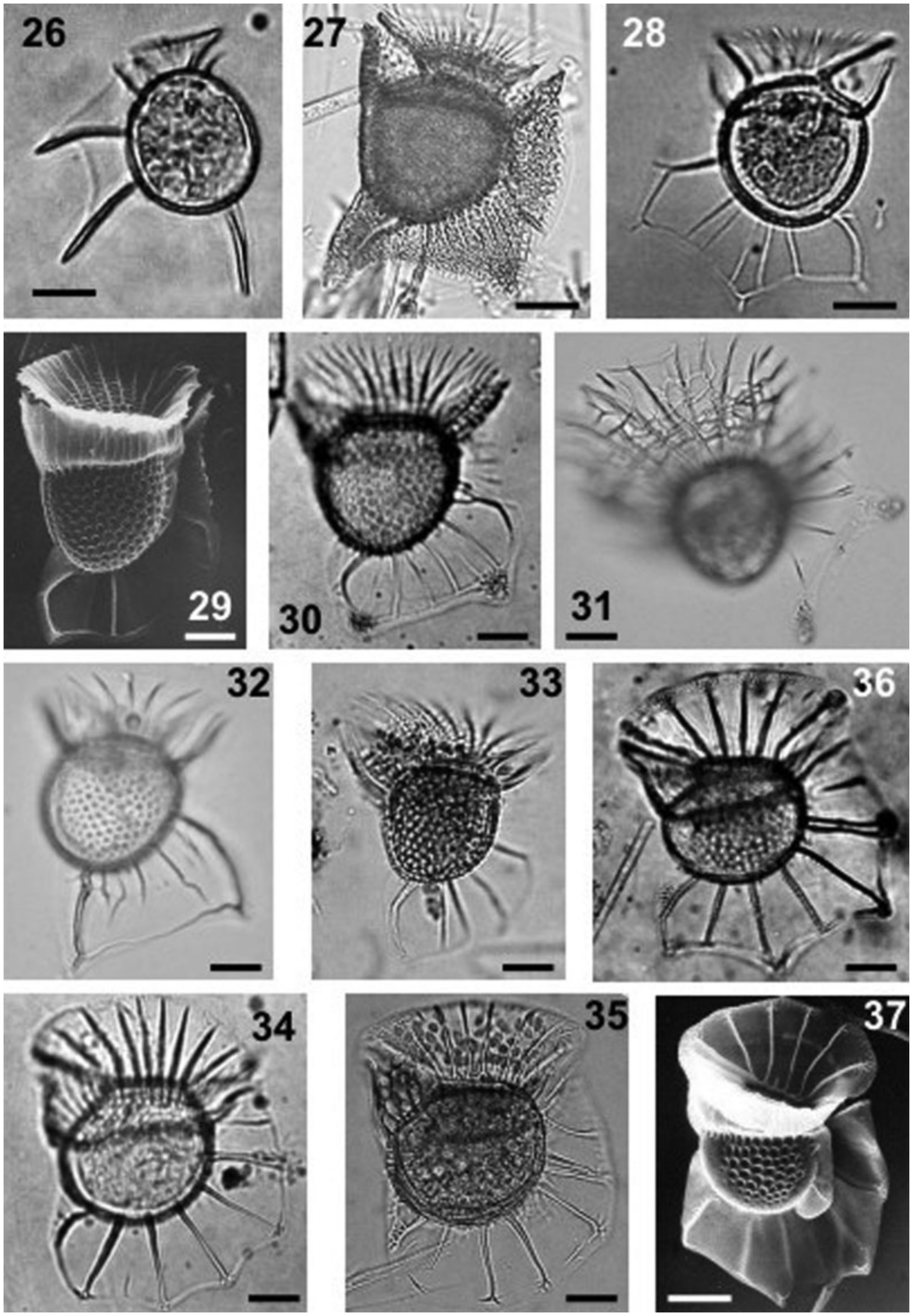


**Fig. 26–37.** Light microscopy (LM) and scanning electron microscopy (SEM). Figure 26. *Dinophysis schuettii*, LM. Figure 27. *Ornithocercus formosus*, LM. Figure 28. *Ornithocercus magnificus*, LM. Figures 29 & 30. *Ornithocercus heteroporoides*, SEM and LM. Figure 31. *Ornithocercus splendidus*, LM. Figure 32. *Ornithocercus heteroporus*, LM. Figure 33. *Ornithocercus cristatus*, LM. Figures 34 & 35. *Ornithocercus orbiculatus*, LM. Figures 36 & 37. *Ornithocercus steinii*, LM and SEM. Scale bars: Figures 27,28,31,34–37, 20 μm; Figures 26,29,30,32,33, 10 μm.

*Synonym*: *Parahistioneis crateriformis* (Stein) Kofoid & Skogsberg

Schiller, 1933, p. 211, figure 200a,b.

*Dimensions*: 84 μm L, 66 μm W.

*Local distribution*: localities in Colima.

*General distribution*: tropical to subtropical.

*Histioneis para* Murray & Whitting
(Figure 65)

*References*: Murray & Whitting, 1899, pl. 32, figure 4a,b; Schiller, 1933, p. 215, figure 205a,b; Balech, 1988, p. 65, pl. 15, figure 4; Gómez, 2005b, figure 30; Rivera Tenenbaum *et al.*, 2006, p. 134.

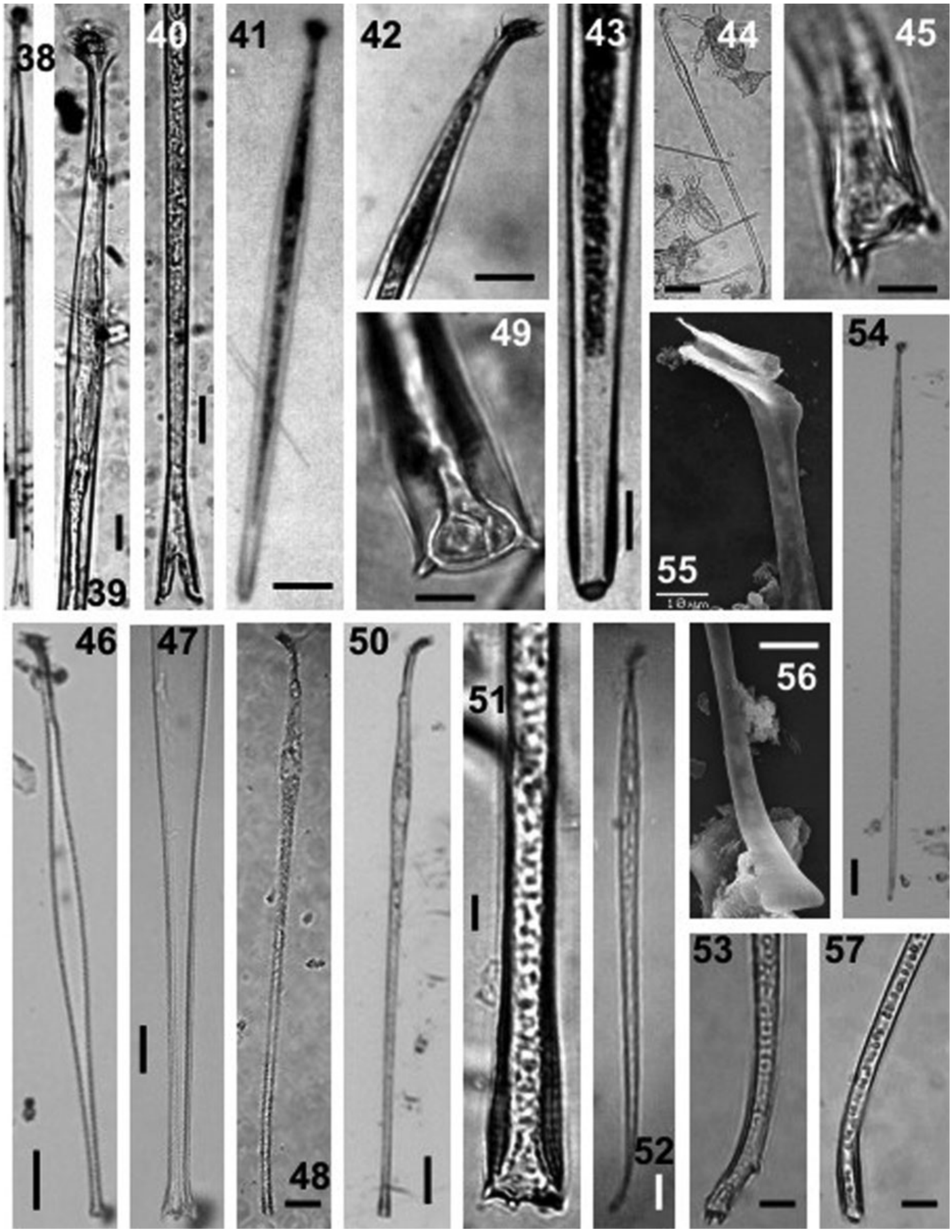


**Fig. 38–57.** Light microscopy (LM) and scanning electron microscopy (SEM). Figures 38–40. *Amphisolenia michoacana*, complete cell, anterior and posterior parts, respectively, LM. Figures 41–43. *Amphisolenia fusiformis*, complete cell, anterior and posterior parts, respectively, LM. Figures 44 & 45. *Amphisolenia palmata*, complete cell and terminal process, LM. Figures 46 & 47. *Amphisolenia palaeotheroides*, complete cell and terminal process, LM. Figures 48 & 49. *Amphisolenia lemmermanni*, complete cell and terminal process, LM. Figures 50 & 51. *Amphisolenia rectangulata*, complete cell and terminal process, LM. Figures 52 & 53. *Amphisolenia bidentata*, complete cell and terminal process, LM. Figures 54–57. *Amphisolenia truncata*, complete cell, anterior and posterios parts, respectively, LM. Scale bars: Figure 44, 100 μm; Figures 38,41,46,48,50,52,54, 50 μm; Figures 39,40,42,47, 20 μm; Figures 43,45,49,51,53, 55–57, 10 μm.

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*Synonym*: *Parahistioneis para* (Murray & Whitting) Kofoid & Skogsberg
Kofoid & Skogsberg, 1928, p. 601, figure 85, 6; Taylor, 1976, p. 53, pl. 9, figures 87 & 88, pl. 41, figure 490.
*Dimensions*: 85 μm L, 35 μm W.
*Local distribution*: localities in Jalisco and Michoacán.
*General distribution*: tropical to subtropical.

*Histioneis pulchra* Kofoid
(Figure 64)

*References*: Kofoid, 1907, p. 205, pl. 16, figure 99; Taylor, 1976, p. 47, pl. 10, figure 95.
*Dimensions*: 130 μm L, 48 μm W.
*Local distribution*: localities in Jalisco.
*General distribution*: tropical to subtropical.

*Histioneis schillerii* Böhm
(Figure 62)

*References*: Böhm, 1931, p. 499, figures 5 & 6; Schiller, 1933, p. 244, figure 238a,b; Hernández-Becerril, 1988b, p. 427, figure 13; Gómez, 2005b, figure 16.
*Dimensions*: 102 μm L, 59 μm W.
*Local distribution*: localities in Michoacán.
*General distribution*: tropical to subtropical.
*Remarks*: this species is considered as a synonym of *H. mitchellana* Murray & Whitting by Taylor (1976).

Genus *Metaphalacroma* Tai & Skogsberg
*Metaphalacroma skogsbergii* Tai
(Figure 60)

*References*: Tai & Skogsberg, 1934, p. 458, figure 11; Balech, 1988, p. 38, pl. 5, figures 3 & 4.
*Dimensions*: 58 μm L, 53 μm W.
*Local distribution*: localities in Michoacán.
*General distribution*: temperate to subtropical.
New record for the Mexican Pacific.

Genus *Ornithocercus* Stein
*Ornithocercus cristatus* Matzenauer
(Figure 33)

*References*: Matzenauer, 1933, p. 447, figure 11; Balech, 1967, p. 93, pl. 2, figures 38–46.
*Synonyms*: *Dinophysis moresbyensis* Wood
Wood, 1963a, p. 7, figure 18.
? *Ornithocercus carpentariae* Wood
Wood, 1963b, p. 5, figure 11.
*Dimensions*: 65 μm L, 38 μm W.
*Local distribution*: localities in Jalisco, Michoacán, Oaxaca and Chiapas.
*General distribution*: tropical to subtropical.

*Ornithocercus formosus* Kofoid & Michener
(Figure 27)

*References*: Kofoid & Skogsberg, 1928, p. 577, figure 91, pl. 17, figures 4 & 5; Schiller, 1933, p. 207, figure 197a–d; Taylor, 1976, p. 48, pl. 7, figure 75.
(as *Ornithocercus quadratus* in Hernández-Becerril, 1988b, p. 427, figures 11 & 41).
*Dimensions*: 98 μm L, 70 μm W.
*Local distribution*: one locality in Jalisco.
*General distribution*: tropical to subtropical.

*Ornithocercus heteroporoides* Abé
(Figures 29 & 30);

*Reference*: Abé, 1967b, p. 83, figure 29a–c.
*Dimensions*: 66–69 μm L, 61–63 μm W.
*Local distribution*: localities in Michoacán.
*General distribution*: temperate to subtropical.
*Remarks*: this species and *Ornithocercus heteroporus* Kofoid are closely related, however, *O. heteroporoides* appears with a body larger and its cingular lists more developed than the former. *Ornithocercus heteroporus* has its left cingular list triangular, with no lobes.

*Ornithocercus heteroporus* Kofoid
(Figure 32)

*References*: Kofoid, 1907, p. 207, pl. 12, figure 70; Abé, 1967b, p. 81, figure 28a,b; Taylor, 1976, p. 48, pl. 8, figure 83; Balech, 1988, p. 59, pl. 14, figure 4; Steidinger & Tangen, 1997, p. 436, pl. 13.
*Synonym*: *Ornithocercus biclavatus* Wood
Wood, 1954, p. 211, figure 66.
*Dimensions*: 66 μm L, 55 μm W.
*Local distribution*: from Jalisco to Chiapas.
*General distribution*: tropical to subtropical.

*Ornithocercus magnificus* Stein
(Figure 28)

*References*: Abé, 1967b, p. 88, figure 32a–d; Norris, 1969, p. 178, figures 1–15; Taylor 1976, p. 49, pl. 7, figures 67–69, pl. 42, figure 505a,b; Balech, 1988, p. 61, pl. 14, figures 7 & 8; Steidinger & Tangen, p. 436, pl. 13.
*Dimensions*: 85–96 μm (90 μm) L, 43–50 μm (48 μm) W.
*Local distribution*: from Jalisco to Chiapas.
*General distribution*: tropical to subtropical.

*Ornithocercus orbiculatus* Kofoid & Michener
(Figures 34 & 35)

*References*: Kofoid & Skogsberg, 1928, p. 559, pl. 17, figure 7; Schiller, 1933, p. 203, figure 193; Balech, 1988, p. 61, pl. 15, figure 2.
*Dimensions*: 90–95 μm (93 μm) L, 88–94 μm (92 μm) W.
*Local distribution*: localities in Jalisco and Michoacán.
*General distribution*: tropical to subtropical.

*Ornithocercus splendidus* Schütt
(Figure 31)

*References*: Kofoid & Skogsberg, 1928, p. 521, figures 77 & 85, pl. 16, figures 2 & 4, pl. 17, figure 3; Abé, 1967b, p. 81, figure 27a–c; Taylor, 1971, figures 13–17; Taylor, 1976, p. 52, pl. 8, figures 85 & 86, pl. 40, figure 486, pl. 42, figure 504; Balech, 1988, p. 59, pl. 14, figures 5 & 6; Steidinger & Tangen, 1997, p. 437, pl. 13.
*Dimensions*: 105 μm L, 68 μm W.
*Local distribution*: from Jalisco to Chiapas.
*General distribution*: tropical to subtropical.

*Ornithocercus steinii* Schütt
(Figures 36 & 37)

*References*: Schiller, 1933, p. 202, figure 192a–f; Abé, 1967b, p. 94, figure 35a–c; Taylor, 1976, p. 52, pl. 7, figures 72 & 73; Balech, 1977, p. 26, figures 1–14; Balech, 1988, p. 61, pl. 15, figure 1; Steidinger & Tangen, p. 437, pl. 13.

*Synonym*: *Ornithocercus serratus* Kofoid

Kofoid, 1907, p. 207, figure 95; Jörgensen, 1923, p. 38, figure 52.

*Dimensions*: 98–108 μm (105 μm) L, 88–94 (92 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: tropical to subtropical.

Family AMPHISOLENIACEAE Lindemann
Genus *Amphisolenia* Stein
*Amphisolenia bidentata* Schröder
(Figures 52 & 53)

*References*: Schiller, 1933, p. 178, figure 169a–e; Abé, 1967b, p. 111, figure 42a–k; Taylor, 1976, p. 28, pl. 2, figures 21 & 22, pl. 3, figures 21b & 22b; Balech, 1988, p. 69, pl. 17, figures 2, 3 & 13; Hernández-Becerril, 1988a, p. 521, figures 3–5; Steidinger & Tangen, 1997, p. 426, pl. 10.

*Dimensions*: 667–754 μm (726 μm) L, 18–25 μm (21 μm) W.

*Local distribution*: from Jalisco to Chiapas.

*General distribution*: tropical to subtropical.

*Amphisolenia fusiformis* Ceballos-Corona
& Hernández-Becerril sp. nov.
(Figures 41–43 & 66A–C)

*Diagnosis*: *cellula solitaria, crassa. Cellula fusiforme, elongata. Testa conspicua, episoma plana. Alae cingulares anteriores et posteriores parvae. Alae sulcales parvae. Collum rectus. Corpo medio leniter inflato, leniter plus angustus ex extremitas posterior. Margines rectae et expolitae. Extremitas posterior rotunda, habens ora conspicua, spinae vel processus terminalis carentes. Chloroplasti carentes*?

*Description*: cell found solitary, large. Cell fusiform, elongate and uniformly wider at the third part of the body (mid-body), then tapering slightly toward caudal part. Head conspicuous, reduced epitheca, cingular lists approximately equal, little developed. Neck short and sulcal lists also reduced. Margins of the body are straight and smooth. The terminal portion ends somewhat rounded, with a perceptible rim and no process, spines or spinules. No chloroplasts are apparent. One single cell found.

*Dimensions*: 516 μm L, 26 μm W.

*Iconotype*: Figure 66A–C has been chosen as Iconotype of the species.

*Type locality*: Bahia de Maruata, Michoacán, Mexico (18°13′36″N 103°11′21″ W).

*Etymology*: the species has been named for its fusiform shape.

*Amphisolenia michoacana* Ceballos-Corona
& Hernández-Becerril sp. nov.
(Figures 38–40 & 67A–C)

*Diagnosis*: *cellula solitaria, crassa. Cellula elongata. Testa conspicua, episoma plana. Alae cingulares anteriores et posteriores parvae. Alae sulcales parvae. Collum rectus et brevis, umerus conspicuus. Corpo medio inflato, leniter plus angustus ex extremitas posterior. Extremitas posterior curvata tenera et bifurcata. Duo processus posteriores, breves, aequales, curvatus. Spinae parvae terminalis praesentes ex processus posteriores. Chloroplasti carentes*?

*Description*: solitary cell, very elongate and inflated about the third anterior part (mid-body). Conspicuous head, reduced epitheca, anterior and posterior cingular lists

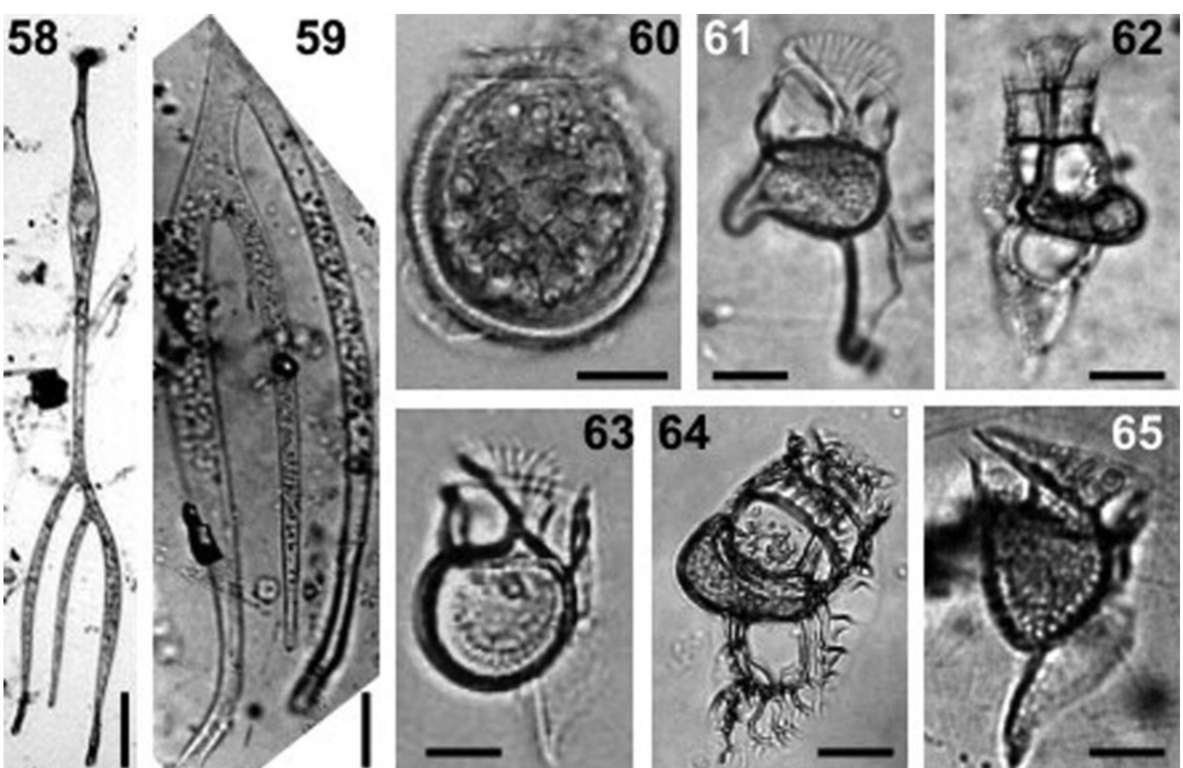


**Fig. 58–65.** Light microscopy. Figures 58 & 59. *Amphisolenia thrinax*. Figure 60. *Metaphalacroma skogsbergi*. Figure 61. *Histioneis biremis*. Figure 62. *Histioneis schilleri*. Figure 63. *Histioneis crateriformis*. Figure 64. *Histioneis pulchra*. Figure 65. *Histioneis para*. Scale bars: Figure 58, 100 μm; Figure 59, 50 μm; Figures 60–65, 20 μm.

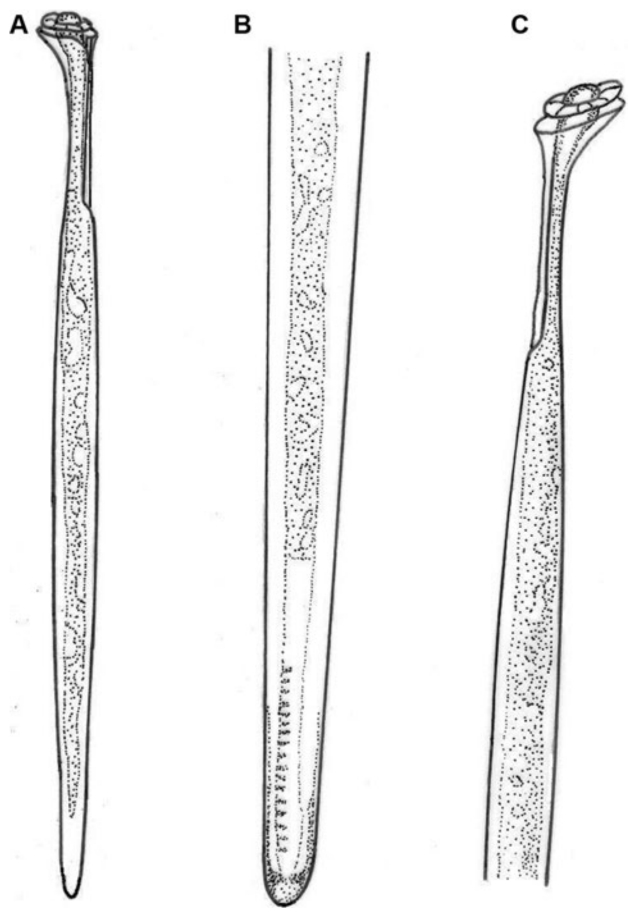


**Fig. 66A–C.** *Amphisolenia fusiformis*, complete cell, posterior and anterior parts, respectively.

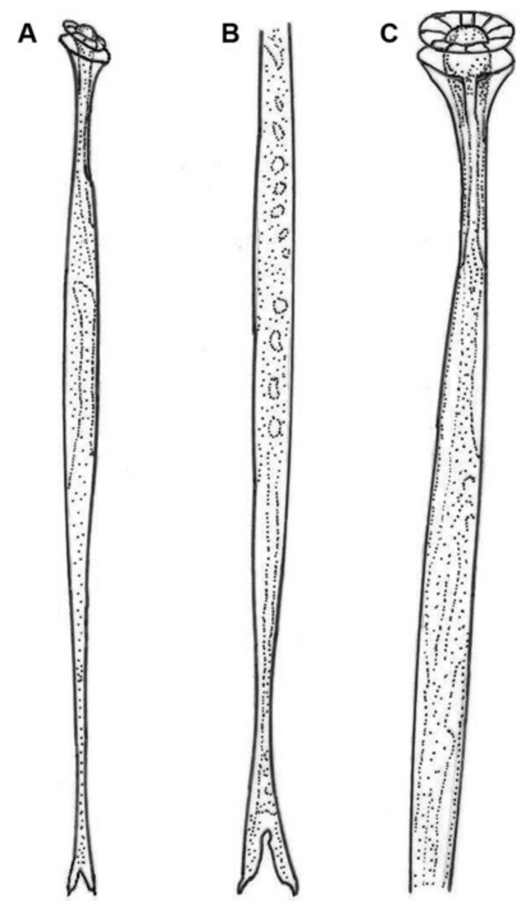


**Fig. 67A–C.** *Amphisolenia michoacana*, complete cell, posterior and anterior parts, respectively.

similar, poorly developed. Neck relatively straight and short, with sulcal lists reduced, shoulder conspicuous. Middle part of the body (mid-body) uniformly wider, becoming smoothly narrower toward the caudal part. The caudal portion is delicately curved at its base and bifurcates into two short, symmetric processes, each of them carries a single spine at the tip. Some inclusions in the cell were apparent. A single cell was found.

*Dimensions*: 625 μm L, 21 μm W.

*Iconotype*: Figure 67A–C has been chosen as iconotype of the species.

*Type locality*: Bahia de Maruata, Michoacán, Mexico (18°13′36″N 103°11′21″ W).

*Etymology*: the species has been named because it was originally found in the Mexican State of Michoacán.

*Amphisolenia lemmermannii* Kofoid
(Figures 48 & 49);

*References*: Schiller, 1933, p. 179, figure 170a,b; Balech, 1988, p. 70, pl. 17, figures 8 & 12; Hernández-Becerril, 1988b, p. 427, figure 14.

*Dimensions*: 671–790 μm L, 20–22 μm W.

*Local distribution*: localities in Jalisco, Colima and Michoacán.

*General distribution*: tropical to subtropical.

*Amphisolenia palaeotheroides* Kofoid
(Figures 46 & 47)

*References*: Kofoid, 1907, p. 199, pl. 14, figure 84; Kofoid & Skogsberg, 1928, p. 472, figure 56, pl. 11, figures 2–4; Schiller, 1933, p. 181, figure 172; Rampi, 1952, figure 5; Taylor, 1976, p. 29, pl. 2, figure 31, pl. 3, figure 31b.

*Dimensions*: 480 μm L, 25 μm W.

*Local distribution*: localities in Michoacán.

*General distribution*: tropical to subtropical.

*Amphisolenia palmata* Stein
(Figures 44 & 45)

*References*: Stein, 1883, pl. 21, figures 11–15; Schiller, 1933, p. 180, figure 171a,b; Abé, 1967b, p. 113, figure 43a–k; Balech 1988, p. 69, pl. 17, figures 4–7.

*Dimensions*: 780 μm L, 25 μm W.

*Local distribution*: localities in Jalisco.

*General distribution*: warm waters (tropical to subtropical).

*Amphisolenia rectangulata* Kofoid
(Figures 50 & 51)

*References*: Kofoid, 1907, p. 200, pl. 14, figure 83; Abé, 1967b, p. 109, figure 41a–d; Balech 1988, p. 186, pl. 83, figures 3–6.

*Dimensions*: 650–780 μm L, 20 μm W.

*Local distribution*: localities in Jalisco.

*General distribution*: tropical to subtropical.

*Amphisolenia thrinax* Schütt
(Figures 58 & 59)

*References*: Schiller, 1933, p. 183, figure 176; Abé, 1967b, p. 114, figure 44a–f; Taylor, 1976, p. 30, pl. 2, figure 20; Balech, 1988, p. 187, pl. 18, figures 5, 6 & 9.

*Dimensions*: 876 μm L, 48 μm W.

*Local distribution*: localities in Jalisco and Colima.

*General distribution*: tropical to subtropical.

New record for the Mexican Pacific.

*Amphisolenia truncata* Kofoid & Michener
(Figures 54–57)

*References*: Jörgensen, 1923, p. 40, figure 58; Schiller, 1933, p. 178, figure 168.

*Dimensions*: 800 μm L, 25 μm W.

*Local distribution*: localities in Jalisco and Colima.

*General distribution*: tropical to subtropical.

# DISCUSSION

## Diversity and distribution

A total of 41 species included in five genera of the order Dinophysiales was reported. The largest diversity was due to the genus *Dinophysis*, with 18 species, followed by *Amphisolenia* (9 species) and *Ornithocercus* (8 species). Two new records are annotated and illustrated: *Metaphalacroma skogsbergii*, and *Amphisolenia thrinax*. And additionally, the species *Amphisolenia rectangulata*, *A. palmata*, *A. truncata*, *Dinophysis apicata*, *D. hindmarchii*, *Histioneis biremis*, *H. crateriformis*, *H. pulchra*, *Ornithocercus cristatus*, *O. heteroporoides* and *O. orbiculatus* are illustrated for the first time in the waters of the Mexican Pacific. In our study, two species of the genus *Amphisolenia* were newly described: *Amphisolenia fusiformis* and *A. michoacana*.

Species found in our study that are associated to the production of okadaic acid or dinophysistoxin (which causes DSP) (Taylor *et al.*, 2003) were basically *Dinophysis* species, such as *D. acuminata*, *D. caudata*, *D. fortii*, *D. mitra* and *D. rotundata*, however, no case of high cell densities of these species or poisoning (DSP) was reported in the study area or in the study period.

The diversity of the order Dinophysiales appears to be relatively low in our study, especially for samples studied that were obtained from a large area in the Mexican Pacific, and with respect to the more than 200 species recognized in *Dinophysis* (Sournia, 1986), or the list of 145 species of *Dinophysis* + *Phalacroma* (104 + 41) and 65 species of *Histioneis* (Gómez, 2005a). The revision of the order in Mexican waters (including both Mexican littorals, the Atlantic—Gulf of Mexico and the Mexican Caribbean—and the Pacific) listed 90 taxa (species and varieties) in 11 genera (Hernández-Becerril *et al.*, 2003), and more recently, Okolodkov & Gárate-Lizárraga (2006) provided a list of dinoflagellates from the Mexican Pacific (with no illustrations) and included 41 species of *Dinophysis*, 12 *Ornithocercus*, ten *Histioneis* and nine *Amphisolenia* species.

From the former two papers, it is clear that more studies need to be carried out to confirm occurrences of certain species and which records seem doubtful, for instance *Dinophysis norvegica* and *D. sacculus*, with limited distribution to the Mediterranean Sea and the North Atlantic, respectively. And although introduction of species (particularly dinoflagellates) may be possible, these two species show preferences for colder waters. We note the lack of a complete, contemporary account of dinoflagellates (with descriptions, measurements and illustrations) from Mexican waters.

The species assemblages found in our study have an important tropical and subtropical component (28 species), whereas the species with temperate to tropical distribution are 13. Species of definite cold-water affinity were not represented. This is consistent with other works in other close or adjacent areas such as the Gulf of California and the Gulf of Tehuantepec (Hernández-Becerril, 1988b, c; Licea *et al.*, 1995; Meave & Hernández-Becerril, 1998).

## Taxonomy

There is an ongoing debate on the distinction and reliable characters with taxonomic value of the two closely related genera *Dinophysis* and *Phalacroma*. As pointed out above, the simultaneous and independent transfer of species of *Phalacroma* to *Dinophysis* (Abé, 1967a; Balech, 1967), merged them in one single genus (see list of basynonyms in many *Dinophysis* species cited here). According to traditional morphological criteria, the presence of a dome-shaped epitheca, which is conspicuous in *Phalacroma*, was one of the reasons to separate both genera (Stein, 1883; Kofoid & Skogsberg, 1928), although later detailed morphological studies, especially at the sulcus level, provided evidence that no significant difference existed between them (Abé, 1967a; Balech, 1967).

Hallegraeff & Lucas (1988) proposed additional criteria to separate both genera: morphology of the cells (areolation of the thecae, megacytic forms), type of nutrition (essentially photosynthetic or heterotrophic forms) and toxicity and ecology (coastal and oceanic forms); Steindinger & Tangen (1997) also considered the two genera apart. However, it is not easy to recognize the reproductive and nutritious biology, or the ecological characteristics of the species, moreover if they cannot be cultured, and the traditional morphological criteria are not practical or convincing.

Molecular phylogenies are based in protocols using single cells for PCR and have been carried out for a very limited number of species of members of the Dinophysiales, basically *Dinophysis* (Rehnstam-Holm *et al.*, 2002; Edvarsen *et al.*, 2003). In the phylogenetic trees produced, the separation of one heterotroph species, *D. rotundata* is significantly supported, but no conclusions on the possible reinstatement of *Phalacroma* were drawn (Edvarsen *et al.*, 2003). Until new insights (morphological, ultrastructural, ecological, molecular and evolutive) are available on this conflict, we will consider that there are no significant differences between both genera and will use the name *Dinophysis* in priority.

On the other hand, we also consider that species of the genus *Parahistioneis* Kofoid & Skogsberg, established to accommodate certain species of *Histioneis* with 'distinct' morphological characters (lack of 'rib' in the posterior cingular list and anterior cingular list with no peduncular shape) (Kofoid & Skogsberg, 1928) are undistinguishable from species of *Histioneis*; Balech (1971, 1988) mentioned that these characters are variable and show overlap, therefore he proposed *Parahistioneis* as a synonym of *Histioneis*. We followed these former criteria.

Smaller and slightly different forms of *Dinophysis*, which were described as new species in the past, are now currently considered as synonyms of other species, among them:

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*Dinophysis dens* Pavillard, *D. skagii* Paulsen, *D. parvula* (Schütt) Balech, and even *D. diegensis* are related to *Dinophysis acuta* Ehrenberg, *D. acuminata*, *D. rotundata* and *D. caudata*, respectively, as part of complex life cycles (Hernández-Becerril, 1992; MacKenzie, 1992; Reguera & González-Gil, 2001; Dodge, 2003; Gómez, 2005a).

This may also be the case for many other forms of the Dinophysiales, in particular *Ornithocercus*. Species such as *O. cristatus* might be considered as 'gametes', cysts or life stages (schizonts or immature cells) of other species, although current evidence is still lacking (e.g. small cells inside larger ones, intergrades). Hernández-Becerril & Bravo-Sierra (2004) recently showed smaller cells of a member of the Dinophysiales, *Dinofurcula* cf. *ultima* and speculated on this subject.

The two species newly described here, on the basis of one specimen, *Amphisolenia fusiformis* and *Amphisolenia michoacana*, are absolutely conspicuous and unmistakably recognized, due to their size and general outline together. *Amphisolenia fusiformis* has a shape completely different from any other species of the genus: no other species is so uniform in width, which only close to the caudal part becomes slightly narrower, with a rounded end and a rim at the very end, and no projections or spines; most species of the genus show a wider mid-body. A species superficially similar is *Amphisolenia laticincta* Kofoid, which is much smaller than *A. fusiformis* and its body becomes considerably narrower toward its end; additionally its cingular lists are more separated from each other than in *A. fusiformis*.

Regarding *Amphisolenia michoacana*, the anterior part of the body is similar to many other species of the genus (head, neck and wider mid-body), but in this species the caudal portion bifurcates into two short symmetric processes, which do not spread widely or become branch-like as for example in *A. bifurcata* Murray & Whitting; the processes in *A. michoacana* show a single spine at the end. No species is like *Amphisolenia michoacana* regarding these characters. No closely related species are apparent in the extant species of *Amphisolenia*. Cell inclusions are present in *Amphisolenia michoacana*, although they are not apparent in *Amphisolenia fusiformis*. In other *Amphisolenia* species various endosymbionts (Cyanobacteria, Bacteria and Eukariots) have been found (Lucas, 1991).

These two species, as with most species of the genus, are extremely rare (only one specimen of each detected); many species have been described on the basis of one single specimen (Kofoid, 1907; Wood, 1954; Hernández-Becerril & Meave, 1999). But until detailed field studies are done on some genera of the order (*Histioneis*, *Amphisolenia*, etc.) (Gómez, 2005a), we will not be able to understand about life cycles and consequently the number of 'recognized' species will remain the same.

## ACKNOWLEDGEMENTS

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