



## **Marine planktonic dinophysoid dinoflagellates (order Dinophysales): 60 years of species-level distributions in Australian waters**

Authors: Hallegraeff, Gustaaf M., Eriksen, Ruth S., Davies, Claire H., and Uribe-Palomino, Julian

Source: Australian Systematic Botany, 35(6) : 469-500

Published By: CSIRO Publishing

URL: <https://doi.org/10.1071/SB21023>

---

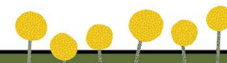
BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



# Marine planktonic dinophysoid dinoflagellates (order Dinophysales): 60 years of species-level distributions in Australian waters

Gustaaf M. Hallegraef<sup>A,\*</sup> , Ruth S. Eriksen<sup>A,B</sup> , Claire H. Davies<sup>B</sup> and Julian Uribe-Palomino<sup>C</sup>

For full list of author affiliations and declarations see end of paper

**\*Correspondence to:**

Gustaaf M. Hallegraef  
Institute for Marine and Antarctic Studies,  
University of Tasmania, Private Bag 129,  
Tas. 7001, Australia  
Email: [gustaaf.hallegraef@utas.edu.au](mailto:gustaaf.hallegraef@utas.edu.au)

**Handling Editor:**

Darren Crayn

**Received:** 24 June 2021

**Accepted:** 10 November 2022

**Published:** 9 December 2022

**Cite this:**

Hallegraef GM *et al.* (2022)  
*Australian Systematic Botany*  
35(6), 469–500. doi:[10.1071/SB21023](https://doi.org/10.1071/SB21023)

© 2022 The Author(s) (or their employer(s)). Published by CSIRO Publishing.

This is an open access article distributed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License ([CC BY-NC-ND](https://creativecommons.org/licenses/by-nc-nd/4.0/))

OPEN ACCESS

## ABSTRACT

We reviewed 9350 Australian species-level records and confirmed 64 species of the marine planktonic dinoflagellate genera *Dinophysis* Ehrenb. (17 species), *Phalacroma* F.Stein (12), *Metaphalacroma* L.S.Tai (1), *Pseudophalacroma* Jörg. (1), *Ornithocercus* F.Stein (7), *Histioneis* F.Stein (11 spp.), *Parahistioneis* Kof. & Skogsb. (4), *Histiophysis* (Kof. & Mich.) Kof. & Skogsb. (1), *Citharistes* F.Stein (2) and *Amphisolenia* F.Stein (8), from the period 1938–2019. The widespread *D. acuminata* Clap. & J.Lachm., *D. acuta* Ehrenb., *D. caudata* Kent, *D. fortii* Pavill., and *D. tripos* Gourret have attracted attention as causative organisms of diarrhetic shellfish poisoning in temperate Australian waters. We discriminate between *Dinophysis* and *Phalacroma*. We newly report from Australian waters *O. assimilis* Jörg., *Metaphalacroma skogsbergii* L.S.Tai, *Parahistioneis pieltainii* Osorio-Taffal, *Amphisolenia extensa* Kof., *A. inflata* G.Murr. & Whitt. and *A. rectangulata* Kof. We rediscovered *Histiophysis rugosa* (Kof. & Mich.) Kof. & Skogsb. here illustrated with two cells from the Coral Sea. The ornate tropical genera *Ornithocercus* and *Histioneis* are excellent warm-water indicators, reflecting the southward reach of the East Australian and Leeuwin currents, whereas *D. truncata* Cleve is a cold-water Subantarctic species.

**Keywords:** Australia, Australian oceans, diarrhetic shellfish poisoning, *Dinophysis*, dinophysoid dinoflagellates, *Histioneis*, *Ornithocercus*, *Phalacroma*, tropical indicator species.

## Introduction

Marine dinophysoid dinoflagellates include the widespread, laterally flattened *Dinophysis* Ehrenb. (mostly with chloroplasts; type species *D. acuta* Ehrenb.) and *Phalacroma* F.Stein (mostly without chloroplasts; type species *P. porodictyum* F.Stein), but also the ornate subtropical and tropical genera *Amphisolenia* F.Stein (type species *A. globifera* F.Stein), *Citharistes* F.Stein (type species *C. regius* F.Stein), *Histioneis* F.Stein (type species *H. remora* F.Stein) and *Ornithocercus* F.Stein (type species *O. magnificus* F.Stein).

Pioneering studies on dinophysoid dinoflagellates were conducted by Von Stein (1883) who from global plankton collections described five new genera and four new *Dinophysis*, eleven *Phalacroma*, two *Amphisolenia*, one *Citharistes*, six *Histioneis* and one *Ornithocercus* species. Kofoed *et al.*, using material collected on an expedition with the US Fish Commission Steamer ‘Albatross’ from October 1904 to March 1905 along the eastern Pacific (Kofoed and Michener 1911; Kofoed and Skogsberg 1928; Tai and Skogsberg 1934) documented 132 species of dinophysoid dinoflagellates (88 new to science) belonging to 11 genera (5 new). Comparable studies have since been conducted on the tropical Mexican Pacific by Esqueda-Lara and Hernández-Becerril (2010) and Hernández-Becerril *et al.* (2021), the western Pacific by Omura *et al.* (2012) and the eastern Pacific by Zinssmeister *et al.* (2017). Dinophysoid dinoflagellates in the Indian Ocean were characterised by Taylor (1976), and from the South West Atlantic by Balech (1988). Smaller regional studies include *Dinophysis* from Vietnamese waters (Lee *et al.* 2012), and dinophysoids from the Gulf of Mexico (Okolodkov 2014), and from Pakistan waters (Gul and Saifullah 2007, 2010; Saifullah *et al.* 2008).

Australian waters were first surveyed by Wood (1954, 50 spp., 1963a, 1963b, 67 further species); however, his work, although impressive in sample coverage, was hampered by poorly reproduced line drawings and limited taxonomic discrimination. In the period 1978–1984, as part of a series of CSIRO Division of Fisheries & Oceanography cruises, Hallegraeff and co-workers made new water and net sample collections from New South Wales (NSW) coastal waters (Hallegraeff and Reid 1986), East Australian Current eddies (Jeffrey and Hallegraeff 1987), the Coral Sea, North West Shelf and Gulf of Carpentaria (Hallegraeff and Jeffrey 1984). In 2007, a collaboration between CSIRO and the Integrated Marine Observing System (IMOS) introduced two further initiatives, namely, the National Reference Station network (NRS, established in 2009) and the Australian Continuous Plankton Recorder program (AusCPR, established in 2009). The NRS consists of a network of reference stations around Australia (Darwin, Ningaloo, Rottnest Island, Esperance, Kangaroo Island, Maria Island, Port Hacking, North Stradbroke Island, Yongala; Eriksen *et al.* 2019; Fig. 1) collecting information on biogeochemical properties in addition to monthly plankton sampling. The AusCPR program uses research vessels and commercial ships of opportunity to tow a torpedo-like device that collects plankton samples (Richardson *et al.* 2006). These AusCPR tows collect

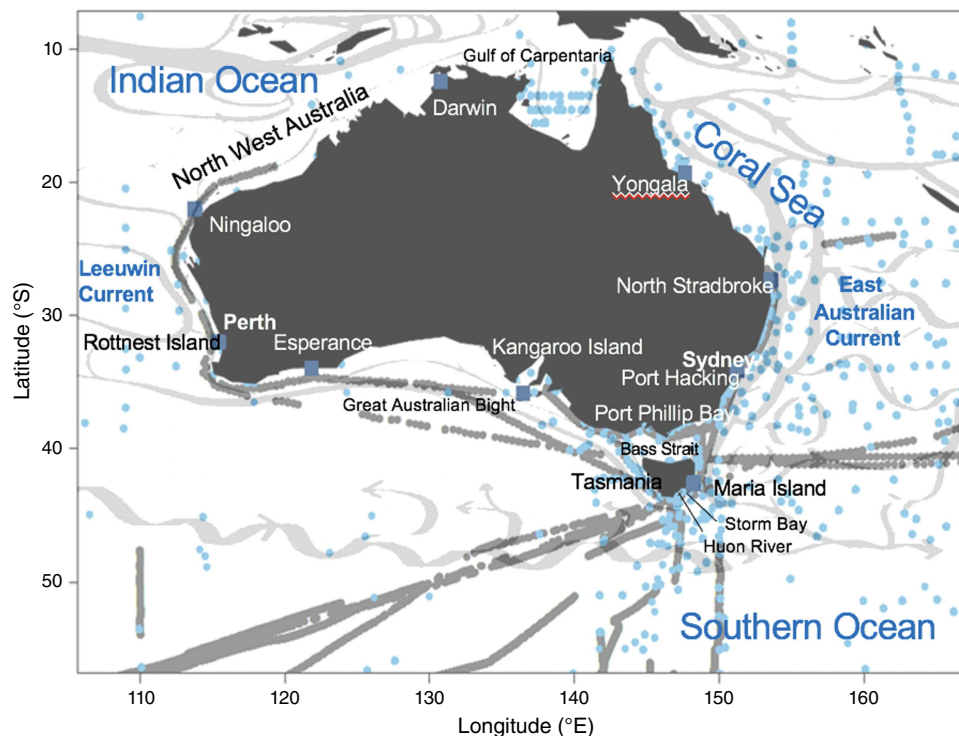
plankton offshore over large spatial and temporal scales on repeated transects around Australia. In 2012, the CSIRO initiated the development of a historical phytoplankton database, with the objective to digitise and centralise known Australian phytoplankton species presence and abundance records (Davies *et al.* 2016).

We here summarise and update dinophysoid species taxonomy in Australian tropical, subtropical, and temperate marine environments over the period 1938–2019, on the basis of 252 new National Reference Station and 129 Continuous Plankton Recorder samples, compare them with 9350 historical records curated in the Australian phytoplankton database, and then describe diversity, distribution and ecosystem implications.

## Materials and methods

The full data base consulted for this study is summarised in Table 1 and sampling locations mentioned in the text are shown in Fig. 1. We also included recent sample collections in the Australian sector of the Indian Ocean made by R.V. *Investigator* along 110°E.

Three sampling approaches were used for both recent and historical data, as specified in Table 1.



**Fig. 1.** Map of Australia with the sampling locations mentioned in the text. The Integrated Marine Observing System National Reference Stations (NRS; Darwin, Ningaloo, Rottnest Island, Yongala, North Stradbroke, Port Hacking, Maria Island) and Continuous Plankton Recorder (CPR) transects (dark grey bands) have been combined with literature data (blue dots). Surface currents (in light grey) are based on Wijeratne *et al.* (2018).

**Table 1.** Methods used for dinophysoid observations from Australian waters from the period 1978–2019, compared with historic observations going back to the 1930s.

Authors	Period	Locality	Niskin bottles	Phytoplankton net	LM or SEM	Number of dinophysoid taxa
Wood (1954)	1938–1954	Australia-wide	–	Plankton tows (mesh not stated)	LM	50
Wood (1963a, 1963b)	1954–1963	Coral Sea, Indian Ocean	–	Plankton tows (mesh not stated)	LM	79
Taylor (1976)	1963–1964	Adjacent Indian Ocean	–	Number 25 mesh, 200-m depth to surface	LM, SEM	48
Hallegraeff and Jeffrey (1984), Hallegraeff and Reid (1986), Jeffrey and Hallegraeff (1987), Hallegraeff et al. (2010)	1978–2010	Australia-wide	8–30 L	37- $\mu$ m free-fall surface to depth (100–200 m)	LM, SEM	50
National Reference Stations, Eriksen et al. (2019)	2009–2019	Australia-wide	A pooled 1-L subsample, composed of 500-mL samples taken at 10-m intervals from surface to 50-m depth		LM	24
Continuous Plankton Recorder, Richardson et al. (2006)	2009–2019	Australia-wide, offshore		270- $\mu$ m mesh; 6–10-m depth subsurface tow	LM, SEM	12

LM, light microscopy; SEM, scanning electron microscopy.

- (1) Net sampling provided material for species taxonomy by light and electron microscopy. For oceanic surveys, we used a 37- $\mu$ m free-fall plankton net with a weighted ring (Heron 1982) to propel it downward from surface to 100- to 200-m depth, but for selected inshore and off-shore collections we used a small conical net (mouth diameter 23 cm, length 40 cm, cod-end diameter 4.5 cm) made of 20- $\mu$ m monofilament nylon mesh, sampled from surface to 20-m depth. Zooplankton net sample collections using 100- $\mu$ m mesh nets also proved to generate excellent dinophysoid material.
- (2) Water bottle sampling using 1-, 5-, 8- or 30-L Niskin bottles to sample from different depths. Water samples of 1-L volume or more were preserved (Lugol's iodine solution, buffered formalin or glutaraldehyde) and concentrated by settling or centrifugation for quantitative cell counts by using an inverted or compound microscope.
- (3) The Continuous Plankton Recorder (CPR) collects plankton continuously from a standard depth of 6–10 m, towed behind ships of opportunity. The plankton cells are collected onto a constantly moving band of silk, which is wound into a tank of 4% formaldehyde. Although the silk mesh is 270  $\mu$ m, it does retain many smaller cells down to 2  $\mu$ m because of the nature of the twisted silk threads, the mesh constituting 30–40% of the mesh area, and through clogging. At the end of a voyage, the silks are cut into ~5-cm sections (representing ~5 nautical miles or ~9.26 km) and 20 fields analysed by light microscopy using a 63 $\times$  objective and 10 $\times$  ocular. The statistics of converting counts from silks to cell concentrations are described by Richardson et al. (2006).

Not all dinophysoid cells could be routinely identified to species level from all samples.

### Light microscopy

Selected samples were examined under the microscope on board ship as soon as possible after collection while in the living state. Most samples were preserved either in Lugol's iodine or using 2% formaldehyde fixative (buffered with hexamine). Cells were photographed with bright-field and differential interference contrast by using an Axioskop 2 Plus Zeiss microscope with Zeiss Axiocam HR digital camera. Samples processed as part of the NRS or CPR surveys were examined using phase contrast on a Leica DM2000 or DM6 microscope with Canon EOS 5D MkII camera. CPR silks were examined using a specially modified stage that enabled counting across the entire silk segment.

### Scanning electron microscopy

Seawater samples (100 mL–3 L) were filtered gently onto Nuclepore filters (pore diameter 1  $\mu$ m) immediately after collection. The filters were rinsed with 100 mL of distilled water to remove salt crystals and then air dried. Small pieces



of filter were mounted on aluminium stubs, coated with gold, gold–palladium or platinum–palladium (5–20-nm layer thickness) and examined with a JEOL JSM-35C or JSM 840, Philips 515 or Hitachi SU70 scanning electron microscope (SEM) at 1.5–25 kV. Filtration immediately after collection minimised aggregation with detritus and structural deformation during air drying did not pose serious problems for dinophysoid cells.

## Dinophysoid species composition

Full names with taxonomic authorities of all species discussed are listed in Table 2, and number of occurrence records and selected abundance estimates are compiled in Table 3.

All data are available online at <https://portal.aodn.org.au/search?uuid=75f4f1fc-bee3-4498-ab71-aa1ab29ab2c0>.

Dinophysales undergo vegetative division by desmoschisis in which the mother cell material is distributed half-and-half between the two daughter cells, but there are some parts of the cell (e.g. sails) that cannot be symmetrically distributed (Taylor 1973). As a result, recently divided daughter cells can exhibit morphological differences of ribs, lists, spines, sails and thecal ornamentation compared with the mother cell. Concerning lists and ribs in the left sulcal lists, R1 goes to one daughter and R2 and R3 to the other daughter cell. Likewise, it is now well known from field population studies and from cultures, that dinoflagellates can undergo depauperating divisions to produce two small cells that were historically sometimes designated as a different species (Reguera and González-Gil 2001; Silva and Faust 2019).

## Dinophysis and Phalacroma

*Dinophysis* cells are laterally flattened and divided into a small epitheca (top portion of cell) and a large hypotheca (bottom half; Fig. 2–32). The girdle is bordered by lists and the sulcus is also normally bordered by lists extending for a variable length along the hypotheca. *Dinophysis* and *Phalacroma* species overlap morphologically, but they can be separated by the development and direction of the cingular lists (Fig. 3), in combination with the height and shape of the epitheca. *Dinophysis* species have a much reduced epitheca and associated funnel-shaped anterior cingular lists (ACL) that curve upwards, but with *Phalacroma*, because of the larger epitheca, the girdle lists are horizontal (Fig. 33–53). The separation of *Dinophysis* and *Phalacroma* was first questioned by Tai and Skogsberg (1934), and, because of comparable plate tabulations, the two genera were synonymised by Abe (1967) and Balech (1967). However, on the basis of molecular phylogenetic data, *Phalacroma* was reintroduced and epitypified by Jensen and Daugbjerg (2009) and its diagnosis emended to

‘Epitheca large but  $< \frac{1}{4}$  of the cell length. It is visible above the cingular lists, and flattened to convex in outline. Cingular lists are narrow and horizontal and can possess ribs’ (p. 1147). Gómez (2021) formally proposed to conserve the name *Phalacroma* F.Stein over the little used name *Prodinophysis* Balech, which was created because of the earlier use of this name for the trilobite genus *Phalacroma* Hawle & Corda. Many of the species can also be separated by the presence (*Dinophysis*) or absence (*Phalacroma*) of chloroplasts (Hallegraef and Lucas 1988), but there exist exceptions; for example, *D. hastata* F.Stein is colourless, whereas *Ph. mitra* F.Schütt contains kleptoplastids of hapto-phyte origin. The theca may be porate and have areoles or reticulations (Hallegraef and Lucas 1988). For species identification, important features are size and shape of the cells, especially the outline of the main body and sulcal lists, whereas plate tabulation details are rarely used for taxonomy. The Australian Phytoplankton Database (Davies et al. 2016) as of May 2021 contained 8082 distribution records of taxa belonging to *Dinophysis* and 952 to *Phalacroma*.

Prominent *Dinophysis* in Australian temperate waters are blooms of *D. acuminata* Clap. & J.Lachm. (4487 location records) and *D. fortii* Pavill. (447 records), with cell densities of up to 7380 cells L<sup>-1</sup> having been recorded in Sullivans Cove, Tasmania, and up to 14 000 cells L<sup>-1</sup> in the Huon River, Tasmania respectively (Wallace 2011; G. M. Hallegraef, unpubl. data). *D. acuminata* is distinguished by its small size (38–58 µm long, 30–39 µm wide) and usually regular oval cell shape with some cells displaying minute protrusions on the bottom of the hypotheca (Fig. 2). This species is highly variable, commonly referred to as the *D. acuminata* species complex (Larsen and Moestrup 1992; Wolny et al. 2020), and the taxa *D. boehmii* Paulsen, *D. borealis* Paulsen, *D. ellipsooides* Kof. and *D. lachmanii* Solum are all considered to be synonyms. We never conclusively identified the closely related *D. sacculus* Stein in Australian waters. *D. skagii* Paulsen has been interpreted as a life-cycle stage of *D. acuminata* (Reguera and González-Gil 2001). *D. acuminata* intergrades with *D. ovum* F.Schütt, which has the right sulcal list (RSL) ending close to the base of the second rib R2 of the left sulcal list (LSL; Raho et al. 2008), whereas in *D. acuminata* this list ends near the middle point between the bases of R2 and R3 (Fig. 3, 4, arrows). However, studies on Korean strains of *D. acuminata* and *D. ovum* could not categorically discriminate between the two species by morphological nor genetic criteria using the *cox1* gene (Park et al. 2019). In this study, we did not conclusively identify *D. ovum* from Australian waters, and numerous cells that at first impression resembled *D. ovum* (Fig. 4) all exhibited the RSL features matching the definition of *D. acuminata*.

*Dinophysis acuta* Ehrenb. (134 records; Fig. 5) is in size similar to *D. fortii* (60–70 µm long, 35–40 µm wide; Fig. 6–9) and best identified by the prominent triangular posterior end of the hypotheca and with the cell body being

**Table 2.** Taxonomic authorities of all dinophysoid taxa discussed and past and current Australasian records.

Taxon	Basionym reference and synonyms	It	EAC	CS	Gulf of Carpentaria	NW Shelf	WA	HI-S	Indian Ocean	Figures in the present work
<i>Dinophysis acuminata</i> Clap. & J.Lachm.	Claparède and Lachmann 1859, p. 408, pl. 20, fig. 17	+++	+++		+	+	+	+		Fig. 2–4
<i>D. acuta</i> Ehrenb.	Ehrenberg 1843, p. 18, pl. 1–4	+	+							Fig. 5
<i>D. brevisulcus</i> L.S.Tai & Skogsb.	Tai and Skogsb. 1934, p. 430		+						+	Fig. 54
<i>D. caudata</i> Sav.-Kent	Saville-Kent 1881, p. 455, 460	+	+++	+	+	+	+	+	+	Fig. 13, 14
<i>D. caudata</i> var. <i>caudata penduculata</i> (J.Schmidt) Jörg.	<i>D. homuncula</i> f. <i>pedunculata</i> J.Schmidt				+					Fig. 15
<i>D. exigua</i> Kof. & Skogsb.	Kofoid and Skogsb. 1928, p. 239, fig. 30		+	+		+			+	Fig. 32
<i>D. expelled</i> Kof. & Mich.	Kofoid and Michener 1911, p. 292; synonym: <i>Phalacroma expulsum</i> (Kof. & Mich.) Kofoid & Skogsb., 1928			+		+			+	Fig. 27, 28
<i>D. hastata</i> F.Stein	Von Stein 1883, pl. 19, fig. 12	+	+	+	+	+	+		++	Fig. 24, 25
<i>D. fortii</i> Pavill.	Pavillard 1924, p. 881	+++	+							Fig. 6–9
<i>D. miles</i> Cleve f. <i>indica</i> Ostenf. & J.Schmidt	Ostenfeld and Schmidt 1901, p. 170				+	+	+		+	Fig. 18–20
<i>D. schroederi</i> Pavill.	Pavillard 1909, fig. 5	+	+	+						Fig. 10, 11
<i>D. schuettii</i> G.Murr. & Whitt.	Murray and Whitting 1899, pl. 31, fig. 10		+	+					++	Fig. 21–23
<i>D. similis</i> Kof. & Skogsb.	Kofoid and Skogsb. 1928, p. 247, fig. 31: 1, 2		+	+					+	Fig. 29, 30
<i>D. sphaerica</i> F.Stein	Von Stein 1883, pl. 20, Fig. 3–9		+		+		+			Fig. 31
<i>D. tripos</i> Gourret	Gourret 1883, pl. 3, fig. 53	+	++	+	+		+	+		Fig. 16, 17
<i>D. truncata</i> Cleve	Cleve 1901, 925, fig. 7	+						+		Fig. 12
<i>D. uracantha</i> F.Stein	Von Stein 1883, pl. 20, Fig. 22, 23		+							Fig. 26
<i>Phalacroma argus</i> F.Stein	Von Stein 1883, pl. 1, fig. 15–17		+	+					+	Fig. 42
<i>Ph. circumsutum</i> G.Karsten	Karsten 1907, p. 421, pl. 53, fig. 8		+	+		+			+	Fig. 52, 53
<i>Ph. cuneus</i> F.Schütt	Schütt 1895, pl. 3, fig. 14; synonym: <i>Dinophysis cuneus</i> (F.Schütt) T.H.Abé		+	+	+	+			++	Fig. 41
<i>Ph. doryphorum</i> F.Stein	Von Stein 1883, pl. 19, fig. 1–4; synonym: <i>Dinophysis doryphora</i> (F.Stein) T.H.Abé		+	+		+			++	Fig. 51
<i>Ph. favus</i> Kof. & Mich.	Kofoid and Michener 1911, p. 289		+	+			+		+	Fig. 39
<i>Ph. hindmarchii</i> G.Murr. & Whitt.	Murray and Whitting 1899, pl. 31, fig. 5	+	+	+						Fig. 40
<i>Ph. partner</i> F.Schütt	Schütt 1895, pl. 4, fig. 18			+		+			++	Fig. 38
<i>Ph. operculoides</i> F.Schütt	Schütt 1895, p. 148, pl. 2, fig. 11 (1 and 3); non <i>Ph. ovum</i> F.Schütt, 1895	+	+	+						Fig. 48–50

(Continued on next page)

Table 2. (Continued)

Taxon	Basionym reference and synonyms	It	EAC	CS	Gulf of Carpentaria	NW Shelf	WA	HI-S	Indian Ocean	Figures in the present work
<i>Ph. ovum</i> F.Schütt	Schütt 1895, pl. 2, fig. 11 (sub. 2); synonym: <i>Dinophysis amandula</i> Sournia, 1973, p. 18	+	+		+	+			+	Fig. 45–47
<i>Ph. parvulum</i> (F.Schütt) Jörg.	<i>Ph. porodictyum</i> var. <i>parvula</i> F.Schütt, pp. 4, 148, pl. 2, fig. 13	+	+	+			+		++	Fig. 34
<i>Ph. porodictyum</i> F.Stein	Von Stein 1883, pl. 18, fig. 1–14 (1883)			+	+	+			+	Fig. 43, 44
<i>Ph. rapper</i> F.Stein	Von Stein 1883, pl. 19, fig. 5–8		+	+					+	Fig. 35–37
<i>Ph. rotundatum</i> (Clap. & J.Lachm.) Kof. & Michener	<i>Dinophysis rotundata</i> Claparède and Lachmann 1859, pl. 20, fig. 16		+		+	+				Fig. 33
<i>Metaphalacroma skogsbergii</i> L.S.Tai	Tai and Skogsberg 1934, pp. 82, 380–482				+				+	Fig. 55
<i>Pseudophalacroma nasutum</i> (F.Stein) Jörg.	Jørgensen 1923, p. 4, fig. 1		+	+					+	Fig. 56
<i>Ornithocercus assimilis</i> Jörg.	Jørgensen 1923, pp. 37, 48, fig. 51; synonym: <i>O. quadratus</i> f. <i>assimilis</i> Kofoid & Skogsberg, 1928			+						Fig. 62, 64
<i>O. heteroporus</i> Kof.	Kofoid 1907, fig. 70; synonyms: <i>O. biclavatus</i> E.J.F.Wood, 1954, <i>O. triclavatus</i> E.J.F.Wood, 1954		+	+	+	+			++	Fig. 65–67
<i>O. magnificus</i> F.Stein	Von Stein 1883, pl. 23, fig. 1–6		+	+	+	+	+		++	Fig. 57–60
<i>O. quadratus</i> F.Schütt	Schütt 1900, fig. 1–4		+	+	+	+			++	Fig. 61, 63
<i>O. splendidus</i> F.Schütt	Schütt 1892, fig. 82, 83		+	+					+	Fig. 68–70
<i>O. steinii</i> F.Schütt	Schütt 1900, fig. 5–7		+	+	+	+			++	Fig. 71
<i>O. thumii</i> (A.W.F.Schmidt) Kof. & Skogsb.	Kofoid and Skogsberg 1928, p. 540 (1928)	+	+	+	+	+			++	Fig. 72–75
<i>Histioneis carinata</i> Kof.	Kofoid 1907, pl. 16, fig. 98								+	Fig. 83
<i>H. cymbalaria</i> F.Stein	Von Stein 1883, pl. 22; synonym: <i>H. depressa</i> Schiller, 1928?			+						Fig. 86
<i>H. elongata</i> Kof. & Mich.	Kofoid and Michener 1911, p. 295, no. fig.								+	Fig. 80, 81
<i>H. garrettii</i> Kof.	Kofoid 1907, pl. 16 (97); synonym: <i>Parahistioneis garrettii</i> (Kof.) Kofoid & Skogsberg, 1928			+					+	Fig. 76
<i>H. highleyi</i> G.Murr. & Whitt.	Murray and Whitting 1899, pl. 32, fig. 5								+	Fig. 84
<i>H. inclinata</i> Kof. & Mich.	Kofoid and Michener 1911, 297								+	Fig. 82
<i>H. joergensenii</i> J.Schiller	Schiller 1928			+						Fig. 88
<i>H. longicollis</i> Kof.	Kofoid 1907, p. 204, pl. 16, fig. 100		+	+					+	Fig. 87
<i>H. milneri</i> G.Murr. & Whitt.	Murray and Whitting 1899, p. 334, pl. 33, fig. 1; synonyms: <i>H. hippoeroides</i> Kof. & Mich.; <i>H. depressa</i> J.Schiller			+		+			+	Fig. 78, 79
<i>H. mitchellana</i> G.Murr. & Whitt.	Murray and Whitting 1899, pl. 33, fig. 3; synonym: ? <i>H. pulchra</i> Kof., 1907			+					+	Fig. 77
<i>H. schilleri</i> Böhm	Böhm 1931, p. 499, fig. 5, 6								+	Fig. 86

(Continued on next page)

Table 2. (Continued)

Taxon	Basionym reference and synonyms	It	EAC	CS	Gulf of Carpentaria	NW Shelf	WA	HI- S	Indian Ocean	Figures in the present work
<i>Parahistioneis para</i> G.Murr. & Whitt.	Kofoid and Skogsberg 1928, p. 601; synonym: <i>P. conica</i> Böhm								+	Fig. 89
<i>P. crateriformis</i> (F.Stein) Kof. & Skogsb.	Von Stein 1883, pl. 22 (5–6); synonym: <i>P. crateriformis</i> (F.Stein) Kofoid & Skogsberg 1928; ? <i>H. reticulata</i> Kof.			+					+	Fig. 92
<i>P. paraformis</i> Kof. & Skogsb.	<i>Histioneis paraformis</i> (Kof. & Skogsb.) Balech, 1971; synonym: <i>P. acuta</i> Böhm								+	Fig. 90
<i>P. pietainii</i> Osorio-Tafall	Osorio-Tafall 1942, p. 444, pl. 35, fig. 13, 14; synonym: ? <i>H. isselii</i> Fortii, 1932			+						Fig. 91
<i>Histiophysis rugosa</i> (Kof. & Mich.) Kof. & Skogsb.	Kofoid and Skogsberg 1928, pp. 333–334, pl. 5, fig. 5, 93			+					+	Fig. 96–98
<i>Citharistes apsteinii</i> F.Schütt	Schütt 1895, p. 16, pl. 5, fig. 24			+					+	Fig. 94, 95
<i>C. regius</i> F.Stein	Von Stein 1883, p. 24, pl. 22, fig. 1–4		++	++		+	+		++	Fig. 93
<i>Amphisolenia bidentata</i> Schröder	Schröder 1900, p. 0, pl. 1: fig. 16								+	Fig. 99–103
<i>A. clavipes</i> Kof.	Kofoid 1907, p. 197, pl. 14, fig. 90								+	Fig. 108
<i>A. extensa</i> Kof.	Kofoid 1907, p. 198, pl. 13, fig. 78			+						Fig. 111
<i>A. inflata</i> G.Murr. & Whitt.	Murray and Whitting 1899, p. 332, pl. 31, fig. 2			+					+	Fig. 104
<i>A. palaeotheroides</i> Kof.	Kofoid 1907, p. 199, pl. 14, fig. 84								+	Fig. 105
<i>A. palmata</i> F.Stein	Von Stein 1883, pl. 21 (11–15)			+					+	Fig. 107
<i>A. rectangulata</i> Kof.	Kofoid 1907, p. 200, pl. 14, fig. 83.		+	+		+	+		+	Fig. 109, 110
<i>A. thrinax</i> F.Schütt	Schütt 1892, p. 299, fig. 81									Fig. 106

EAC, East Australian Current; CS, Coral Sea; WA, Western Australia; SA, South Australia; Tas, Tasmania; number of records in the Australian Phytoplankton Data Base, and from Continuous Plankton Recorder (CPR) and National Reference Stations (NRS) are indicated; +, present; ++, common; +++, abundant.

**Table 3.** Number of occurrence records of dinophysoid dinoflagellate species in the Australian region, either in the historic Phytoplankton Data Base, or recent Continuous Plankton Recorder (CPR) or National Reference Station (NRS) surveys.

Species	Occurrence records			Cells L <sup>-1</sup>					
	Phytoplankton Data Base	CPR	NRS	Tas	EAC	GBR	North Australia	WA	GAB
<i>Dinophysis acuminata</i>	4467	6	14	Up to 7380 <sup>A</sup>	3.33; up to 3000 <sup>B</sup>				3.33
<i>D. acuta</i>	132	1	2		3.33				
<i>D. caudata</i>	1784	10	40		0.67–10; up to 12 000 <sup>C</sup>	3.33			3.33
<i>D. hastata</i>	63								
<i>D. fortii</i>	443	0	4	Up to 14 000 <sup>D</sup>					
<i>D. miles</i>	13	1	25		0.67				
<i>D. schroederi</i>	34								
<i>D. schuettii</i>	51								
<i>D. tripos</i>	510	32	42		0.67–20				0.67–3.33
<i>D. truncata</i>	52	0	1						
<i>Dinophysis</i> spp.	255	2	3						
<i>Phalacroma argus</i>	47								
<i>Ph. cuneus</i>	13								
<i>Ph. doryphorum</i>	65	2							
<i>Ph. favus</i>	19								
<i>Ph. mitra</i>	75		4						
<i>Ph. parvulum</i>	49								
<i>Ph. rapa</i>	37								
<i>Ph. rotundatum</i>	632	1	20	3.33					
<i>Phalacroma</i> spp.	78	3	2						0.67
<i>Ornithocercus heteroporus</i>	25		1						
<i>O. magnificus</i>	53		3						
<i>O. quadratus</i>	55	6	23		0.67–3.33				0.67
<i>O. thumii</i>	73		3						
<i>Ornithocercus</i> spp.	40		4		0.67	3.33			0.67
<i>Histioneis</i> spp.	75	1	8						
<i>Citharistes</i> spp.	4		1						
<i>Amphisolenia bidentata</i>	64	60	46		0.67–3.33	0.67–3.33	0.67–6.67	0.67	
<i>A. thrinax</i>	8	7	2		0.67	0.67		0.67	
<i>Amphisolenia</i> spp.	34	0	1		0.67–3.67	0.67–3.33		0.67–3.33	0.67

Estimates of abundance levels (cells L<sup>-1</sup>) for selected species are based on CPR offshore counts, supplemented by selected surveys in estuaries as indicated.

<sup>A</sup>Wallace (2011), Sullivans Cove, Tasmania.

<sup>B</sup>Farrell et al. (2020), South Ballina Beach, NSW.

<sup>C</sup>Ajani et al. (2016). Hawkesbury estuary.

<sup>D</sup>G. M. Hallegraeff, Huon River, Tasmania, unpubl. data.



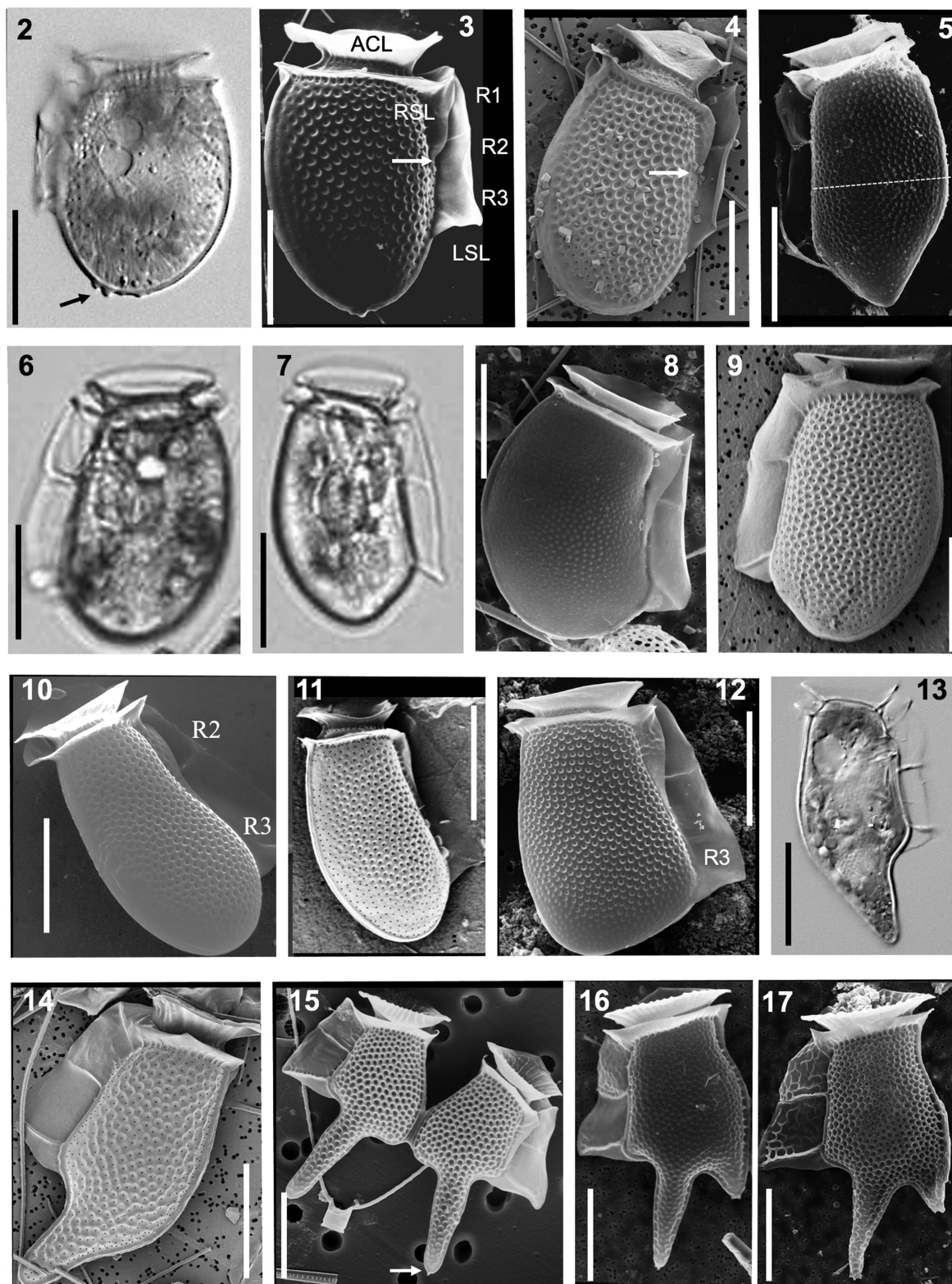


Fig. 2–17. (Caption on next page)

**Fig. 2–17.** Fig. 2–4. *Dinophysis acuminata* with minute protrusions on the bottom of the hypotheca and the right sulcal list (RSL) ending near the middle point of the bases of ribs R2 and R3 of the left sulcal list (LSL) (arrow). Fig. 2. LM. Fig. 3. SEM. Sullivans Cove, Tasmania. Fig. 4. SEM. South Australia. Fig. 5. *D. acuta* with the cell body widest below the middle of the hypotheca (dotted line), and prominent triangular bottom of hypotheca; SEM. Tasmania. Fig. 6–9. *D. fortii* with long LSL extending to 4/5 of cell length, and subovate or bulge-like bottom of hypotheca. Fig. 6–7. LM. Sullivans Cove, Tasmania. Fig. 8. SEM. Sydney coastal waters. Fig. 9. SEM. Ningaloo Reef. Fig. 10, 11. *D. schroederi*, which is 1.8× longer than wide. SEM. Coral Sea. Fig. 12. *D. truncata* with trapezoid hypotheca and posteriorly curved rib R3 of LSL. SEM. West Coast Tasmania. Fig. 13, 14. *D. caudata* with long ventral hypotheca projection. Fig. 13. LM, Tasmania. Fig. 14. SEM. South Australia. Fig. 15. *D. caudata* var. *pedunculata*. Recently divided cell. SEM. Gulf of Carpentaria; Fig. 16–17. *D. tripos* with one long and one short hypothecal projection. SEM. Fig. 16. Storm Bay, Tasmania. Fig. 17. Gulf of Carpentaria. Fig. 3, 4, 7, 8, 10, 11, 12, 13, 16, 17 represent left lateral views, Fig. 2, 5, 6, 9, 14 right lateral views, and Fig. 15 of a dividing pair present both left and right lateral views. Scale bars: 20 µm.

widest below the middle of the hypotheca (Fig. 5, dotted line). The smaller, narrower *D. dens* Pavill. is considered to be a life-cycle stage of *D. acuta* (Reguera et al. 2004). *D. fortii* is typically distinguished by appearing broad, ‘bag-shaped’, with rounded antapices (dorsal bulge; Fig. 6, 8) and very straight ventral margin, but narrower forms can intergrade with *D. acuta* and *D. acuminata*. The LSL of *D. fortii* is much longer than that of *D. acuminata* and can extend to 4/5 of the hypotheca (Fig. 8, 9). *D. acuta* has been widely reported from New Zealand waters (MacKenzie et al. 2005) but rarely from Australian tropical, subtropical or temperate waters. Partial 28S rDNA gene sequences of Tasmanian *D. fortii* were indistinguishable from those of *D. fortii* from France and from *D. acuta* from New Zealand (Wallace 2011). Diarrhetic shellfish toxin profiles between Australia and New Zealand were also similar and it is possible that the New Zealand species designations have been confounded and refer to the same taxon *D. fortii*.

*Dinophysis schroederi* Pavill. (34 records) was encountered in this work only in the Coral Sea. The cells are ~1.8 times longer (70 µm length) than wide, and widest mid-distant between R2 and R3 (Fig. 10, 11). *D. truncata* Cleve (53 records) is a predominantly cold-water, Subantarctic species, which is rare in Tasmanian and South Australian waters, and also known from New Zealand (Burns and Mitchell 1982). Cells are 61–70 µm long and 37–49 µm wide, with a distinctive trapezoid hypotheca with flattened bottom, although this shape varies from smooth and straight to concave and bulbous or concave and wrinkled. The left sulcal list is typically widest at R3 and this rib is curved posteriorly (Fig. 12).

Common in Australian waters are the morphologically distinctive *D. caudata* Kent (1832 records) and *D. tripos* Gourret (589 records). Ajani et al. (2016) reported cell concentrations of 12 000 cells L<sup>-1</sup> for *D. caudata* in the Hawkesbury River. *Dinophysis caudata* (Fig. 13, 14), 70–170 µm long, is irregularly subovate with long ventral hypothecal projections and is widest at the base of the sulcal list. It can be toothed on the posterior end. The most common *D. caudata* morphology in Australian temperate waters compares with var. *abbreviata* Jörgensen (Fig. 13, 14), whereas tropical, more slender forms have been discriminated as *D. caudata* var. *pedunculata* Schmidt (Fig. 15). Wood (1954, fig. 49a–g) noted that each area in Australia seems

to have a characteristic form of *D. caudata* which is reasonably constant for that area. These forms deserve discrimination in future studies (compare Jörgensen 1923). We did not conclusively identify in Australian waters the *D. diegensis* Kofoid-like small cells (Rodríguez et al. 2012) of this species. *Dinophysis tripos* is anterior–posteriorly elongated, 94–105 µm long, with distinctive long antapical projections and short dorsal projections (Fig. 16). Morphologically identical cells are known from both Australian temperate (Fig. 16) and tropical waters, such as Ningaloo Reef, Western Australia, and the Gulf of Carpentaria (Fig. 17). *Dinophysis miles* Cleve f. *indica* Ostenf. & E.J.Schmidt (37 records) is a readily recognisable but rare tropical neritic species with maximum development of dorsal processes, up to 140–165 µm long (Fig. 18–20). The ventral margin of the hypotheca is straight or strongly wavy. Cell division can produce spectacular quadruplets or octuplets (Fig. 19, 20). This species has been exclusively observed by us in the port of Darwin, Gulf of Carpentaria, North-West Shelf and Rottnest Island, but Wood (1954) cites a single record from Port Hacking, NSW.

*Dinophysis schuettii* G.Murr. & Whitt. is a small species, 29–62 µm long, with round to subovate cell body and a curved, reinforced posterior sail that has a median rib joined to the marginal ribs (Fig. 21–23). The left sulcal list between R2 and R3 is concave and shorter than the ribs. The posterior spine is dorsal and curved to the right. This taxon has a predominantly warm-water oceanic distribution. *Dinophysis hastata* F.Stein is the commonest *Dinophysis* in Australian tropical waters (Fig. 24, 25). The medium-sized ovoid cells, 63–70 µm long, have a characteristic left sulcal list with the R3 rib typically curved distally. The cells carry a curved posterior spine, with list, which is directed ventrally. The nearest related species, *D. uracantha* F.Stein (Fig. 26), is distinguished on the basis of the dorso-antapical insertion of the antapical fin (arrowed) as opposed to ventro-antapical insertion in *D. hastata* (Fig. 24). The stylised original illustration of *D. hastata* by Von Stein (1883, pl. 19, fig. 12) shows a subovate cell with central antapical spine; however, later interpretations of this taxon (e.g. Taylor 1976, fig. 52, 54) included off-centre posterior spines. It is likely that more than one species is involved, and our cells in Fig. 24, 25 come closest to what has been called *D. hastata* var. *uracanthides* Jörgensen (see also Esqueda-Lara et al. 2013 for species discrimination within the *D. hastata* complex).



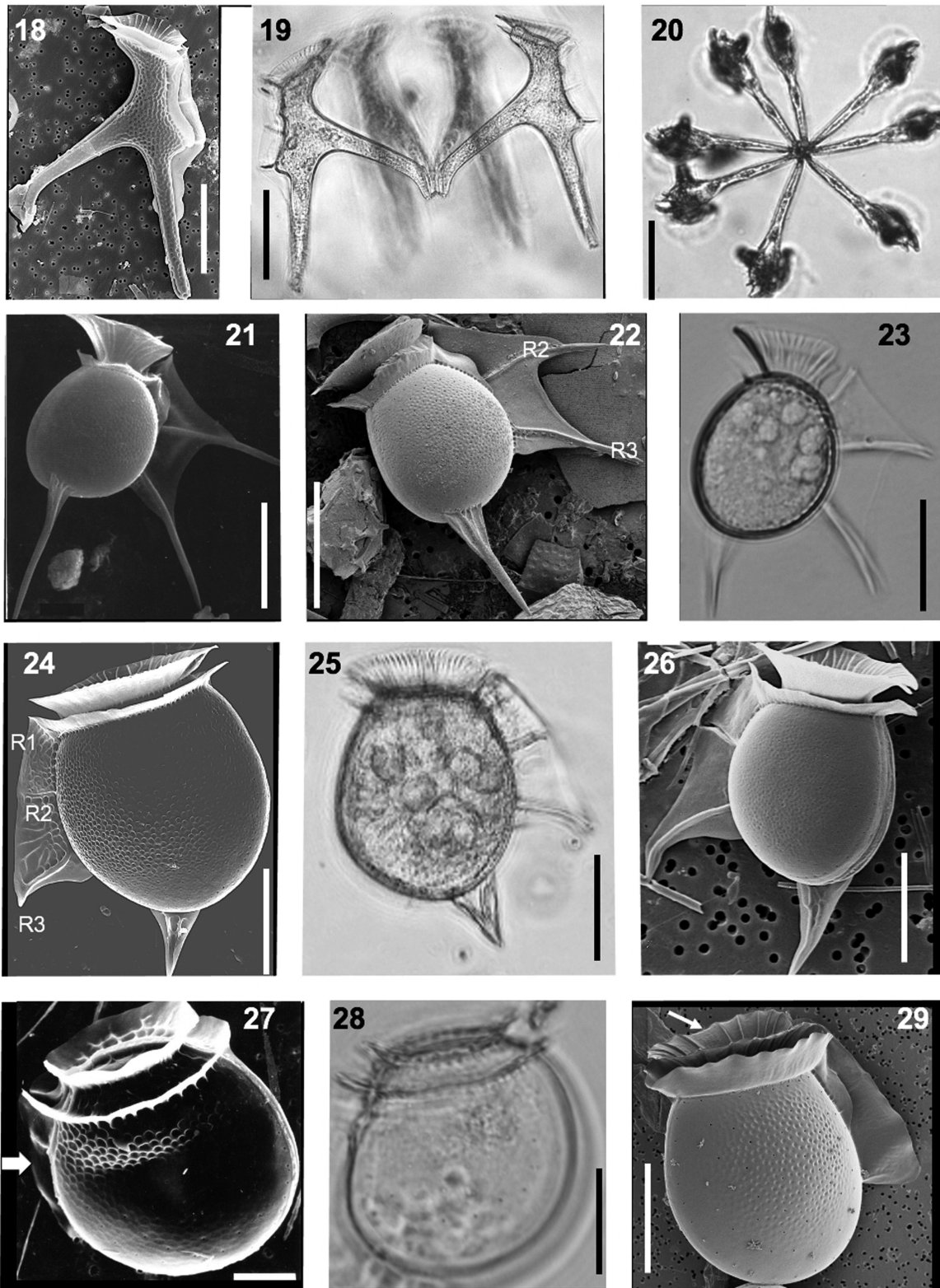


Fig. 18–29. (Caption on next page)

**Fig. 18–29.** Fig. 18–20. *D. miles* with long dorsal hypothecal projection. Fig. 18. SEM. North West Shelf, Australia. Fig. 19. LM. Quadruplet. Fig. 20. LM. Octuplet from Gulf of Carpentaria. Fig. 21–23. *D. schuettii* with long dorsal posterior spine curved to the right, and the left sulcal list between R2 and R3 shorter than the ribs. Fig. 21–22. SEM. Coral Sea. Fig. 23. LM, showing absence of chloroplast and presence of food vacuoles. Fig. 24–25. *D. hastata* with short curved posterior spine directed ventrally, and the left sulcal list with R3 rib curved distally. Fig. 24. SEM. Gulf of Carpentaria. Fig. 25. LM, showing absence of chloroplasts and large food vacuoles. Fig. 26. *D. uracantha* with the dorsal spine inserted ventro-antapically. SEM. North West Australia. Fig. 27–28. *D. expulsa*. Small species, 36  $\mu\text{m}$  high, with a wedge-shaped body with marked depression  $\frac{1}{4}$ – $\frac{1}{3}$  the distance from the lower girdle list to the antapex. Fig. 27. SEM. Fig. 28. LM, Coral Sea. Fig. 29. *D. similis* with subcircular to ovate cell body with the posterior main rib of the left sulcal list well developed. SEM. Indian Ocean. Fig. 18, 21, 22, 23, 25, 29 represent left lateral views, and Fig. 24, 26, 27, 28 right lateral views. Scale bars: Fig. 18–26, 28, 29, 20  $\mu\text{m}$ ; Fig. 27, 10  $\mu\text{m}$ .

*Dinophysis expulsa* Kof. & Mich. (Fig. 27, 28) is a small distinctive species, 36  $\mu\text{m}$  high, readily recognisable in ventral view with a wedge-shaped body with a marked depression (arrowed)  $\frac{1}{4}$ – $\frac{1}{3}$  the distance from the lower girdle list to the antapex. *Dinophysis similis* Kof. & Skogsb. has an asymmetrical ovate cell body with the posterior main rib of the left sulcal list well developed and the anterior girdle list with fine radial spokes (Fig. 29, 30, arrowed). The separation from *D. sphaerica* F.Stein (Fig. 31) is mainly based on the shape of the posterior portion of the LSL. *Dinophysis exigua* Kof. & Skogsb. is a small, 35–40  $\mu\text{m}$  long, subglobular species, slightly compressed in lateral view (Fig. 32). The epitheca is very small and hypotheca is broadly rounded posteriorly. The LSL terminates  $\sim 0.6$  of the cell length, continuously widening from R1 through R3. The RSL terminates at the base of R3. Both previous species exhibit girdle lists that are curving upwards and, hence, unambiguously belong to *Dinophysis*.

By contrast, *Ph. rotundatum* (Clap. & J. Lachm.) Kof. & Mich. (Fig. 33) belongs to a group of small to medium-sized species, 36–56  $\mu\text{m}$  long, with a simple rotund lateral outline, without striking morphological features. Balech (1976a) redefined this taxon from Norwegian waters as having the LSL extending to  $> 1/2$  and almost  $3/4$  the length of the hypotheca (arrowed). *Phalacroma parvulum* (F.Schütt) Jörg. (Fig. 34) is 30–35  $\mu\text{m}$  long, with subcircular lateral outline, deepest in the middle. The girdle lists are horizontal, approximately as wide as the girdle furrow.

The three strongly areolate species of *Ph. mitra* F.Schütt, *Ph. rapa* F.Stein, and *Ph. favus* Kof. & Mich. are common in tropical neritic waters. In our study, *Ph. rapa* (Fig. 35–37) was the most widespread. In *Ph. rapa*, the left ventral margin from R1 to R3 is angled, making the LSL extend out at approximately a 45–60° angle perpendicular to the depth axis. In the closely related *Ph. mitra*, the posterior portion of the hypotheca is concave from R3 to the antapex (Fig. 38), whereas *Ph. favus* is distinguished by its posterior finger-like projection (Fig. 39). *Phalacroma hindmarchii* G.Murr. & Whitt. shares the feature of a projecting antapex, but has a higher epitheca and the theca is more finely areolate (Fig. 40).

*Phalacroma cuneus* F.Schütt is a medium-sized species, 80–90  $\mu\text{m}$  long, that is broadest anteriorly and narrowest posteriorly (Fig. 41). The left sulcal list is curved distally. The thecal surface is distinctive in being strongly reticulate with a pore in almost every depression. *Phalacroma argus* F.Stein has a higher epitheca, but similar but more delicate

reticulate ornamentation (Fig. 42). The interpretation of *Ph. porodictyum* F.Stein by different authors has been inconsistent. The cells illustrated in Fig. 43, 44 are obovate or subellipsoidal in lateral outline, deepest at or somewhat behind the girdle. The RSL usually ends at or somewhat behind a point midway between the fission rib and the posterior main rib of the LSL. The thecal wall is faintly areolate with distinctive scattered larger pores.

### The complex problem of *Ph. ovum* and *Ph. operculoides*

Large ovoid or almond-shaped *Phalacroma* cells with strongly raised epitheca have been variously referred to as *Ph. ovum* F.Schütt, *Ph. operculoides* F.Schütt, *Ph. porodictyum* F.Stein or *D. amandula* (Balech) Sournia, *D. amandula* Sournia or *Ph. amandula* (Balech) Sournia (e.g. Zinssmeister et al. 2017). The names *Ph. operculoides* (as the basionym of *Dinophysis operculoides* F.Schütt (Balech)) and *Dinophysis amandula* (Balech) Sournia are recognised in Algaebase (M. D. Guiry and G. M. Guiry, National University of Ireland, Galway Ireland, see <https://www.algaebase.org>), but *Ph. ovum* is listed as an invalid name, for which Schütt (1895, p. 90), stating ‘the taxonomic or nomenclatural status (or both) in some way is unresolved and requiring further investigation’ made an error by only mentioning the name *Ph. ovum* in the text when referring to pl. 2, fig. 11 (sub. 2; type illustration reproduced here as Fig. 45), but this figure was erroneously labelled as *Ph. operculoides* Schütt (1895, p. 148). The other illustrations of *Ph. operculoides* by Schütt’s pl. 2, fig. 11 (sub. 1 and 3) (reproduced here as Fig. 48) clearly are a different species. Although numerous later authors remarked that Schütt (1895) included two apparently different species, the taxonomic solutions proposed to solve this problem have varied.

Jørgensen (1923) accepted the name *Ph. operculoides* for Schütt’s pl. 2, fig. 11 (sub. 2) because the other figures were uncertain. Instead, Kofoed and Skogsborg (1928) interpreted Schütt’s pl. 2, fig. 11 (sub. 2) as *Ph. ovum* and pl. 2, fig. 11 (sub. 1 and 3) as *Ph. operculoides*. Balech (1967) accepted the taxon *Ph. operculoides* Schütt (which he transferred to *Dinophysis*), but when seeking to transfer *Ph. ovum* to *Dinophysis* recognised that this name was preoccupied by the distinct taxon *D. ovum* Schütt. Balech (1967) therefore created the new name *D. amygdala* for the larger ‘almond-shaped’ cell of Schütt’s (1895) pl. 2, fig. 11 (sub. 2). Sournia (1973) subsequently recognised



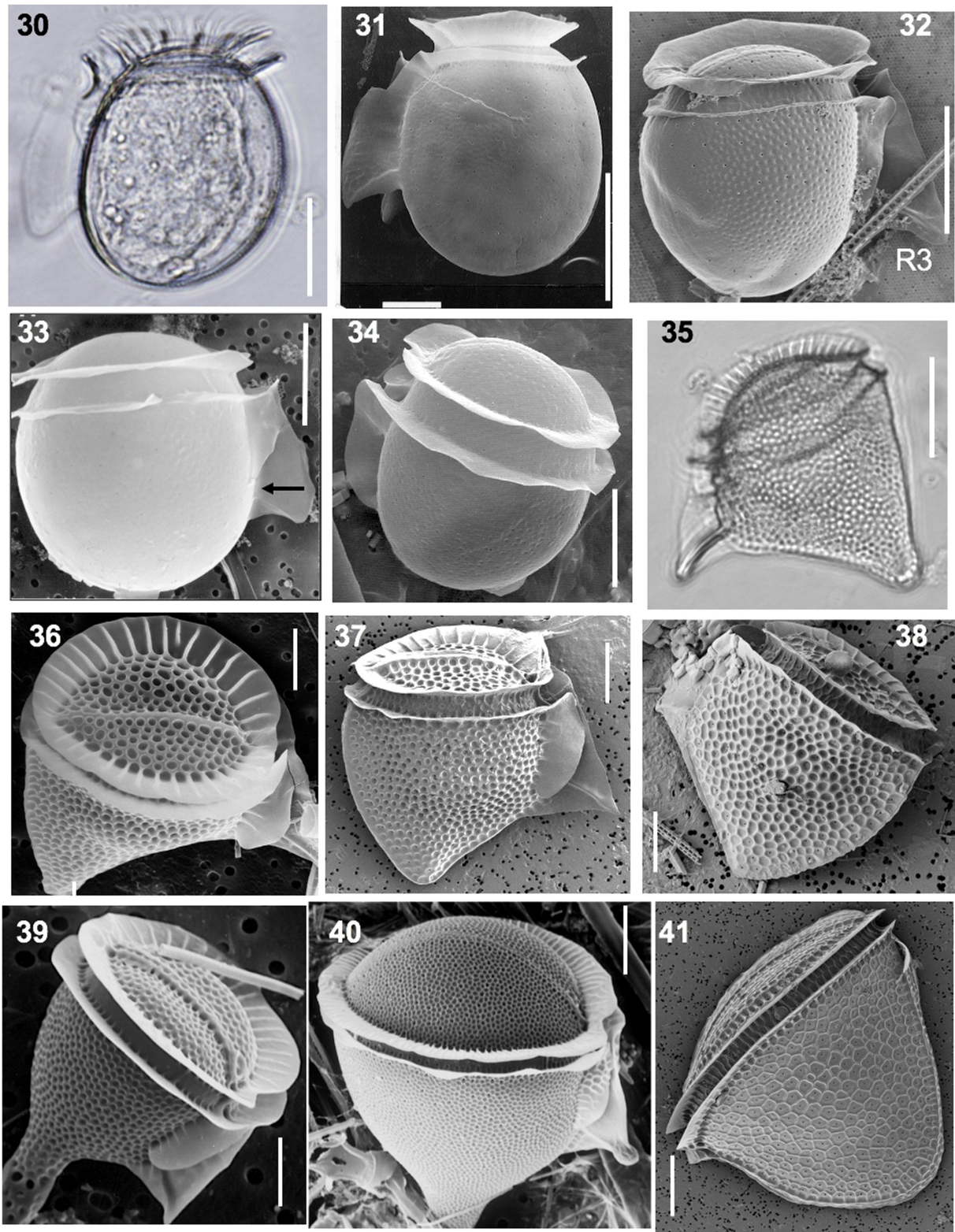


Fig. 30–41. (Caption on next page)



**Fig. 30–41.** Fig. 30. *D. similis*. LM. Coral Sea. Fig. 31. *D. sphaerica* with long posterior portion of the left sulcal list. SEM. Coral Sea. Fig. 32. *D. exigua* is slightly compressed in lateral view. The LSL terminates ~0.6 of the cell length, continuously widening from R1 through R3. The RSL terminates at the base of R3. SEM. Indian Ocean. Fig. 33. *Phalacroma rotundatum*, 36–56 µm long, with dome-shaped epitheca and rotund lateral outline, without striking morphological features. SEM. Tasmanian waters. Fig. 34. *Ph. parvulum*, 30–35 µm long, with subcircular lateral outline, deepest in the middle. The girdle lists are horizontal approximately as wide as the girdle furrow. SEM. Sydney coastal waters. Fig. 35–37. *Phalacroma raba* with the left ventral margin from R1 to R3 angled to make the left sulcal list extend out at 45–60° perpendicular to the depth axis. SEM. North West Shelf. Fig. 38. *Ph. mitra* with concave posterior portion of the hypotheca from R3 to the antapex. SEM. South Australia. Fig. 39. *Ph. favus* with posterior finger-like projection. SEM. Coral Sea. Fig. 40. *Ph. hindmarchii* with projecting apex but finely areolate theca and higher epitheca. Coral Sea. Fig. 41. *Ph. cuneus* with a distinctive strongly reticulate theca with a pore in almost every depression. The left sulcal list is curved distally. SEM. North West Shelf. Fig. 32, 33, 36, 37, 39, 40 represent left lateral views, and Fig. 30, 31, 34, 35, 38, 41 right lateral views. Scale bars: Fig. 30, 31, 35–41, 20 µm; Fig. 32–34, 10 µm.

that this name was preoccupied by *D. amygdalus* Paulsen (1949, p. 43, fig. 12B–D) and hence proposed the new name *D. amandula* Sournia. Under the International Code for Nomenclature, ICN Article 53.2 (Turland et al. 2018), when two names are so similar (*amandula* is Latin; *amygdala* is Greek, both meaning almond) that they are likely to be confused, they are to be treated as homonyms (see also Balech 1976b). Jensen and Daugbjerg (2009) produced convincing molecular evidence that *Ph. cf. ovum* belongs in *Phalacroma*. Options to solve this complex nomenclatural problem will be discussed in a separate communication.

In our work, the strongly poroid cells in Fig. 46, 47 from the East Australian Current and North West Australia compare to Schütt's first species, referred here as *Ph. ovum*, but the smooth-walled cells with both minute and larger scattered pores in Fig. 49, 50 from the East Australian Current and Indian Ocean compare to *Ph. operculoides* F.Schütt. As pointed out by Balech (1988, pl. 10, fig. 16–17), the first species has a LSL that is narrower at the level of the R2 rib where it exhibits a reinforcement (Fig. 46, arrow), and the latter species has an oval cell shape, usually >50 µm long, the right sulcal fin almost extending to R3, with a straight border between R2 and R3.

The finely areolated cell in our Fig. 47 compares to what Taylor (1976) from the Indian Ocean referred to as *D. porodictyum* (pl. 4, fig. 45), but which is clearly distinct in ornamentation from our *Ph. porodictyum* illustrated in Fig. 43, 44. Delgado and Fortuño (1991) illustrated by SEM from the Mediterranean an identical areolated cell, which they identified as *Dinophysis amandula* Sournia (pl. 37, fig. a).

### Other *Phalacroma*, *Dinophysis* and the related *Metaphalacroma* and *Pseudophalacroma*

*Phalacroma doryphorum* F.Stein has straight girdle lists and carries a characteristic triangular ribless posterior sail not connected to the LSL (Fig. 51). The ventral edge of the LSL is almost straight. Surface markings comprise shallow depressions with scattered pores. The similar *Ph. circumsutum* G.Karsten has the strong, single spine supporting the posterior list directed postero-ventrally, and exhibits more strongly ornamentation (Fig. 52, 53). Both species were rare in the Coral Sea, Great Australian Bight and Indian Ocean.

Fig. 54 with a very short sulcal list corresponds to *Dinophysis brevisulcus* L.S.Tai et Skogsb. as illustrated by Taylor (1976) from the Indian Ocean (pl. 4, fig. 34). This taxon is borderline between *Dinophysis* and *Phalacroma*, but the horizontal girdle lists (not curved upwards) suggest an affinity to the latter. We refrain from making a formal transfer until more material or, ideally, molecular sequences become available.

*Metaphalacroma skogsbergii* L.S.Tai (Fig. 55) belongs to a monospecific genus of uncertain taxonomic status and resembles the microcephalic, only known benthic dinophysoid genus *Sinophysis* Nie & Wang. This is a small subcircular dinophysoid with areolate theca, and the epitheca small and less wide than the hypotheca. The left and right girdle lists are very narrow and the posterior circular list resembles a collar. Zinssmeister et al. (2017) provided a comparable SEM (fig. 3l) from the tropical eastern Pacific. *Pseudophalacroma nasutum* (F.Stein) Jörg., first described as *Phalacroma nasutum* Stein, was discriminated by Jörgensen (1923) from *Phalacroma* in having a prolongation of the 'longitudinal furrow' (sulcus) extending ~2/3 of the distance from girdle to apex. The cell shape is similar to that of *Ph. rotundatum*, but the ornamentation of the theca is much coarser with pit-like areolation, and no ribs are visible on the sulcal lists (Fig. 56). A single individual was observed by us in the Coral Sea and Wood (1954) reported one individual each from Port Hacking and Eden, NSW. Zinssmeister et al. (2017) provided a comparable SEM of *P. nasutum* (fig. 3k) from the tropical eastern Pacific.

Other *Dinophysis* and *Phalacroma* species illustrated as poorly reproduced small line drawings by Wood (1954, 1963a, 1963b) include *D. arctica* Mereschk., *D. okamurai* Kof. & Skogsb., *D. micropterygia* P.Dangeard, *D. parva* J.Schiller, *D. recurva* Kof. & Skogsb., *D. tuberculata* Mangin, *D. ventrecta* J.Schiller, *Ph. acutum* (F.Schütt) Pavill., *Ph. apicatum* Kof. & Skogsb., *Ph. contractum* Kof. & Skogsb., *Ph. dolichopterygium* G.Murr. & Whitt., *Ph. elongatum* Jörg., *Ph. irregulare* M.Lebour, *Ph. lens* Kof. & Skogsb., *Ph. lenticula* Kof., *Ph. minutum* Cleve, *Ph. mucronatum* Kof. & Skogsb., *Ph. operculatum* F.Stein, *Ph. porosum* (Kof. & Mich.) Kof. & Skogsb., *Ph. pulchellum* M.Lebour, *Ph. pulchrum* (Kof. & Mich.) Jörg., *Ph. rudgei* G.Murr. & Whitt., *Ph. striata* Kof. and the newly created taxa *D. hyalina* E.J.F.Wood, *D. carpentariae*

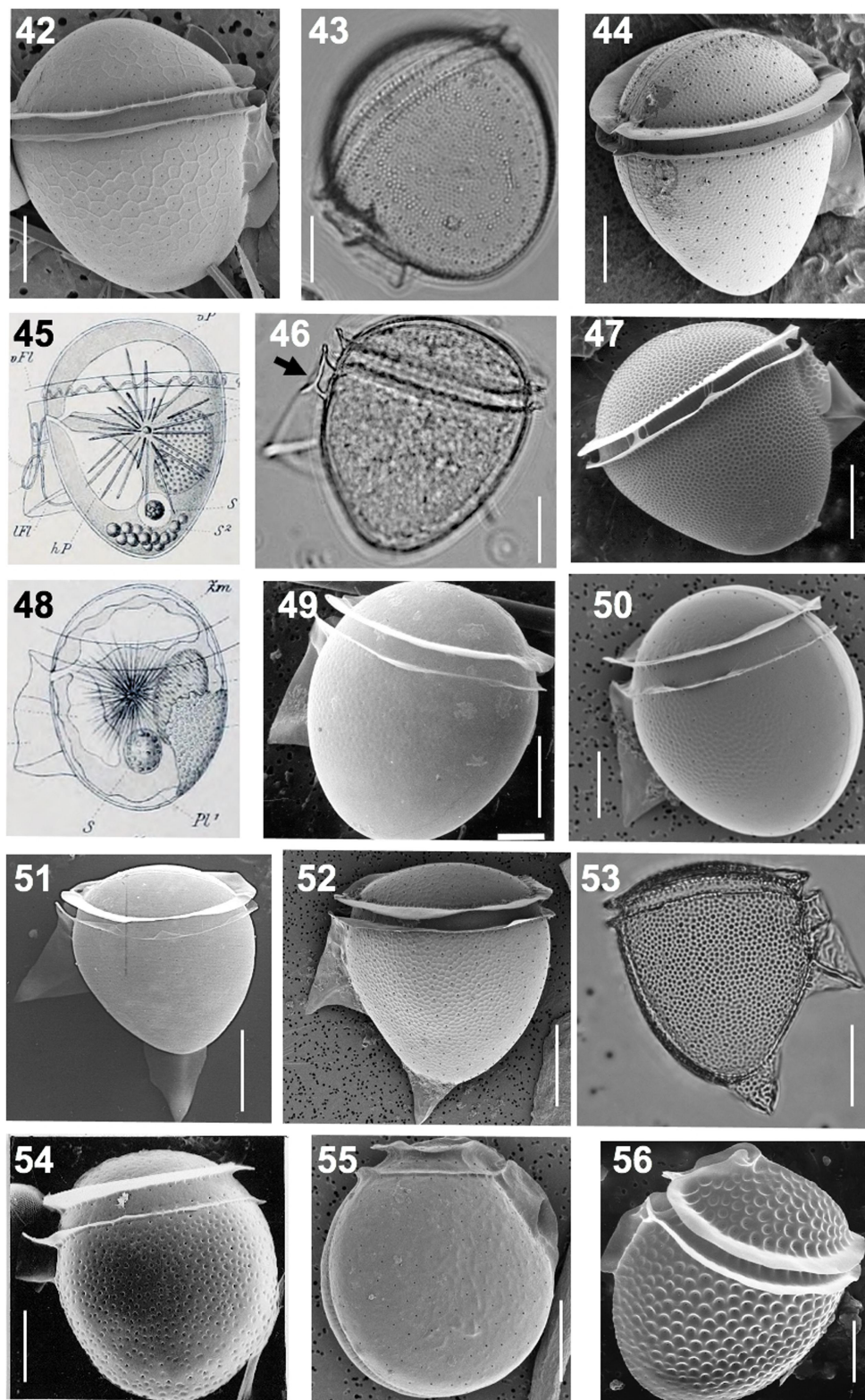


Fig. 42–56. (Caption on next page)

**Fig. 42–56.** Fig. 42. *Ph. argus* with a high epitheca and delicate reticulate ornamentation. SEM. Coral Sea. Fig. 43–44. *Ph. porodictyum* with finely areolate theca with scattered larger pores. Obovate species with the right sulcal list ending at a point midway between the fission rib and the posterior main rib of the left sulcal list. Fig. 43. LM. Fig. 44. SEM. Coral Sea. Fig. 45–46. *Ph. ovum*. Ovoid cell with finely areolate theca and medium sulcal lists. Fig. 45. Type illustration of Schütt (1895), *Ergebn. Plankton-Expedition Humboldt-Stiftung* fig. 11 (sub. 2), erroneously labelled as *Ph. operculoides*. Fig. 46. LM. East Australian Current. Fig. 47. SEM. North West Australia. Fig. 48–50. *Ph. operculoides* with smooth thecal surface and long sulcal list. Fig. 48. Type illustration of Schütt (1895), *Ergebn. Plankton-Expedition Humboldt-Stiftung* fig. 11 (sub. 1 and 3). Fig. 49. SEM. East Australian Current. Fig. 50. SEM. Indian Ocean. Fig. 51. *Ph. doryphorum* with straight girdle lists and a characteristic triangular ribless posterior sail not connected to the left sulcal list. SEM. Coral Sea. Fig. 52–53. *Ph. circumsutum* with the antapical spine directed ventrally. Fig. 52. SEM. Indian Ocean. Fig. 53. LM. Great Australian Bight. Fig. 54. *D. brevisulcus* with very short sulcal list. SEM. Sydney coastal waters. Fig. 55. *Metaphalacroma skogsbergii*, with epitheca small and less wide than hypotheca. The left and right girdle lists are very narrow and the posterior cingular list resembles a collar. SEM. Tasmania. Fig. 56. *Pseudophalacroma nasutum* with no ribs on the sulcal lists, and strongly areolate theca. SEM. Indian Ocean. Fig. 42, 44, 47, 53, 55 represent left lateral views, and Fig. 43, 45, 46, 48, 49, 50, 51, 52, 54, 56 right lateral views. Scale bars: 20 µm.

E.J.F.Wood, *D. opposita* E.J.F.Wood, *D. pacifica* E.J.F.Wood, *D. moresbyensis* E.J.F.Wood, *Ph. alata* E.J.F.Wood, *Ph. jibbonense* E.J.F.Wood, *Ph. mawsonii* E.J.F.Wood, *Ph. thompsonii* E.J.F.Wood, *Ph. triangulare* E.J.F.Wood and *Ph. whiteleggei* E.J.F.Wood. We did not confidently identify any of these taxa in our surveys.

### Ornithocercus

In total, seven *Ornithocercus* species were encountered in Australian waters, and the Australian Phytoplankton Database contains 282 distribution records. They are small to medium-sized (trans-diameter 30–40 µm; height 70–80 µm) species, with a circular full body in lateral view, with extensive ornate sulcal and cingular list and rib systems that characterise the species. Ribs and lists are formed at the extremities of plates, near the sutures. Body-surface markings consist of pores or areolae. *Ornithocercus* all lack chloroplasts, but they often carry cyanobacterial ectosymbionts in their cingular chamber. Species of this genus can be differentiated by size and shape, notably of their list features even though these are subject to maturational changes (Taylor 1973). The most common species in Australian waters are *O. magnificus* F.Stein (40–45 µm long, with a trilobed posterior sail, typically 3 ribs extend towards the median lobe; Fig. 57–60), *O. quadratus* F.Schütt (45–62 µm long, with square posterior sail, lacking median posterior lobes; Fig. 61, 63), *O. heteroporus* Kof. (Fig. 65–67) and *O. thumii* (A.W.F.Schmidt) Kof. & Skogsb. 1928 (misspelled by Wood 1954 as *O. thurni*; with multilobed sails). *Ornithocercus heteroporus* is the smallest species, 26–33 µm long, 57–83 µm high, with a bilobed posterior LSL. Its name is deceptive because the pores and areolae are no different from *O. quadratus* or *O. magnificus*. Following Taylor (1973), we consider *O. biclavatus* E.J.F. Wood to be a junior synonym of *O. heteroporus*, from which it differs only in the presence of rugose reticular masses occupying the lobes of the LSL (Fig. 67). The variability of *O. heteroporus*, including forms with nearly square sulcal lists (Fig. 66) to the more typical bilobed sulcal lists in mature cells (Fig. 65, 67), is accounted for in its type description (Kofoid and Skogsberg 1928). The most ornate *O. splendidus* F.Schütt (50–60 µm

long, with very extensive, posterior reticulate cingular lists; Fig. 68–70) and the type species *O. steinii* F.Schütt (Fig. 71) have rarely been observed in Australian waters. *Ornithocercus steinii*, 55–65 µm long, is often confused with *O. thumii*, but in *O. steinii* the b-rib terminates within the dorsal lobe, as opposed to that in *O. thumii* where the b-rib of the LSL terminates in a position distinctly ventral to the dorsal lobe of the list (Fig. 72–75). In *O. quadratus* and *O. magnificus*, one or two of the ribs are found on the inner side of the lists (usually the c-rib), whereas others are positioned on the outside; however, in *O. steinii* and *O. thumii* all ribs occur on one side of the LSL (Taylor 1973). We newly report from Australian waters *O. assimilis* Jörgensen 1923 emend. T.Wilke and Hoppenrath (Fig. 62, 64), previously treated as a form of *O. quadratus* but distinguishable by its posteriorly bent fission rib and dense reticulation of mature anterior sulcal lists (Wilke et al. 2018). Although Wood's (1954) distribution records of *Ornithocercus* were mainly confined to Australia's eastern coast from Moreton Bay to Maria Island, Hallegraeff and Jeffrey (1984) added many new records from the Coral Sea, Gulf of Carpentaria and North West Shelf. The ongoing IMOS surveys have added new records from tropical Darwin, Ningaloo, Rottnest Island, and the Indian Ocean off North West Australia. Other *Ornithocercus* species reported from Australian waters by Wood (1954) include *O. australis* E.J.F.Wood (never reported since), *O. carolinae* Kof., *O. carpentariae* E.J.F.Wood (never reported since), *O. formosus* Kof. & Mich., and *O. geniculatus* P.Dangard. We did not observe these taxa in our surveys.

### Histioneis and Parahistioneis

*Histioneis* species are heterotrophic, small dinophysoids (20–30 µm wide, up to 90 µm long) with large subcircular, reniform or subreniform cell bodies with ornate list and rib systems and a large cingular chamber. They are a readily recognisable group, best collected in deep water-column net samples; however, species are poorly characterised owing to uncertainty of the degree of variability in cell size and girdle and list features accompanying maturity (Gómez 2007). The posterior cingular list is often cup-shaped, with the largest



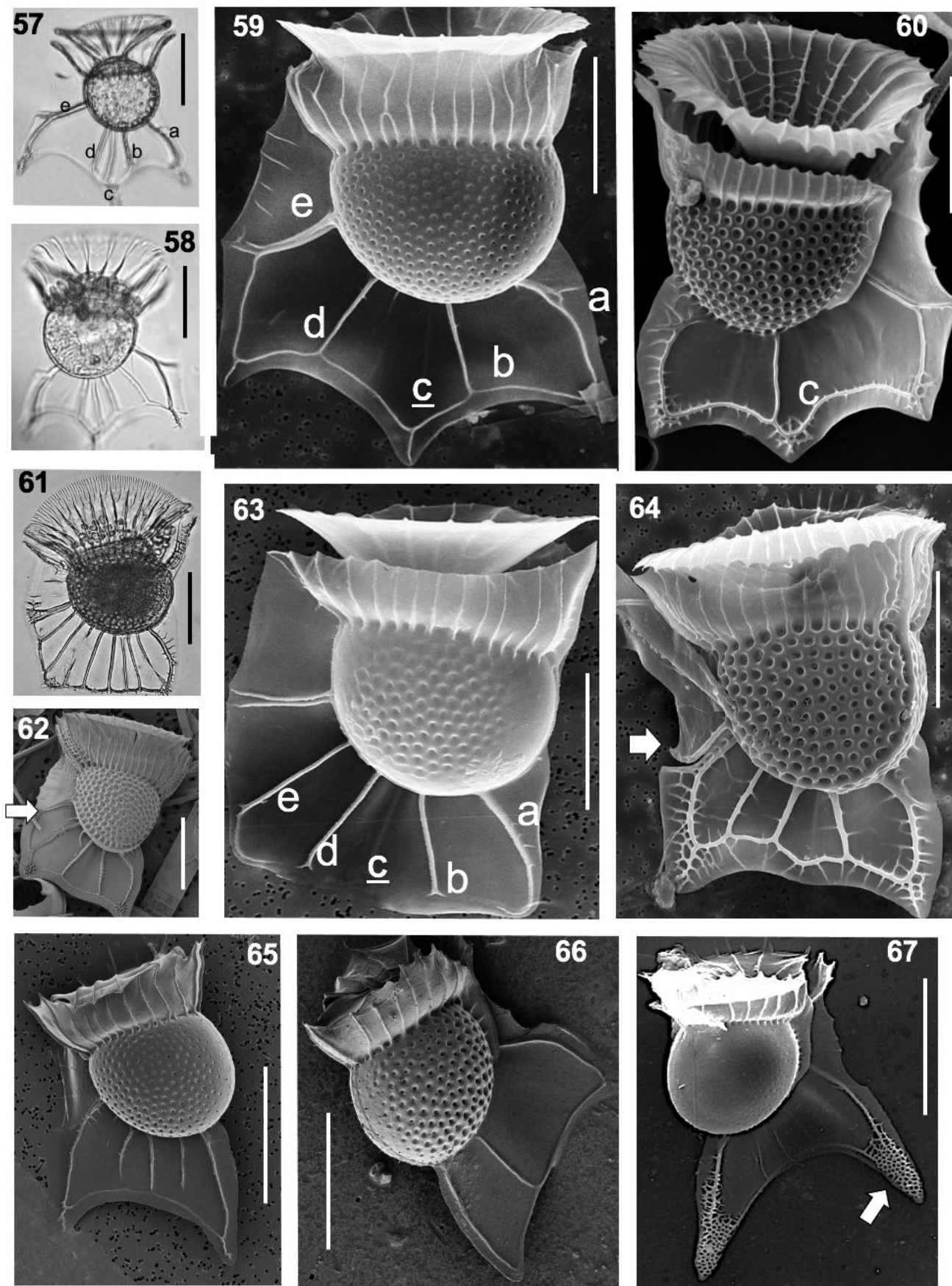


Fig. 57–67. (Caption on next page)

**Fig. 57–67.** Fig. 57–60. *Ornithocercus magnificus* with a trilobed posterior sail and typically three ribs, labelled b, c, d, extending towards the median lobe of the sulcal list. The annotation  $\underline{c}$  denotes that that rib is positioned on the other side of the sulcal list, just visible to shine through; Fig. 57. LM. Timor Sea. Fig. 58. LM. East Australian Current. Showing cyanobacterial ectosymbionts in the cingular chamber. Fig. 59. SEM. Gulf of Carpentaria. Left lateral view. Fig. 60. SEM. Right lateral view. Fig. 61, 63. *O. quadratus* with square posterior sail, and lacking median posterior lobes. Fig. 62. LM. East Australian Current. Showing cyanobacterial ectosymbionts in the cingular chamber. Fig. 63. SEM. East Australian Current. Left lateral view. Fig. 62, 64. *O. assimilis* with posteriorly bent fission rib (arrows) and reticulation of mature anterior sulcal lists. Fig. 65–67. *O. heteroporus* with bilobed posterior left sulcal list. Fig. 65. SEM. Indian Ocean. Left lateral view. Fig. 66. SEM. Indian Ocean. Right lateral view. Fig. 67. SEM. Coral Sea. Mature cell with more strongly lobed sulcal list and reticulate ornamentation of lobes (arrow). Fig. 58, 60, 66, 67 represent left lateral views, and Fig. 57, 59, 61, 63, 64, 65 right lateral views. Scale bars: 20  $\mu\text{m}$ .

portion of cingulum being posterior and with vertical support ribs. The anterior cingular area is reduced, sometimes turned into a funnel with a small anterior cingular list. The membranous right sulcal list is reduced but the left sulcal list is extensive, sometimes including a window formed by the R2 rib bending posteriorly and anastomosing with the R3 rib. The cell body carries surface markings of pores or areolae.

In total, 11 *Histioneis* species were confirmed from Australian waters, and the Australian Phytoplankton Database contains 79 distribution records. *Histioneis* cells contain a large cingular chamber that hosts cyanobacterial ectosymbionts. The small, 30–32  $\mu\text{m}$  long *H. garretii* Kof. (Fig. 76) represents a transition between *Ornithocercus* and *Histioneis*, with a large epitheca and long narrow left sulcal fin. In our material, *H. mitchellana* G.Murr. & Whitt. (130  $\mu\text{m}$  long, with rounded tapering of reticulated sulcal list; Fig. 77), and *H. milneri* G.Murr. & Whitt. (reniform cell body with highly developed sulcal list with accessory lists; Fig. 78, 79) were the most common. *Histioneis milneri* is considered synonymous with *H. helenae* G.Murr. & Whitt. and *H. hippoperoides* Kof. & Mich. (Gómez 2007). Other taxa identified include *H. elongata* Kof. & Mich. (90–110  $\mu\text{m}$  long, with a long striated R3 rib; Fig. 80, 81), *H. inclinata* Kof. & Skogsb. (27  $\mu\text{m}$  long, with simple rounded body short left sulcal fin; Fig. 82), *H. carinata* Kof. (with narrow boat-shaped cell body; Fig. 83), *H. highleyi* G.Murr. & Whitt. (with Y-shaped areolated hypotheca; Fig. 84), *H. cymbalaria* F.Stein (25  $\mu\text{m}$  long, with loop-shaped enforcement of the quadrangular window in its long left sulcal fin; Fig. 85), *H. schilleri* Böhm (small form with pointed tapering of sulcal list; Fig. 86), *H. longicollis* Kof. (round cell body with ventrally inclined sulcal list with circular window; Fig. 87) and *H. joergensenii* J.Schiller (with triangular window in left sulcal fin; Fig. 88).

Considering the poorly defined genus *Histioneis*, unlike Balech (1988), but in agreement with Zinssmeister et al. (2017), we maintained the separate genus *Parahistioneis* Kof. & Skogsb., which is distinguished by the absence of the cross-rib in the lower cingular list (arrowed in Fig. 88) and tends to have solid-walled heavily areolated cells. This genus was represented by *P. para* G.Murr. & Whitt. (with hemispherical hypotheca and straight left sulcal fin, Fig. 89;

synonymous with *P. conica* Böhm), *P. paraformis* Kof. et Skogsb. (42  $\mu\text{m}$  long, with hemispherical hypotheca and dorsally curved sulcal fin; Fig. 90; synonymous with *P. acuta* Böhm), *P. pieltainii* Osorio-Tafall (Fig. 91; with very heavily areolated cell body and reticulated left sulcal fin) and the shorter, stubbier *P. crateriformis* (F.Stein) Kof. & Skogsb. sometimes considered to be synonymous with *H. reticulata* Kof. (Fig. 92). Our cell tentatively identified as *P. pieltainii* is smaller than *P. diomedea* (Kof. & Mich.) Kof. & Skogsb. but distinct from *P. karstenii* (Kof. & Mich.) Kof. & Skogsb. in the direction of the terminal fin and more closely matches the deeply areolated cells illustrated by Osorio-Tafall (1942) from Mexico.

Other *Histioneis* species illustrated as line drawings from Australian waters by Wood (1954) include *H. cerasus* Böhm, *H. costata* Kof. & Mich., *H. hyalina* Kof. & Mich., *H. inornata* Kof. & Mich., *H. megalocopa* F.Stein, *H. panaria* Kof. & Skogsb., *H. panda* Kof. & Mich., *H. pietschmannii* Böhm, *H. remora* F.Stein, *H. rotundata* Kof. & Mich., *H. tubifera* Böhm, *H. variabilis* Schiller and *H. vouckii* J.Schiller. Several species newly characterised by Wood (1963b) have rarely or never been reported since, including *H. aequatorialis* E.J.F.Wood, *H. australiae* E.J.F.Wood, *H. bougainvilleae* E.J.F.Wood, *H. diamantinae* E.J.F.Wood, *H. lanceolata* E.J.F.Wood, *H. moresbyensis* E.J.F.Wood, *H. planeta* E.J.F.Wood, *H. simplex* E.J.F.Wood and *P. gascoynensis* E.J.F.Wood. We did not observe these taxa in our surveys.

*Citharistes* represents an unusual modification of the dinophysoid cell structure, with the small to medium-sized cell body deeply excavated on its dorsal side to create a C-shape in right lateral view. Enclosure of the cavity has been achieved by a shift in orientation of the lower girdle list and with the upper girdle list moved out of the 'phaeosome' chamber. The left sulcal list extends with ribs from the posterior cingular area to near the posterior part of the strongly areolate cell body. The smaller, 27–30  $\mu\text{m}$  high, *C. regius* F.Stein (Fig. 93) was detected in the Indian Ocean and Coral Sea, and the larger, 59–65  $\mu\text{m}$  high, *C. apsteinii* F.Schütt (Fig. 94, 95) was detected in the Coral Sea only. The latter species has a flat bottom, and rounded dorsal side of hypotheca. There exist only five distribution records of this genus in the Australian Phytoplankton Database and 49 global records in OBIS.



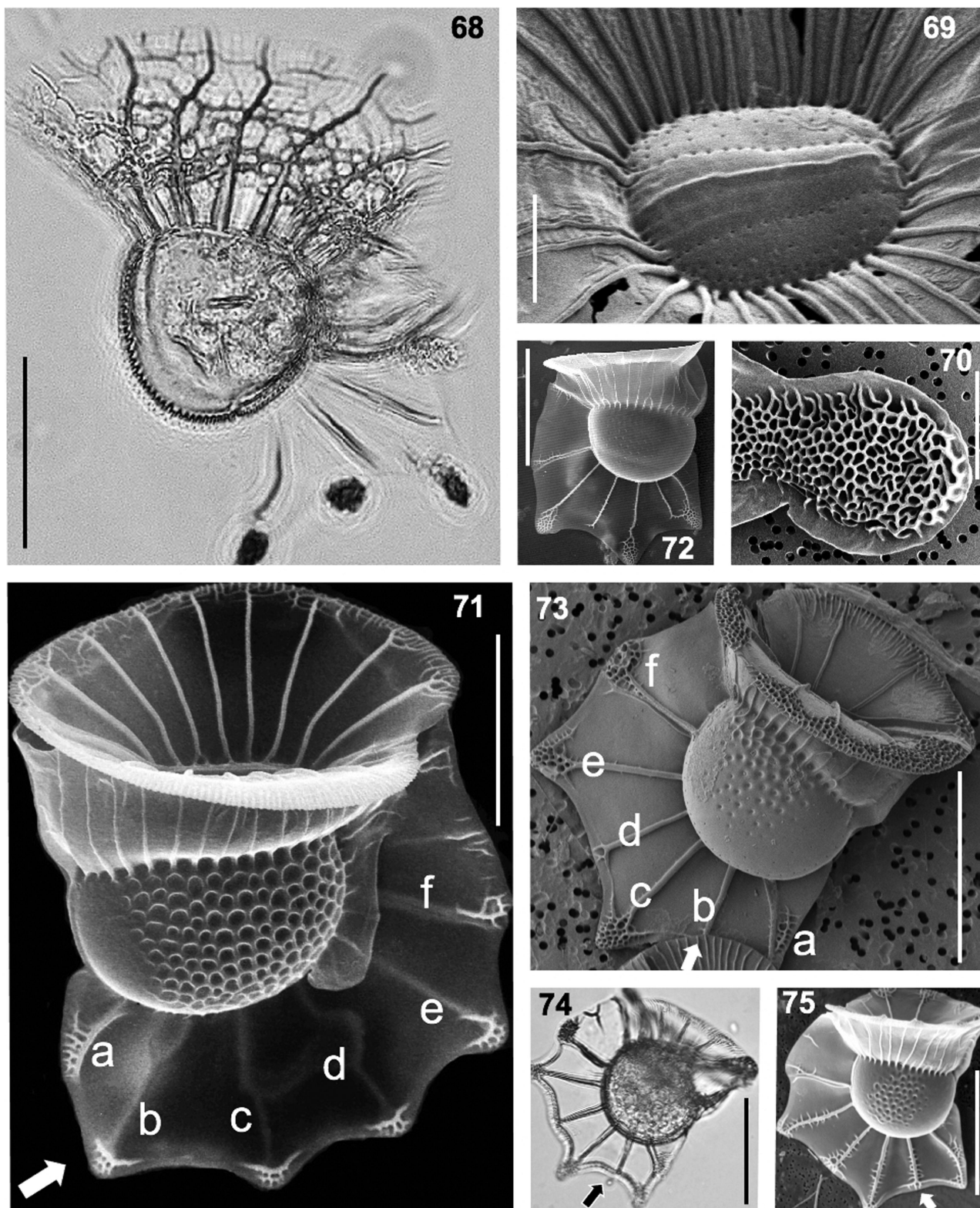


Fig. 68–75. (Caption on next page)

**Fig. 68–75.** Fig. 68–70. *O. splendidus* with very extensive, posterior reticulate cingular lists. Fig. 68. LM. Left lateral view. Fig. 69. SEM. Anterior view of epitheca. Fig. 70. SEM. Detail of reticulate ornamentation of sulcal list lobe ending, Stradbroke Island. Fig. 71. *O. steinii*. Right lateral view with the b-rib (arrow) terminating within the dorsal lobe. All ribs occur on the other side of the left sulcal list. SEM. Gulf of Carpentaria. Fig. 72–75. *O. thumii*. Left lateral views, with all ribs visible on the same side of the sulcal list. The b-rib of the left sulcal list terminates in a position distinctly ventral to the dorsal lobe of the list. Fig. 72. SEM. North West Shelf. Fig. 73. SEM. Coral Sea. Fig. 74. LM. Timor Sea. Fig. 75. SEM. Gulf of Carpentaria. Fig. 68, 71 represent left lateral views, and Fig. 72, 73, 74, 75 right lateral views. Scale bars: Fig. 68, 71–75, 20  $\mu\text{m}$ ; Fig. 69, 70, 5  $\mu\text{m}$ .

## Histiophysis

Our rediscovery of the genus *Histiophysis* (Kof. & Mich.) Kof. & Skogsb., intermediate between *Histioneis* (with an extending sulcal list) and *Dinophysis* (with upwardly curved cingular lists), deserves special mention. Initially described as *Dinophysis rugosa* by Kofoid and Michener (1911), on the basis of a single individual collected in 1904 at a depth of 0–549 m in the Eastern Tropical Pacific during a voyage by the US Fish Commission Steamer *Albatross*, 15°5'S, 99°19'W, this taxon was later transferred to *Histiophysis rugosa* (Kof. & Mich., 1911) Kof. & Skogsb., 1928 (Kofoid and Skogsb. 1928, pp. 333–334, pl. 5, fig. 5, type illustration here reproduced as Fig. 98).

In our work, we collected two individuals from the Coral Sea, one on RV Sprightly cruise SP16/80, on 14 November 1980, 19.30°S, 152.40°E (Fig. 96), and a further one 6 years later on FRV Soela cruise SO1/86, on 26 January 1986, 23.00°S, 155.00°E (Fig. 97), in both cases using surface to 150-m deep 37- $\mu\text{m}$  mesh net drops. This is a medium-sized species, with 45- $\mu\text{m}$  body length, 35- $\mu\text{m}$  body width, 62- $\mu\text{m}$  total cell length, which is broadly ovate in lateral view, broadly rounded posteriorly and narrowly rounded anteriorly. It is deepest just behind the middle. The epitheca is ~0.26 times as deep as the hypotheca, and its shape is gently convex. Dorsally the transverse furrow is 0.20 times the greatest depth of the body and approximately twice as wide as ventrally. The posterior cingular list is ~0.1 times the length of the body from the apex. The hypotheca is subcircular, somewhat narrower anteriorly than posteriorly, and its margins are confluent. The anterior cingular list has a well developed funnel shape, which flares approximately twice as much dorsally as ventrally, with the dorsal side more concave than the ventral; with a flat, slightly inclined top and it has on each valve ~11–13 ribs. The posterior cingular list is narrower and more inclined than is the anterior, it lacks ribs but is heavily reticulated, a feature never seen in *Dinophysis*. The RSL is long, narrow, and heavily reticulated and extends to the fission rib of the LSL. The LSL ends somewhat ventrally to the antapex and increases gradually in width posteriorly. Its ventral margin is strongly curved and somewhat dorsal margin has a postero-ventral inclination of ~25°, is gently sigmoid, concave anteriorly and convex posteriorly, forms an acute angle of ~60° with the ventral margin, and its length is ~0.46 times the greatest depth of the body. The list has only one rib, the fission rib, located at a point approximately two-thirds the way from the apex to the antapex, deflected

posteriorly at ~20°, and measuring 0.20 times the greatest depth of the body. In front of this rib the list is coarsely reticulated, most of the meshes being elongated transversely, and the margin is finely undulating. Behind this rib, the list is finely reticulated, and the margin is smooth. The thecal wall is finely, deeply and regularly areolated. Phaeosomes were described in the girdle of the type, but not seen in our formalin-preserved Coral Sea material.

*Amphisolenia* species are dinophysoid dinoflagellates, with the epitheca and cingulum forming a very small anterior 'head' on top a very thin and narrow body up to >1 mm in length (Fig. 99–101). Cells have often been interpreted as composed of a head, neck, shoulder, narrow body, sometimes with an inflated mid-region, and a foot. A portion of the plate surfaces are covered with pores (Fig. 103) The neck and shoulder have the sulcal plates and lists. The cingulum is circular (Fig. 100). The genus was represented by eight species in our material. *Amphisolenia bidentata* Schröder (with a foot end with two antapical spines; Fig. 103), is widespread. *A. inflata* Murr. & Whitt. (with inflated central cell body; Fig. 104), *A. palaeotheroides* Kof. (with a differentiated foot with heel spine and 3 antapical spines; Fig. 105), the spectacular Neptune's fork shaped *A. thrinax* F.Schütt (with 2 lateral antapical branches arising from the main antapical stem; Fig. 106), *A. palmata* F.Stein (with 3 antapical spines; Fig. 107), *A. clavipes* Kof. (with curled foot end; Fig. 108), *A. rectangulata* Kofoid (with 4 antapical spines; Fig. 109, 110 and *A. extensa* Kof. (club-shaped areolate foot without spines; Fig. 111) were mostly observed as single specimens in the Coral Sea or Indian Ocean only. In total, 211 distribution records of this genus exist in the Australian Phytoplankton Database. Other *Amphisolenia* species illustrated as line drawings by Wood include *A. astralagus* Kof. & Mich., *A. bifurcata* Murr. & Whitt., *A. bispinosa* Kof., *A. brevicauda* Kof., *A. curvata* Kof., *A. globifera* F.Stein, *A. laticincta* Kof., *A. lemmermanii* Kof., *A. schauinslandi* Lemmerm., *A. schroederi* Kof. and the related *Triposolenia bicornis* Kof. (Wood 1963b). We did not observe these taxa in our surveys.

## On the identity of *Ornithocercus*, *Histioneis*, *Citharistes*, *Amphisolenia*, *Phalacroma* and *Dinophysis* ecto- and endosymbionts

The tropical dinophysoid genera *Ornithocercus*, *Histioneis* and *Citharistes* commonly host coccoid symbionts (referred



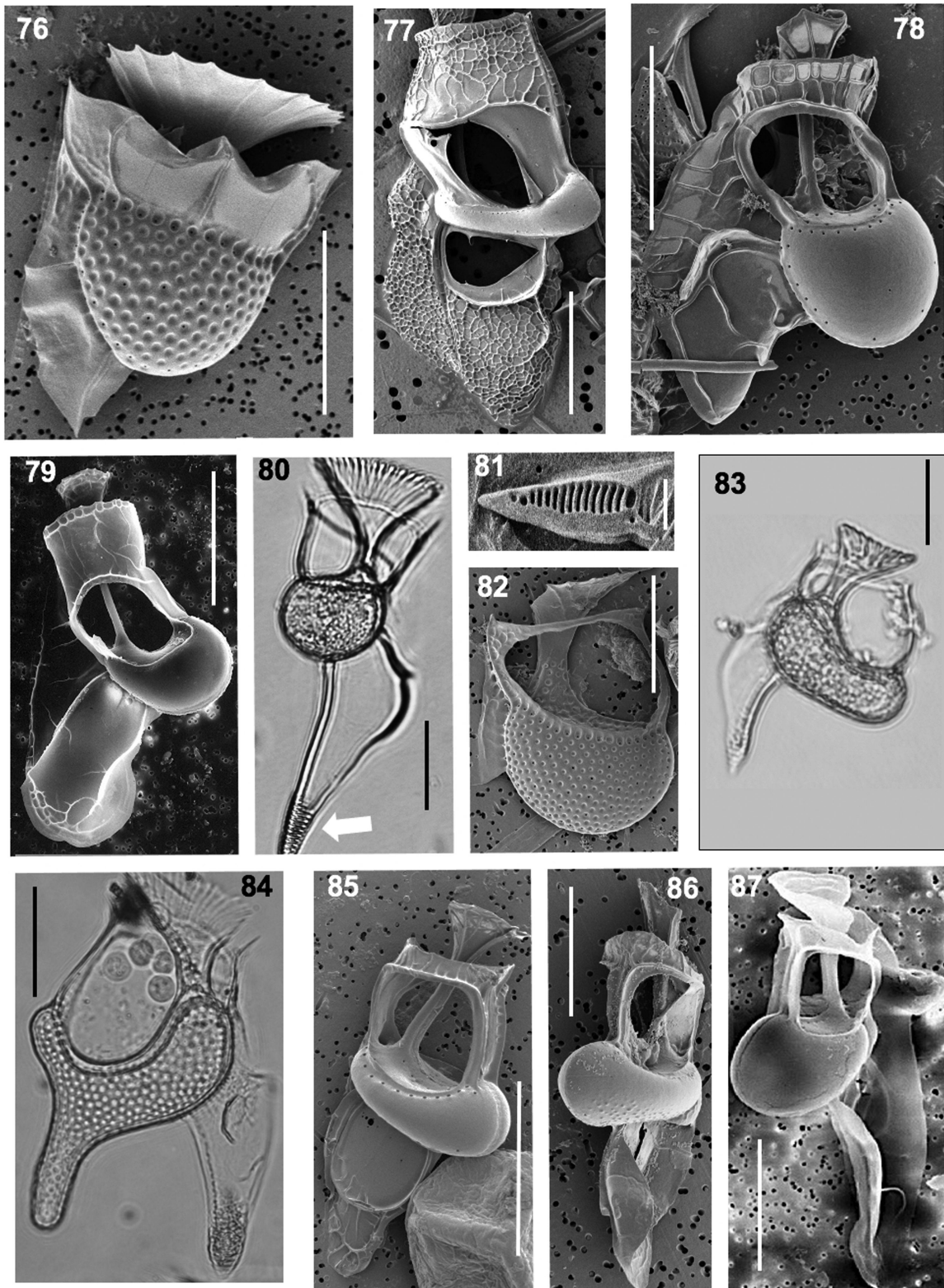


Fig. 76–87. (Caption on next page)

**Fig. 76–87.** Fig. 76. *Histioneis garrettii*, a transition between *Ornithocercus* and *Histioneis*, with a comparatively large epitheca and long narrow left sulcal fin. SEM. Indian Ocean. Fig. 77. *H. mitchellana*, with rounded tapering of reticulated sulcal list. SEM. Coral Sea. Fig. 78–79. *H. milneri*, with reniform cell body with highly developed sulcal list with accessory lists. Fig. 78. SEM. Indian Ocean. Fig. 79. SEM. Coral Sea. Fig. 80–82. *H. elongata*, with a long striated R3 rib (arrow). Fig. 80. LM. Coral Sea. Fig. 81. SEM. Detail of R3 rib. Fig. 82. *H. inclinata*. Small, simple cell body with spatula shaped left sulcal fin. SEM. Indian Ocean. Fig. 83. *H. carinata* with narrow boat shaped cell body. LM. Coral Sea. Fig. 84. *H. highleyi* with Y-shaped areolated hypotheca. LM. Coral Sea. Fig. 85. *H. cymbalaria* with loop-shaped enforcement of the quadrangular window in its long left sulcal fin. SEM. Indian Ocean. Fig. 86. *H. schilleri* with pointed tapering of sulcal list. SEM. Indian Ocean. Fig. 87. *H. longicollis* with round cell body with ventrally inclined sulcal list with circular window. SEM. Coral Sea. Fig. 80, 84, 86, 87 represent left lateral views, and Fig. 76, 77, 78, 79, 82, 83, 85 right lateral views. Scale bars: Fig. 76–80, 82–87, 20  $\mu\text{m}$ ; Fig. 81, 5  $\mu\text{m}$ .

to as ‘phaeosomes’ in older literature; Schütt 1895), either externally associated with their girdle lists (Fig. 58, 61), or internally contained within special chambers (Fig. 84, 95). Lucas (1991) was the first to characterise these pigmented phaeosomes from Australian dinophysoids by transmission electron microscopy, which allowed him to discriminate three or four prokaryote morphotypes, often present in mixtures within the same dinoflagellate host. Some 22 years later, Foster et al. (2006) used molecular polymerase chain reaction (PCR) techniques to confirm their identity as three clades of *Prochlorococcus* and one strain of *Synechococcus*. Kim et al. (2021), using 16S rDNA, confirmed three genetic types of *Synechococcales* in *Ornithocercus*, similarly often present in mixtures, some being host-specific but others common to the genus or shared with *Histioneis*, *Amphisolenia* and *Citharistes*. Lucas (1991) also identified one or two types of eukaryote endosymbionts inside *Amphisolenia* (Fig. 102, 104). Some 25 years later, by using molecular techniques, their identity was confirmed by Daugbjerg et al. (2013) as pelagophytes. The kleptochloroplasts of several *Dinophysis* and *Phalacroma* species were characterised by transmission electron microscopy by Hallegraef and Lucas (1988), and subsequently identified by genetic methods as having either cryptomonad affinities (*D. fortii*, *D. acuminata*; Hackett et al. 2003; see also Schnepf and Elbrächter 1988), or a mixture of cryptophytes, haptophytes and cyanobacteria (in *D. miles*; Qiu et al. 2011). Chloroplasts were absent in *D. hastata*, *D. schuettii*, *Ph. favus*, *Ph. parvulum*, *Ph. cuneus*, but an unidentified eukaryote symbiont was observed within *Ph. rapa* (Hallegraef and Lucas 1988). Koike et al. (2005), by using genetic methods, later identified kleptoplastids of haptophyte origin symbiont in the related *Ph. mitra* (see also Tarangkoon et al. 2010).

### Diarrhetic shellfish toxin (DST) producers

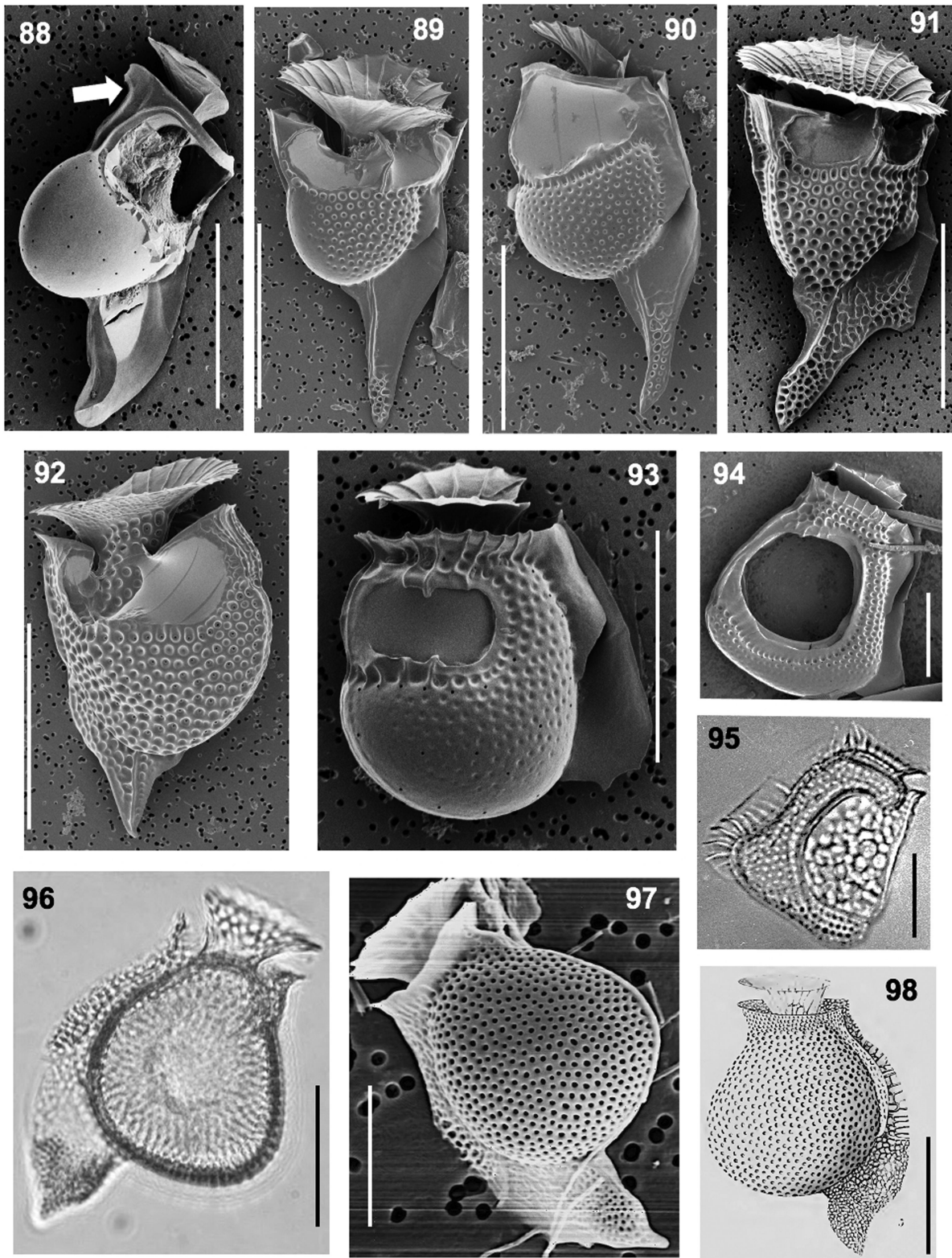
At least 10 *Dinophysis* and two *Phalacroma* species, namely *Ph. mitra* and *Ph. rotundatum*, have been demonstrated to contain diarrhetic shellfish toxins, DST (Reguera et al. 2012), whereas others potentially could be toxigenic but are commonly present in too low cell concentrations to cause problems. Evidence for toxigenicity of the only heterotrophic species, *Ph. rotundatum*, is doubtful (González-Gil et al. 2011). This taxon may be not a toxin-producer *de*

*novo*, but a vector of DST toxins taken from its tintinnid prey they had previously fed on. In Australian waters, the key species of concern able to achieve high cell abundances are *D. acuminata*, *D. caudata*, *D. fortii*, and *D. tripos*. *D. tripos* has never been conclusively associated, yet, with any toxic event in Australian waters. A significant human poisoning event occurred in 1997 in Ballina, NSW, resulting in 102 people being affected, with 56 hospitalisations, resulting from bivalve consumption of pipis (*Plebidonax deltoides*) contaminated with PTX-seco acids and dinophysistoxin-3 (DTX-3) from *D. acuminata* and *D. caudata* (Quaine et al. 1997; Burgess and Shaw 2001). In March 1998, a second outbreak was reported, in which 20 cases of DSP were reported (Hallegraef et al. 2021). Since then, DSTs have been a major food-safety challenge for the NSW pipi industry, with up to 40% of pipis in an end-product market survey between 2015 and 2017 returning positive results for DST, and two market-place samples above the regulatory limit (Farrell et al. 2018). DST in pipis and *Dinophysis* concentrations continue to be monitored in the Ballina area (Farrell et al. 2020). DSTs have also been occasionally detected in shellfish from Tasmania. During 2003–2004, high seasonal abundance of *D. acuminata* and associated *D. fortii* (up to 7380 cells  $\text{L}^{-1}$  for *D. acuminata*, 500 cells  $\text{L}^{-1}$  for *D. fortii*) in Sullivan’s Cove, Hobart, was associated with the detection of okadaic acid (OA) + dinophysistoxin-1 (DTX-1) in the digestive gland of non-commercial mussels (*Mytilus edulis*) with pectenotoxin-2 (PTX-2), PTX-2 seco acids and 7-epi-PTX-2 SA also being present (Wallace 2011). In Tasmania, DST was responsible for a recall of mussels from Spring Bay in 2016 (0.56  $\text{mg kg}^{-1}$  okadaic acid equivalent). Although a low risk, positive DST detections also occurred in shellfish from South Australia in 2000–2001 (Madigan et al. 2006) and Western Australia (but never exceeding regulatory levels of 0.20  $\text{mg kg}^{-1}$  OA equivalents).

### Phylogenetic relationships

Several molecular phylogenetic investigations have attempted to evaluate dinophysoid character evolution as hypothesised on the basis of morphology, but with limited results. On current evidence, planktonic dinophysoids are not monophyletic (Go’mez et al. 2012). Genetic studies of *Dinophysis* species have largely focused on the toxigenic species *D. acuminata*, *D. acuta*, *D. caudata*, *D. norvegica*





**Fig. 88–98.** (Caption on next page)



**Fig. 88–98.** Fig. 88. *Histioneis joergensenii*, with triangular window in the left sulcal list. The cross-rib in the lower cingular list that distinguishes *Histioneis* from *Parahistioneis* is arrowed. SEM. Indian Ocean. Fig. 89. *Parahistioneis para* with hemispherical hypotheca and straight ventral ending left sulcal fin. SEM. Coral Sea. Fig. 90. *P. paraformis* with curved left sulcal fin. SEM. Indian Ocean. Fig. 91. *P. pieltanii*. Heavily reticulated cell. SEM. Indian Ocean. Fig. 92. Short stumpy cell of *P. crateriformis*. SEM. Indian Ocean. Fig. 93. *Citharistes regius* with the small cell body deeply excavated on its dorsal side to create a C-shape in right lateral view. SEM. Indian Ocean. Fig. 94–95. *C. apsteinii* with a flat bottom and rounded dorsal side of hypotheca. Fig. 94. SEM. Fig. 95. LM. Coral Sea, showing cyanobacterial endosymbionts in phaeosome chamber. Fig. 96–98. *Histiophysis rugosa*, intermediate between *Histioneis* and *Dinophysis*. The thecal wall is finely, deeply and regularly areolated. The left sulcal list has only one rib, the fission rib; in front of this rib the list is coarsely reticulated, behind this rib the list is finely reticulated. Fig. 96. LM, Fig. 97. SEM. Coral Sea. Fig. 98. Type illustration by Kofoid and Skogsborg's (1928) pl. 5, fig. 5. *Memoirs Museum Comparative Zoology* vol. 51. Fig. 88, 89, 90, 92, 93, 94, 98 represent left lateral views, and Fig. 92, 95, 96, 97 right lateral views. Scale bars: 20  $\mu\text{m}$ .

Clap. & J.Lachm. and *D. tripos*. Striking morphological differences between, for example, *D. norvegica* and *D. acuminata* (Edwardsen *et al.* 2003) and within the *D. acuminata*–*D. sacculus* F.Stein complex (Séchet *et al.* 2021), or attempts to separate *D. acuminata* and *D. ovum* (Park *et al.* 2019; Raho *et al.* 2008), have all encountered very limited genetic support. Generally, species of Dinophysales are best discriminated using a combination of sequences of the mitochondrial *cox1* gene and the *ITS1*–*SSU* rDNA *ITS2* gene, and with poor results by using *LSU* rDNA (Edwardsen *et al.* 2003; Gómez *et al.* 2011; Handy *et al.* 2009). Identical *LSU* rDNA sequences were thus observed for the morphologically distinctive *D. tripos*, *D. miles* and *D. odiosa* (Pavill.) L.S.Tai & Skogsb. (Jensen and Daugbjerg 2009). Similarly, Jensen and Daugbjerg (2009) found identical *LSU* rDNA gene sequences for *O. quadratus* and *O. steinii*, and *SSU* sequences of two *O. quadratus* varieties (var. *quadratus* (Jörg.) Taylor and f. *schuettii* Kofoid & Skogsb.) were identical in the study by Gómez *et al.* (2011). However, uniform genetic support has now been achieved for the separation of *Phalacroma* from *Dinophysis* (Jensen and Daugbjerg 2009), which we adopted here throughout.

Lack of success in culturing most dinophysoid species has limited our understanding of morphological variability by individual taxa and has contributed to the paucity of molecular sequences available. The first cultures of mixotrophic *Dinophysis* were achieved only in 2006 by feeding with the phototrophic ciliate *Mesodinium rubrum*, which in turn had been fed with cryptomonads such as *Teleaulax*, *Plagioselmis* and *Geminigera* (Park *et al.* 2006). As far as known to us, heterotrophic dinophysoids have not yet been cultured, with the exception of feeding experiments with freshly caught dinoflagellates in laboratory experiments, such as, for example, *Ph. rotundatum* feeding on the ciliate *Tiarina fusus* (Hansen 1991). The extreme rarity of tropical genera such as *Histioneis* and *Amphisolenia* undoubtedly has contributed to the fact that many species have never been reported since their initial description (Wood 1954, 1963a, Gómez 2007; 1963b). This is reflected in the extraordinary number of 91 *Histioneis* species formally described, of which 35 taxa have been observed only once, so-called ‘orphan’ taxa (Gómez 2007). *Histioneis*, *Parahistioneis* and *Ornithocercus* species remain especially poorly characterised owing to uncertainty of degree of variability in cell size and girdle and list features

accompanying maturity (Taylor 1973). Similarly, non-descriptive small *Ph. rotundatum*-like taxa have rarely been correctly identified to species level (Daugbjerg *et al.* 2019).

### Species distributions

The island continent of Australia is surrounded by surface and subsurface boundary currents that flow along the continental shelf and slope. The unique feature of this circulation is that along both eastern and western coasts, boundary currents transport warm-water southward via the East Australian and Leeuwin currents respectively (Fig. 1, Wijeratne *et al.* 2018). These boundary currents are enhanced through inflows from the South Pacific and South Indian Ocean basins, and represent an important conduit for the poleward heat and mass transport and inter-ocean water exchange in the tropics. Table 3 compiles the number of occurrence records for the most common taxa, ranging from 4467 for *D. acuminata*, 1754 for *D. caudata*, but being down to 246 for all combined *Ornithocercus* and 75 for all combined *Histioneis* species. Typical background abundance levels from routine offshore Continuous Plankton Recorder tows ranged from 0.67 to 3.33 cells  $\text{L}^{-1}$ , and typically 5–10 *Ornithocercus* or *Histioneis* cells were observed of 100–1000 net-phytoplankton cells (0.0001–1% of total phytoplankton volume; Hallegraeff and Jeffrey 1984); however, selected surveys in estuaries have yielded *Dinophysis* concentrations of 3000–14 000 cells  $\text{L}^{-1}$ . Table 2 tabulates regional distribution patterns of all taxa discussed.

Some dinophysoids such as *D. acuminata*, *D. caudata*, *D. fortii* and *D. tripos* occur both in tropical and temperate Australian waters (Fig. 112), but many others have strong warm-water preferences. Temporal shifts in sampling efforts in the periods 1940–1960, 1960–1980, 1980–2000, and 2000–2019 reflect the focus of different analysts (Wood 1954, 1963a, 1963b; Hallegraeff and Jeffrey 1984; Hallegraeff and Reid 1986; Jeffrey and Hallegraeff 1987; Eriksen *et al.* 2019; IMOS, since 2009; and others). Furthermore, water-column net samples consistently retrieved a higher diversity of dinophysoid species than did Continuous Plankton Recorder silks (CPR; towed offshore and subsurface only) and water-bottle samples (as in the National Reference Stations, NRS). In our work, *D. hastata* was one of the common *Dinophysis* species in

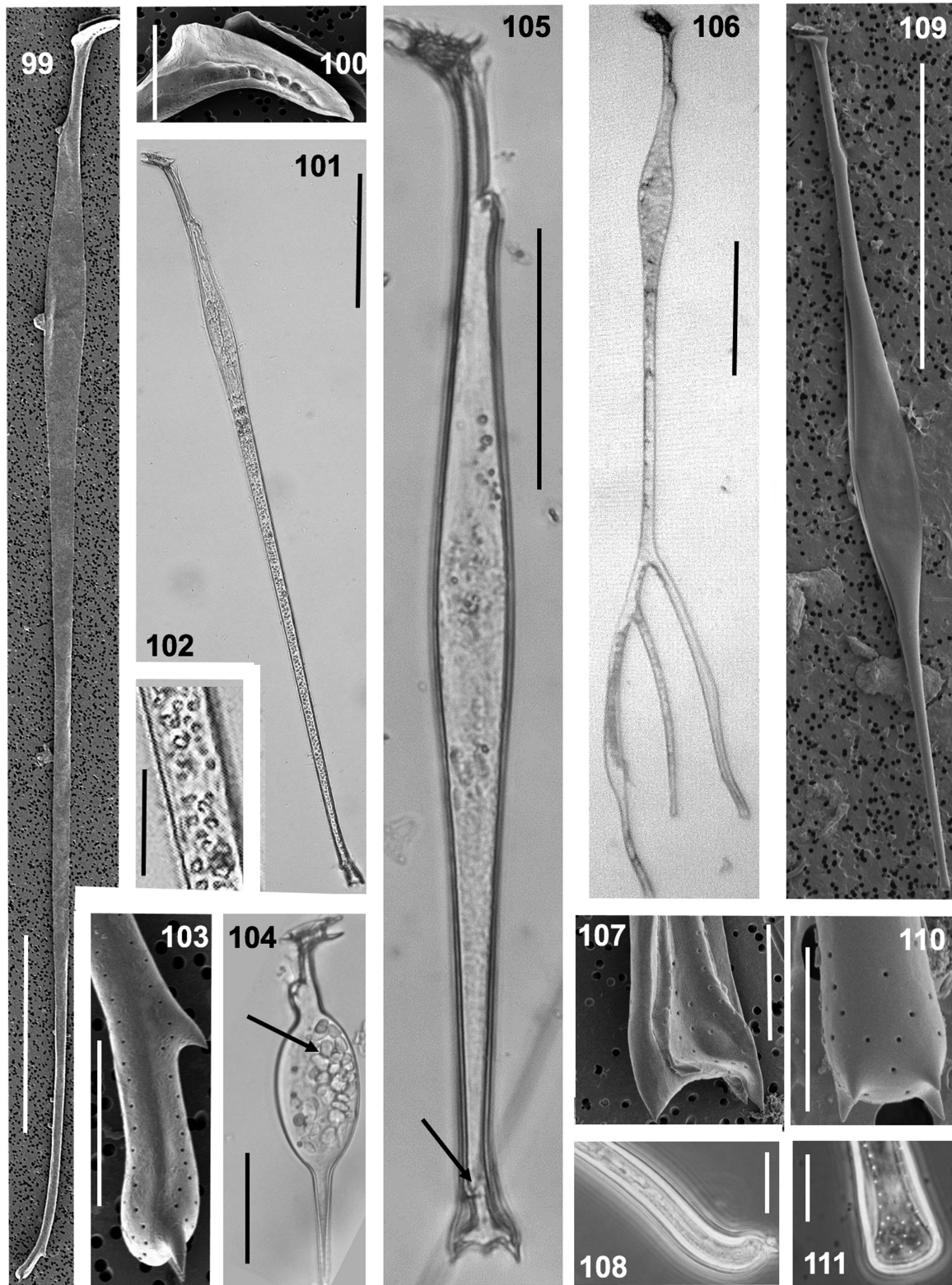
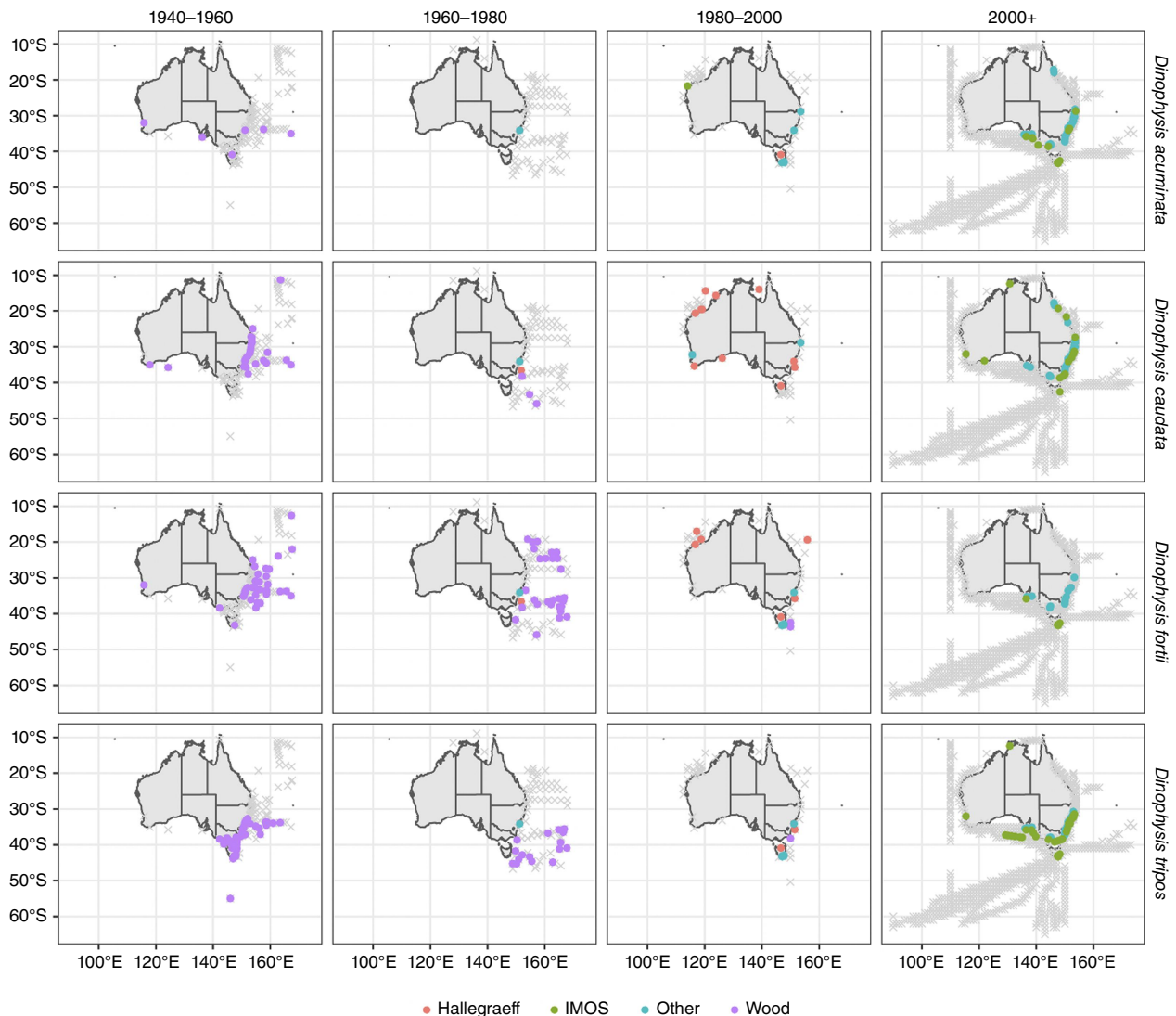


Fig. 99–111. (Caption on next page)



**Fig. 99–111.** Fig. 99–103. *Amphisolenia bidentata*. Fig. 99. SEM. Complete cell from East Australian Current. Fig. 100. SEM. Detail of head end from North West Shelf of Australia. Fig. 101. LM. Complete cell from East Australian Current. Fig. 102. LM. Detail of coccoid endosymbionts. Fig. 103. SEM. Detail of foot end with two antapical spines. Fig. 104. *A. inflata*. Complete cell with inflated cell body and arrows indicate endosymbionts. LM. Coral Sea. Fig. 105. LM. *A. palaeotheroides*, with a differentiated foot with a heel spine (arrow) and three antapical spines. Coral Sea. Fig. 106. *A. thrinax* with two lateral antapical branches arising from the main antapical stem. LM. Stradbroke Island. Fig. 107. *A. palmata*. Detail of foot end with three antapical horns. SEM. Indian Ocean. Fig. 108. *A. clavipes*. Detail of curled foot end. LM. Indian Ocean. Fig. 109–110. *A. rectangulata*. Fig. 109. Complete cell. Fig. 110. Foot end with 4 antapical spines. SEM. Coral Sea. Fig. 111. *A. extensa*. Detail of club-shaped foot end without spines but coarse areolation. Indian Ocean. Fig. 101, 105, 106, 109 represent left lateral views, and Fig. 99, 104 right lateral views. Scale bars: Fig. 99, 101, 105, 107, 109, 100  $\mu\text{m}$ ; Fig. 100, 102, 103, 107, 108, 110, 111, 20  $\mu\text{m}$ .

## 112



**Fig. 112.** Sixty years of Australian distribution records of the most common *Dinophysis acuminata*, *D. caudata*, *D. fortii* and *D. tripos* reflect temporal shifts in sampling locations and techniques among different analysts (Hallegraeff, Wood, IMAS, others) in the periods of 1940–1960, 1960–1980, 1980–2000 and 2000–2019.

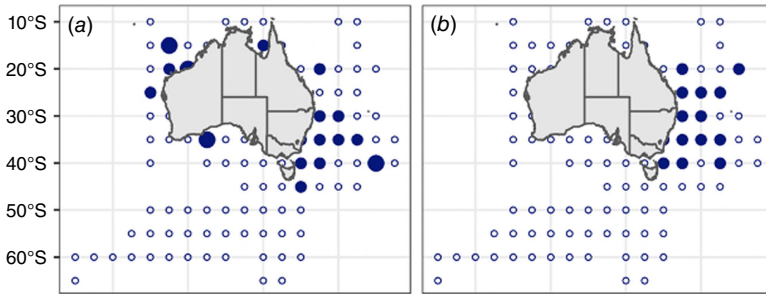


113

Warm offshore indicator

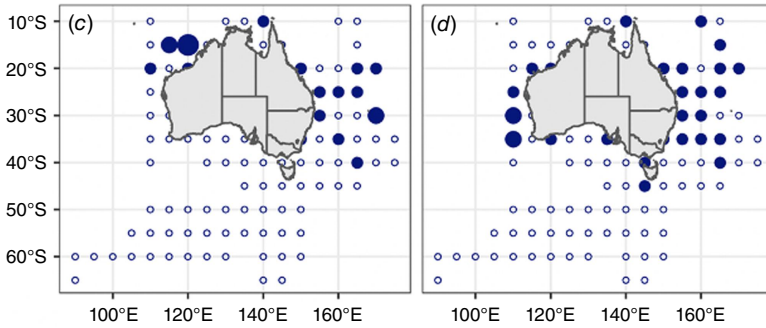
*Dinophysis hastata*

*Dinophysis schuettii*



*Ornithocercus heteroporus*

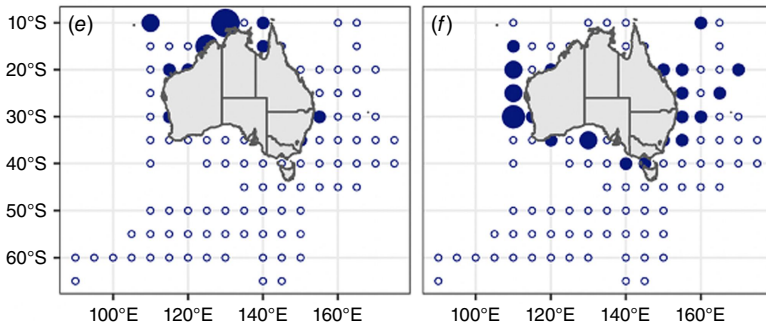
*Ornithocercus magnificus*



Warm inshore indicator

*Dinophysis miles*

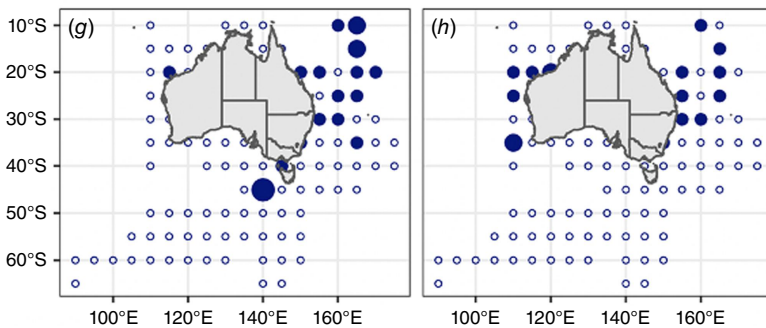
*Ornithocercus quadratus*



Warm offshore inshore indicator

*Phalacroma mitra*

*Phalacroma rapa*



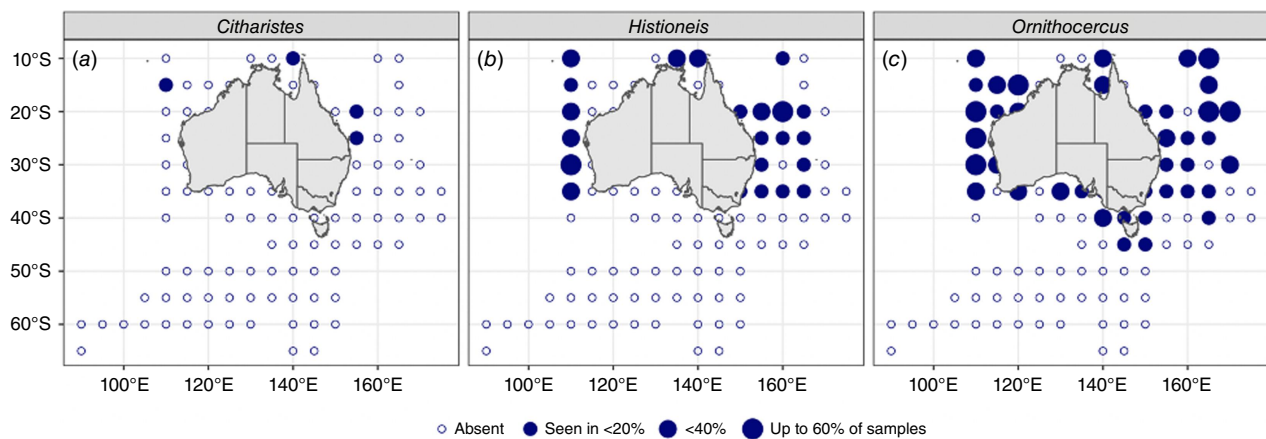
○ Absent ● Seen in <20% ● <40% ● <60% ● <80% ● Up to 100% of samples

**Fig. 113.** Compilation of Australian distribution records of selected warm-water offshore (*D. hastata*, *D. schuettii*, *O. heteroporus*, *O. magnificus*), warm-water inshore (*D. miles*, *O. quadratus*) and combined warm-water inshore or offshore dinophysoid species (*Ph. mitra*, *Ph. rapa*). Open symbols indicate absence of species records.

Australian tropical waters (63 observations; Fig. 113a), whereas *D. miles* was exclusively observed in the Gulf of Carpentaria, North-West Shelf, Darwin, and off Rottnest Island (39 observations; Fig. 113e). *Dinophysis schuettii*

( $n = 51$ ; Fig. 113b) had a predominantly warm-water oceanic distribution in the Coral Sea and East Australian Current, but has been rarely observed in shallow shelf waters of tropical north-western Australia. *Dinophysis*

## 114



**Fig. 114.** Compilation of Australian distribution records of the rare genera *Citharistes* and *Histioneis* and the more common *Ornithocercus*. Open symbols indicate absence of species records.

*truncata* ( $n = 53$ ) is a Subantarctic species, rare in Tasmanian and South Australian waters but also known from New Zealand (Burns and Mitchell 1982). The three strongly areolate species of *Ph. mitra* ( $n = 75$ ; Fig. 113g), *Ph. rapa* ( $n = 37$ ; Fig. 113h) and *Ph. favus* (19) were common in tropical neritic waters. In our study, *Ph. mitra* was the most widespread. *Ornithocercus* and *Histioneis* are stenotherm warm-water species. *O. quadratus* ( $n = 84$ ; Fig. 113f) was more common inshore, and *O. magnificus* ( $n = 56$ ; Fig. 113d) and notably *O. heteroporus* ( $n = 26$ ; Fig. 113c) were more common offshore. The rare genus *Citharistes* has never been reported south of Brisbane (Fig. 113a). Unlike *Dinophysis*, *Phalacroma* and *Ornithocercus*, the genera *Amphisolenia* and *Histioneis* (Fig. 113b) were never observed in estuaries. Although Wood's (1954) distribution records of *Ornithocercus* were mainly confined to Australia's eastern coast, from Moreton Bay to Maria Island, Hallegraeff and Jeffrey (1984) added many new records from the Coral Sea, Gulf of Carpentaria and North West Shelf, and the present IMOS work added numerous new records from coastal stations off Darwin, Ningaloo and Rottneest Island. *Ornithocercus* species only very rarely have been detected as far south as Tasmania off Maria Island (September 1984) and in the Huon River (July 2016, with cyanobacterial symbionts present). These warm-water species can occasionally be carried southward by the East Australian Current and Leeuwin Current (Fig. 1); however, they are not persistent residents in these waters (Fig. 114).

In total, the present work analysed 9350 Australian records of 64 confirmed species of marine planktonic dinophysoid dinoflagellate genera, including the genera *Dinophysis* (17 species; 8082 records), *Phalacroma* (12; 953 records), *Metaphalacroma* (1), *Pseudophalacroma* (1), *Ornithocercus* (7 spp.; 289 records), *Histioneis* (11 spp.; 102 records), *Parahistioneis* (4), *Histiophysis* (1; 2 records), *Citharistes*

(2; 5 records) and *Amphisolenia* (8; 223 records). Wood's (1954) early survey of Australian waters reported a comparable 50 species, but his later observations (Wood 1963a, 1963b) from the Coral Sea and Indian Ocean yielded a further 67, although poorly defined, species, many of which have never been reported since and remain of uncertain status.

Comparable surveys on the tropical Mexican Pacific by Esqueda-Lara and Hernández-Becerril (2010) and Hernández-Becerril et al. (2021) yielded 34–56 species, Omura et al. (2012) reported 73 species from the western Pacific, Balech (1988) reported 82 species from the South West Atlantic, and Zinssmeister et al. (2017) found 75 species from the eastern Pacific. Dinophysoid dinoflagellates in the Indian Ocean were characterised by Taylor (1976) who reported 48 spp. (summarised in Table 4). None of these surveys matched the astounding work by early pioneers such as Kofoid and Michener 1911; Kofoid and Skogsberg 1928; Tai and Skogsberg 1934) in the eastern Pacific documenting 132 species of which 88 were new to science. We newly report from Australian waters *O. assimilis* Jörg., *Metaphalacroma skogsbergii* L.S.Tai, *Parahistioneis pieltainii* Osorio-Taffal, *Amphisolenia extensa* Kof., *A. inflata* G.Murr. & Whitt. and *A. rectangularata* Kof. We should never underestimate the extraordinary observation skills by these early workers as demonstrated here by the rediscovery of *Histiophysis rugosa* (Kof. & Mich.) Kof. & Skogsb. collected in 1904 from the tropical eastern Pacific on the basis of a single individual only, but here observed with two further cells collected from the Coral Sea in 1980 and 1986 respectively. That is, only three cells were observed in the entire world oceans in 100+ years. These rarer tropical species deserve careful attention in monitoring for future range expansions, changes in seasonality or upwelling or incursion of deep tropical waters, but call for water-column net samples for appropriate collection.

**Table 4.** Dinophysoid species numbers reported from various geographic regions.

Species	Present study	Australian waters (Wood 1954, 1963a, 1963b)	Eastern Pacific (Kofoid and Skogsberg 1928)	Eastern Pacific (Zinssmeister et al. 2017)	Central Pacific Mexico (Esqueda-Lara and Hernández-Becerril 2010)	Central Pacific Mexico (Hernández-Becerril et al. 2021)	Western Pacific (Omura et al. 2012)	South West Atlantic (Balech 1988)	Indian Ocean (Taylor 1976)
<i>Amphisolenia</i>	8	5 + 10 + 2	26	9	6	7	10	7	8
<i>Citharistes</i>	2	0	2	1	0	1	2	2	1
<i>Dinofurcula</i>	0	0	2	0	0	0	0	0	0
<i>Dinophysis</i>	17	18 + 8 + 3	20	15	6	7	20	32	11
<i>Histioneis</i>	11	4 + 28 + 0	24	8	4	6	20	12	8
<i>Histiophysis</i>	1	0	1	0	0	0	0	0	0
<i>Heteroschisma</i>	0	0	2	1	0	0	0	3	0
<i>Ornithocercus</i>	7	9 + 5 + 0	9	9	10	8	13	7	7
<i>Metaphalacroma</i>	1	0	0	0	0	0	0	1	0
<i>Parahistioneis</i>	4	2 + 4 + 1	7	3	0	2	4	1	1
<i>Phalacroma</i>	12	26 + 5	31	16	8	25	15	15	11
<i>Pseudophalacroma</i>	1	1	0	2	0	0	1	0	0
<i>Triposolenia</i>	0	0 + 1	8	1	0	0	1	1	1
<b>Total</b>	<b>64</b>	<b>50 + 67 = 117</b>	132	<b>75</b>	<b>34</b>	<b>56</b>	<b>73</b>	<b>70</b>	<b>48</b>



## References

- Abe TH (1967) The armoured dinoflagellata: II. Prorocentridae and Dinophysidae (B). *Dinophysis* and its allied genera. *Publications of the Seto Marine Biological Laboratory* **15**, 37–78. doi:10.5134/175455
- Ajani P, Larsson ME, Rubio A, Bush S, Brett S, Farrell H (2016) Modelling bloom formation of the toxic dinoflagellates *Dinophysis acuminata* and *Dinophysis caudata* in a highly modified estuary, south eastern Australia. *Estuarine, Coastal and Shelf Science* **183**, 95–106. doi:10.1016/j.ecss.2016.10.020
- Balech E (1967) New or interesting dinoflagellates from the Gulf of Mexico and the Caribbean. *Revista Museo Argentina de Ciencias Naturales Bernardino Rivadavia. Hidrobiologia* **2**, 87–135. [In Spanish]
- Balech E (1976a) Some Norwegian *Dinophysis* species (Dinoflagellata). *Sarsia* **61**, 75–94.
- Balech E (1976b) Notas sobre el genero *Dinophysis* (Dinoflagellata). *Physis A* **35**, 183–193. [In Spanish]
- Balech E (1988) Los dinoflagelados del Atlantico sudoccidental. *Publications Especial Instituto Espanol Oceanograficos* **1**, 310. [In Spanish]
- Böhm A (1931) Peridineen aus dem Persischen Golf und dem Golf von Oman. *Achive für Protistenkunde* **74**, 188–197. [In German]
- Burgess V, Shaw G (2001) Pectenotoxins – an issue for public health: a review of their comparative toxicology and metabolism. *Environment International* **27**, 275–283. doi:10.1016/S0160-4120(01)00058-7
- Burns DA, Mitchell JS (1982) Dinoflagellates of the genus *Dinophysis* Ehrenberg from New Zealand coastal waters. *New Zealand Journal of Marine and Freshwater Research* **16**, 289–298. doi:10.1080/00288330.1982.9515972
- Cleve PT (1901) Plankton from the Indian Ocean and the Malay Archipelago. *Kungliga Svenska Vetenskapsakademiens Handlingar* **35**(5), 8–58. [In Swedish]
- Claparède E, Lachmann J (1859) Studies on infusories and rhizopods *Mémoires de l'Institut National Genevois* **6**, 261–482. [In French]
- Daugbjerg N, Jensen MH, Hansen PJ (2013) Using nuclear-encoded *LSU* and *SSU* rDNA sequences to identify the eukaryotic endosymbiont in *Amphisolenia bidentata*. *Protist* **164**, 411–422. doi:10.1016/j.protis.2012.10.001
- Daugbjerg N, Hansen SA, Richardson K (2019) Cryptic diversity of small-sized species of *Phalacroma* (Dinophysales, Dinophyceae) from Denmark Strait (eastern Arctic Greenland). *Phycological Research* **67**, 244–249. doi:10.1111/pre.12366
- Davies CH, Hallegraef G, Ajani P, Armbrrecht L, Bonham P, Brett S, Burford M, Clementson L, Coman F, Coughlan A, Davies D, Dela-Cruz J, Devlin M, Edgar S, Eriksen R, Furnas M, Hassler C, Ingleton T, Leterme SC, McEnnulty F, Miller M, Nayar S, Pritchard T, Proctor R, Purcell D, Slotwinski A, Tattersall K, Thompson P, Tonks M, Trull T, Uribe-Palomino J, Swadlow K, Zammit A, Richardson AJ (2016) A database of marine phytoplankton abundance, biomass and species composition in Australian waters. *Scientific Data* **3**, 160043. doi:10.1038/sdata.2016.43
- Delgado M, Fortuño J-M (1991) Atlas of Phytoplankton of the Mediterranean Sea. *Scientia Marina* **55**(Suppl.), 1–133. [In Spanish]
- Edvardsen B, Shalchian-Tabrizi K, Jakobsen KS, Medlin LK, Dahl E, Brubak S, Paasche E (2003) Genetic variability and molecular phylogeny of *Dinophysis* species (Dinophyceae) from Norwegian waters inferred from single cell analyses of rDNA. *Journal of Phycology* **39**, 395–408. doi:10.1046/j.1529-8817.2003.01252.x
- Ehrenberg CG (1839) Über jetztwirklich noch zahlreich lebende Thier-Arten der Kreideformation der Erde. *Berichtüber die zur Bekanntmachung geeigneten Verhandlungen der Königl. Preuß. Akademie der Wissenschaften zu Berlin* 152–159. [In German]
- Eriksen RS, Davies CH, Bonham P, Coman FE, Edgar S, McEnnulty FR, McLeod D, Miller MJ, Rochester W, Slotwinski A, Tonks ML, Uribe-Palomino J, Richardson AJ (2019) Australia's long-term plankton observations: the Integrated Marine Observing System National Reference Station network. *Frontiers in Marine Science* **6**, 161. doi:10.3389/fmars.2019.00161
- Esqueda-Lara K, Hernández-Becerril DU (2010) 'Marine microplanktonic dinoflagellates of the central Pacific of Mexico (Isabel Island, Nayarit and coasts of Jalisco and Colima). Institute of Marine Sciences and Limnology.' (National Autonomous University of Mexico: Mexico City, Mexico)
- Esqueda-Lara K, Parra-Toriz D, Hernández-Becerril DU (2013) Morphology and taxonomy of *Dinophysis* species of the section *Hastata* (Dinoflagellata), including the description of *Dinophysis conjuncta* sp. nov., from the Mexican marine waters. *Journal of the Marine Biological Association of the United Kingdom* **93**, 1187–1202. doi:10.1017/S0025315412001750
- Farrell H, Ajani P, Murray S, Baker P, Webster G, Brett S, Zammit A (2018) Diarrhetic shellfish toxin monitoring in commercial wild harvest bivalve shellfish in New South Wales, Australia. *Toxins* **10**(11), 446. doi:10.3390/toxins10110446
- Farrell H, Ajani P, Murray S, Baker P, Webster G, Brett S, Barua A, Zammit A, Hill D (2020) Time series of harmful algal blooms in New South Wales. Case Study 1. *Dinophysis* time series at South Ballina Beach. Integrated Marine Observing System, State and Trends of Australia's Oceans Report, IMOS, Hobart, Tas., Australia.
- Foster RA, Collier JL, Carpenter EJ (2006) Reverse transcription PCR amplification of cyanobacterial symbiont16SrRNA sequences from single non-photosynthetic eukaryotic marine planktonic host cells. *Journal of Phycology* **42**, 243–250. doi:10.1111/j.1529-8817.2006.00185.x
- Gómez F (2007) Synonymy and biogeography of the dinoflagellate genus *Histioneis* (Dinophysiales: Dinophyceae). *Revista De Biología Tropical* **55**, 459–477. doi:10.15517/rbt.v55i2.6025
- Gómez F (2021) (2833) Proposal to conserve the name *Phalacroma* (Dinophysales: Dinophyceae). *Taxon* **70**, 1127–1128. doi:10.1002/tax.12576
- Gómez F, López-García P, Moreira D (2011) Molecular phylogeny of dinophysoid dinoflagellates: the systematic position of *Oxyphysis oxytoxoides* and the *Dinophysis hastata* group (Dinophysales, Dinophyceae). *Journal of Phycology* **47**, 393–406. doi:10.1111/j.1529-8817.2011.00964.x
- Gómez F, Moreira D, López-García P (2012) *Sinophysis* and *Pseudophalacroma* are distantly related to typical dinophysoid dinoflagellates (Dinophysales, Dinophyceae). *Journal of Eukaryotic Microbiology* **59**, 188–190. doi:10.1111/j.1550-7408.2011.00598.x
- González-Gil S, Pizarro G, Paz B, Velo-Suárez L, Reguera B (2011) Considerations on the toxigenic nature and prey sources of *Phalacroma rotundatum*. *Aquatic Microbial Ecology* **64**, 197–203. doi:10.3354/ame01523
- Gourret P (1883) Sur les Péridiniens du Golf de Marseille. *Annales du Musée d'Histoire Naturelle de Marseille, Section du Zoologie 1 (Mémoire 8)* 5–114. [In French]
- Gul S, Saifullah SM (2007) Genus *Amphisolenia* Stein from north-west Arabian sea shelf of Pakistan. *Pakistan Journal of Botany* **39**, 561–576.
- Gul S, Saifullah SM (2010) Taxonomic and ecological studies on three marine genera of Dinophysiales from Arabian sea shelf of Pakistan. *Pakistan Journal of Botany* **42**, 2647–2660.
- Hackett JD, Maranda L, Yoon HS, Bhattacharya D (2003) Phylogenetic evidence for the cryptophyte origin of the plastid of *Dinophysis* (Dinophysiales, Dinophyceae). *Journal of Phycology* **39**, 440–448. doi:10.1046/j.1529-8817.2003.02100.x
- Hallegraef GM, Jeffrey SW (1984) Tropical phytoplankton species and pigments of continental shelf waters of north and north-west Australia. *Marine Ecology Progress Series* **20**, 59–74. doi:10.3354/meps020059
- Hallegraef GM, Lucas IAN (1988) The marine dinoflagellate genus *Dinophysis* (Dinophyceae): photosynthetic, neritic and non-photosynthetic, oceanic species. *Phycologia* **27**, 25–42. doi:10.2216/i0031-8884-27-1-25.1
- Hallegraef GM, Reid DD (1986) Phytoplankton species successions and their hydrological environment at a coastal station off Sydney. *Marine and Freshwater Research* **37**, 361–377. doi:10.1071/MF9860361
- Hallegraef GM, Bolch CJS, Hill DRA, Jameson I, Leroi J-M, McMinn A, Murray S, De Salas MF, Saunders K (Eds) (2010) 'Algae of Australia: Phytoplankton of Temperate Coastal Waters.' (CSIRO Publishing: Melbourne, Vic., Australia)
- Hallegraef GM, Schweibold L, Jaffrezic E, Rhodes L, MacKenzie L, Hay B, Farrell H (2021) Overview of Australian and New Zealand harmful algal species occurrences and their societal impacts in the period 1985 to 2018, including a compilation of historic records. *Harmful Algae* **102**, 101848. doi:10.1016/j.hal.2020.101848

- Handy SM, Bachvaroff TR, Timme RE, Wayne Coats D, Kim S, Delwiche CF (2009) Phylogeny of four dinophysiacean genera (Dinophyceae, Dinophysiales) based on rDNA sequences from single cells and environmental samples. *Journal of Phycology* **45**, 1163–1174. doi:10.1111/j.1529-8817.2009.00738.x
- Hansen PJ (1991) *Dinophysis* – a planktonic dinoflagellate genus which can act both as a prey and a predator of a ciliate. *Marine Ecology Progress Series* **69**, 201–204. doi:10.3354/meps069201
- Hernández-Becerril DU, Barón-Campis SA, Ceballos-Corona JGA, Alonso-Rodríguez R, Rincones-Reyes KM, Becerra-Reynoso RT, Arce-Rocha G (2021) ‘Phytoplankton Catalog of the Mexican Central Pacific. Cruises ‘MareaR’ (2009–2019) B/W “El Puma”.’ (National Autonomous University of Mexico) [In Spanish]
- Heron AC (1982) A vertical free fall plankton net with no mouth obstructions. *Limnology & Oceanography* **27**, 380–383. doi:10.4319/lo.1982.27.2.0380
- Jeffrey SW, Hallegraeff GM (1987) Phytoplankton pigments, species and light climate in a complex warm-core eddy of the East Australian Current. *Deep Sea Research – A. Oceanographic Research Papers* **34**, 649–673. doi:10.1016/0198-0149(87)90029-X
- Jensen MH, Daugbjerg N (2009) Molecular phylogeny of selected species of the order Dinophysiales (Dinophyceae): testing the hypothesis of a dinophysoid radiation. *Journal of Phycology* **45**, 1136–1152. doi:10.1111/j.1529-8817.2009.00741.x
- Jørgensen E (1923) Mediterranean Dinophysiaceae. *Report on the Danish Oceanographic Expeditions 1908–10 to the Mediterranean and Adjacent Seas* **2**, 1–48.
- Karsten G (1907) Das Indische Phytoplankton nach dem Material der Deutschen Tiefsee-Expedition 1898–1899. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer ‘Valdivia’ 1898–1899* **112**(2), 221–548. [In German]
- Kim M, Choi DH, Park MG (2021) Cyanobiont genetic diversity and host specificity of cyanobiont-bearing dinoflagellate *Ornithocercus* in temperate coastal waters. *Scientific Reports* **11**, 9458. doi:10.1038/s41598-021-89072-z
- Kofoed CA (1907) Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the US Fish Commission steamer “Albatross”, from October, 1904, to March, 1905. IX. New species of Dinoflagellates. *Bulletin Museum Comparative Zoology* **50**, 161–207.
- Kofoed CA, Michener JR (1911) New genera and species of dinoflagellates. *Bulletin Museum Comparative Zoology Harvard College* **54**, 267–302.
- Kofoed CA, Skogsberg T (1928) The Dinoflagellata: the Dinophysoidae. *Memoirs of the Museum of Comparative Zoology* **21**, 1–766.
- Koike K, Sekiguchi H, Kobiyama A, Takishita K, Kawachi M, Koike K, Ogata T (2005) A novel type of kleptoplastidy in *Dinophysis* (Dinophyceae): presence of haptophyte-type plastid in *Dinophysis mitra*. *Protist* **156**, 225–237. doi:10.1016/j.protis.2005.04.002
- Larsen J, Moestrup Ø (1992) Potentially toxic phytoplankton. 2. Genus *Dinophysis* (Dinophyceae). Leaflet 180, International Council for the Exploration of the Sea, Copenhagen, Denmark.
- Lee TT, Nguyen VN, Fukuyo Y (2012) *Dinophysis* (Dinophyceae) in Vietnamese waters. *Coastal Marine Science* **35**, 73–77.
- Lucas IAN (1991) Symbionts of the tropical Dinophysiales (Dinophyceae). *Ophelia* **33**, 213–224. doi:10.1080/00785326.1991.10429712
- MacKenzie L, Beuzenberg V, Holland P, McNabb P, Suzuki T, Selwood A (2005) Pectenotoxin and okadaic acid-based toxin profiles in *Dinophysis acuta* and *Dinophysis acuminata* from New Zealand. *Harmful Algae* **4**, 75–85. doi:10.1016/j.hal.2003.12.001
- Madigan TL, Lee KG, Padula DJ, McNabb P, Pointon AM (2006) Diarrhetic shellfish poisoning (DSP) toxins in South Australian shellfish. *Harmful Algae* **5**, 119–123. doi:10.1016/j.hal.2004.12.005
- Murray G, Whitting F (1899) New Peridiniaceae from the Atlantic. *Transactions of the Linnean Society of London, Botany* **2**, 321–342.
- Okolodkov YB (2014) Dinophysiales (Dinophyceae) of the National Park Sistema Arrecifal Veracruzano, Gulf of Mexico, with a key for identification. *Acta Botanica Mexicana* **106**, 9–71. doi:10.21829/abm106.2014.217
- Omura T, Iwataki M, Borja VM, Takayama H, Fukuyo Y (2012) ‘Marine phytoplankton of the Western Pacific’. (Kouseisha Kouseikaku: Tokyo, Japan)
- Osorio-Tafall BF (1942) Notes on some marine planktonic dinoflagellates of Mexico, with description of new species. *Anales de la Escuela Nacional de Ciencias Biológicas Mexico* **2**, 435–447. [In Spanish]
- Ostenfeld CH, Schmidt J (1901) Plankton fra det Røde Hav og Adenbugten. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening* **141**–182. [In Danish]
- Park MG, Kim S, HS, Myung G, Kang YG, Yih W (2006) First successful culture of the marine dinoflagellate *Dinophysis acuminata*. *Aquatic Microbial Ecology* **45**, 101–106. doi:10.3354/ame045101
- Park JH, Kim M, Jeong HJ, Park MG (2019) Revisiting the taxonomy of the ‘*Dinophysis acuminata* complex’ (Dinophyta). *Harmful Algae* **88**, 101657. doi:10.1016/j.hal.2019.101657
- Paulsen O (1949) Observations on dinoflagellates. *Kongelige Danske Videnskabernes Selskabs Skrifter* **6**, 1–67. [In Danish]
- Pavillard J (1909) Sur les peridiniens du Golfe de Lion. *Bulletin de la Société Botanique de France* **9**, 227–284. [In French]
- Pavillard J (1924) A propos de la systématique des Péridiniens. *Bulletin de la Société Botanique de France* **70**, 876–882. [In French]
- Qiu D, Huang L, Liu S, Lin S (2011) Nuclear, mitochondrial and plastid gene phylogenies of *Dinophysis miles* (Dinophyceae): evidence of variable types of chloroplasts. *PLoS One* **6**, e29398. doi:10.1371/journal.pone.0029398
- Quaine J, Kraa E, Holloway J, White K, McCarthy R, Delpech V, Trent M, McAnulty J (1997) Outbreak of gastroenteritis linked to eating pipis. *New South Wales Public Health Bulletin* **8**, 103–104.
- Raho N, Pizarro G, Escalera L, Reguera B, Marín I (2008) Morphology, toxin composition and molecular analysis of *Dinophysis ovum* Schütt, a dinoflagellate of the ‘*Dinophysis acuminata* complex’. *Harmful Algae* **7**, 839–848. doi:10.1016/j.hal.2008.04.006
- Reguera B, González-Gil S (2001) Small cell and intermediate cell formation in species of *Dinophysis* (Dinophyceae, Dinophysiales). *Journal of Phycology* **37**, 318–333. doi:10.1046/j.1529-8817.2001.037002318.x
- Reguera B, González-Gil S, Delgado M (2004) Formation of *Dinophysis dens* and *D. diegensis* from laboratory incubations of *Dinophysis acuta* and *D. caudata*. In ‘Proceedings of the Xth International Conference on Harmful Algae’, 21–25 October, 2002, Saint Petersburg, FL, USA. (Eds KA Steidinger, JH Landsberg, CR Tomas, GA Vargo) pp. 440–442. (UNESCO: Paris, France)
- Reguera B, Velo-Suárez L, Raine R, Park MG (2012) Harmful *Dinophysis* species: a review. *Harmful Algae* **14**, 87–106. doi:10.1016/j.hal.2011.10.016
- Richardson AJ, Walne AW, John AWG, Jonas TD, Lindley JA, Sims DW, Stevens D, Witt M (2006) Using continuous plankton recorder data. *Progress in Oceanography* **68**, 27–74. doi:10.1016/j.pocean.2005.09.011
- Rodríguez F, Escalera L, Reguera B, Rial P, Riobó P, de Jesús da Silva T (2012) Morphological variability, toxinology and genetics of the dinoflagellate *Dinophysis tripos* (Dinophysiales, Dinophysiales). *Harmful Algae* **13**, 26–33. doi:10.1016/j.hal.2011.09.012
- Saifullah SM, Gul S, Khan M (2008) The dinoflagellate genus *Ornithocercus* Stein from north Arabian sea shelf of Pakistan. *Pakistan Journal of Botany* **40**, 849–857.
- Schnepf E, Elbrächter M (1988) Cryptophyceae-like double membrane-bound chloroplast in the dinoflagellate, *Dinophysis Ehrenb.*: evolutionary, phylogenetic and toxicological implications. *Botanica Acta* **101**, 196–203. doi:10.1111/j.1438-8677.1988.tb00033.x
- Saville-Kent W (1881) A manual of the infusoria, including a description of all known flagellate, ciliate, and tentaculiferous protozoa. *British and Foreign and an Account of the Organization and Affinities of the Sponges* **1**, 289–720.
- Schiller J (1928) Die planktischen Vegetationen des adriatischen Meeres. C. Dinoflagellata. 1 Teil. Adiniferidea, Dinophysidaceae *Archiv für Protistenkunde* **61**, 45–91.
- Schröder F (1900) Das Phytoplankton des Golfes von Neapel nebst vergleichenden Ausblicken auf das des atlantischen Ozeans. *Mitteilungen aus der Zoologischen Station zu Neapel* **14**, 1–38. [In German]
- Schütt F (1892) Das Pflanzenleben der Hochsee. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung* **1A**, 243–314. [In German]
- Schütt F (1895) The peridines of the Plankton expedition. Part 1. *Results of the Humboldt Foundation’s Plankton Expedition* **4**, 1–170.
- Schütt F (1900) Die Erklärung des centrifugalen Dickenwachstums der Membran. *Botanische Zeitung* **58**(16/17 II), 245–274. [In German]

- Séchet V, Sibat M, Billien G, Carpentier L, Rovillon G-A, Raimbault V, Malo F, Gaillard S, Perrière-Rumebe M, Hess P, Chomérat N (2021) Characterization of toxin-producing strains of *Dinophysis* spp. (Dinophyceae) isolated from French coastal waters, with a particular focus on the *D. acuminata*-complex. *Harmful Algae* **107**, 101974. doi:10.1016/j.hal.2021.101974
- Silva ES, Faust MA (2019) Small cells in the life history of dinoflagellates (Dinophyceae): a review. *Phycologia* **34**, 396–408. doi:10.2216/i0031-8884-34-5-396.1
- Sournia A (1973) Catalogues of species and infraspecific taxa of current marine dinoflagellates published since the revision of J. Schiller. I. Free dinoflagellates. *Beihefte zur Nova Hedwigia* **48**, 1–92. [In French]
- Tai L-S, Skogsberg T (1934) Studies on the Dinophysoidae, marine armored dinoflagellates, of Monterey Bay, California. *Archiv Protistenkunde* **82**, 380–482.
- Tarangkoon W, Hansen G, Hansen PJ (2010) Spatial distribution of symbiont-bearing dinoflagellates in the Indian Ocean in relation to oceanographic regimes. *Aquatic Microbial Ecology* **58**, 197–213. doi:10.3354/ame01356
- Taylor FJR (1973) Topography of cell division in the structurally complex dinoflagellate genus *Ornithocercus*. *Journal of Phycology* **9**, 1–10. doi:10.1111/j.0022-3646.1973.00001.x
- Taylor FJR (1976) Dinoflagellates from the International Indian Ocean Expedition. A report on material collected by the R.V. 'Anton Bruun' 1963–1964. *Bibliotheca Botanica* **132**, 1–234.
- Turland NJ, Wiersma JH, Barrie FR, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Kusber W-H, Li D-Z, Marhold K, May TW, McNeill J, Monro AM, Prado J, Price MJ, Smith GF (Eds) (2018) 'International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)', adopted by the Nineteenth International Botanical Congress, July 2017, Shenzhen, PR China. *Regnum Vegetabile*, vol. 159. (Koeltz Botanical Books: Glashütten, Germany) doi:10.12705/Code.2018
- Von Stein FR (1883) 'Der organism der Infusionsthier nach eigenen Forschungen in systematischer Ordnung.' (Engelmann: Leipzig, German Empire) [In German]
- Wallace GM (2011) Diarrhetic shellfish toxins in Tasmanian coastal waters: causative dinoflagellate organisms, dissolved toxins and shellfish depuration. PhD thesis, School of Plant Science, University of Tasmania, Hobart, Tas., Australia. Available at [https://eprints.utas.edu.au/11846/2/Wallace\\_whole\\_thesis.pdf](https://eprints.utas.edu.au/11846/2/Wallace_whole_thesis.pdf)
- Wilke T, Zinssmeister C, Hoppenrath M (2018) Morphological variability within the marine dinoflagellate *Ornithocercus quadratus* (Dinophysales, Dinophyceae) – evidence for three separate morphospecies. *Phycologia* **57**, 555–571. doi:10.2216/17-126.1
- Wijeratne S, Pattiaratchi C, Proctor R (2018) Estimates of surface and subsurface boundary current transport around Australia. *Journal of Geophysical Research: Oceans* **123**, 3444–3466. doi:10.1029/2017JC013221
- Wolny JL, Egerton TA, Handy SM, Stutts WL, Smith JL, Whereat EB, Bachvaroff TR, Henrichs DW, Campbell L, Deeds JR (2020) Characterization of *Dinophysis* spp. (Dinophyceae, Dinophysiales) from the mid-Atlantic region of the United States. *Journal of Phycology* **56**, 404–424. doi:10.1111/jpy.12966
- Wood EJJ (1954) Dinoflagellates in the Australian region. *Marine Freshwater Research* **5**, 171–351. doi:10.1071/MF9540171
- Wood EJJ (1963a) Dinoflagellates in the Australian region. II. Recent collections. CSIRO Division of Fisheries, Oceanography Technical paper 14, CSIRO, Melbourne, Vic., Australia.
- Wood EJJ (1963b) Dinoflagellates in the Australian region. III. Further collections. CSIRO Division of Fisheries, Oceanography Technical paper 17, CSIRO, Melbourne, Vic., Australia.
- Zinssmeister C, Wilke T, Hoppenrath M (2017) Species diversity of dinophysoid dinoflagellates in the Clarion–Clipperton Fracture Zone, eastern Pacific. *Marine Biodiversity* **47**, 271–287. doi:10.1007/s12526-016-0607-x

**Data availability.** All data are available online from the Australian Phytoplankton Database (<https://portal.aodn.org.au/search?uuiid=75f4ff1fc-bee3-4498-ab71-aa1ab29ab2c0>), the Australian Continuous Plankton Recorder Survey (<https://portal.aodn.org.au/search?uuiid=c1344979-f701-0916-e044-00144f7bc0f4>) and the National Reference Station (<https://portal.aodn.org.au/search?uuiid=dfef238f-d669-3868-e043-08114f8c8a94>).

**Conflicts of interest.** The authors declare that they have no conflicts of interest.

**Declaration of funding.** IMOS is enabled by the National Collaborative Research Infrastructure Strategy (NCRIS). It is operated by a consortium of institutions as an unincorporated joint venture, with the University of Tasmania as Lead Agent.

**Acknowledgements.** We thank Prof. Anthony Richardson for his leadership of the AusCPR program, and Frank Coman, Mark Tonks, Anita Slotwinski and Felicity McEnnulty for help with the ongoing phytoplankton surveys and management of imaging records. Helen Bond from Analytical Services Tasmania kindly shared her Tasmanian *Ornithocercus* observations. We thank Consuelo Carbonell-Moore (Oregon State University, USA) for drawing our attention to the significance of *Histiophysis*. Prof. Martina Doblin kindly gave us access to Investigator IN2019-V03 Indian Ocean samples. We thank Assoc. Prof. Maret Vesik from the Electron Microscope Unit of Sydney University and Dr Karsten Goemann and Dr Sandrin Feig from the Central Science Laboratories of the University of Tasmania for expert assistance with electron microscopy. Comments from three anonymous reviewers greatly improved the paper.

#### Author affiliations

<sup>A</sup>Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Tas. 7001, Australia.

<sup>B</sup>CSIRO Oceans and Atmosphere, Castray Esplanade, Battery Point, Tas. 7004, Australia.

<sup>C</sup>CSIRO Oceans and Atmosphere, Queensland BioSciences Precinct (QBP), Saint Lucia, Qld 4067, Australia.