

EPIPELLIS OIKETIS (BACILLARIOPHYTA) ON HARBOR PORPOISES FROM THE NORTH SEA CHANNEL (BELGIUM)*

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Abstract. *Epipellis oiketis* Holmes, an obligate epizoic diatom living on cetaceans, was found in skin samples of harbor porpoises from Belgian coastal waters. Previously this species was recorded exclusively from porpoises and from tooth and baleen whales in the northern Pacific. We present additional information on the morphology of this diatom and comment on its geographic distribution. Both host dispersal before geographic separation and interspecific transfer may explain its occurrence in the northern part of both oceans. Our observations further corroborate the suggestion that cetacean diatom species probably are more widespread than documented so far.

Key words: Bacillariophyceae, *Phocoena phocoena*, epizoic diatoms, cetaceans, valve morphology, *Cocconeis*

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INTRODUCTION

Diatoms adapted to epi- or endozoic conditions are reported from a wide range of animal groups, especially in the marine realm (e.g., Gibson 1978; Lee *et al.* 1980; Takano 1983; Reimer & Lee 1984; Bavestrello *et al.* 2000; Bigelow & Alexander 2000). The epidermis of mysticete and odontocete cetaceans supports a range of obligate epizoic pennates (e.g., Hart 1935; Hustedt 1952; Nemoto 1956), which are believed to derive a required growth factor from this substrate. To date, studies of this specialized flora have concentrated on the Pacific Ocean and (Sub-)Antarctic waters, leaving that of the more northern Atlantic Ocean and adjacent seas hardly explored (Denys 1997). Even the commonest cetaceans in this area appear to have drawn almost no attention in this respect. This includes the harbor porpoise (*Phocoena phocoena* L.), a small species occurring in coastal areas of almost the entire Northern Hemisphere. Harrison and Thurley (1974) noted an abundance of diatoms on a damaged and diseased porpoise

from a beach near Skegness (eastern England) but the only species identified by R. Ross from this material are two widespread marine-littoral taxa with no particular substrate requirements: *Synedra tabulata* (Ag.) Kütz. [*Tabularia fasciculata* (Ag.) Williams & Round] and *Navicula ramosissima* (Ag.) Cl. This contrasts sharply with observations from Pacific harbor porpoises, which yielded several obligate epizoic diatoms (Holmes *et al.* 1989).

MATERIAL AND METHODS

We obtained skin samples from eight harbor porpoises netted accidentally by fishermen in the North Sea Channel area or beached on the Belgian coast (Table 1). Samples were preserved in alcohol or formaldehyde before treatment with concentrated hydrogen peroxide. Strewn mounts for light microscopy were prepared from the resulting suspension using Naphrax® and examined with an Olympus BX51 microscope and Nomarski interference contrast. Cleaned material on polycarbonate filters was coated with gold and studied with a Philips 550 scanning electron microscope.

* Dedicated to Dr. Kurt Krammer on the occasion of his 85th birthday

Table 1. Sampled specimens of harbor porpoise and occurrence of *Epipellis oiketis* Holmes.

Specimen	Place	Coordinates	Date	Origin	<i>Epipellis</i>
Juvenile male	Blankenberge	51°19'2"N; 3°7'41"E	29-04-2005	beached	no
Juvenile male	Bredene	51°14'59"N; 2°57'36"E	21-04-2005	beached	yes
Juvenile male	De Panne	51°5'38"N; 2°33'34"E	26-12-2005	beached (live)	no
Adult male	De Panne	51°5'42"N; 2°33'43"E	27-12-2005	beached	yes
Adult female	Duinbergen	51°20'44"N; 3°15'30"E	27-02-2005	beached	no
Juvenile	Heist	51°20'35"N; 3°13'55"E	26-04-2007	beached	no
Juvenile female	Koksijde	51°7'13"N; 2°37'49"E	5-04-2005	beached	yes
Juvenile female	open sea	51°14'10"N; 2°30'38"E	18-03-2005	netted	yes

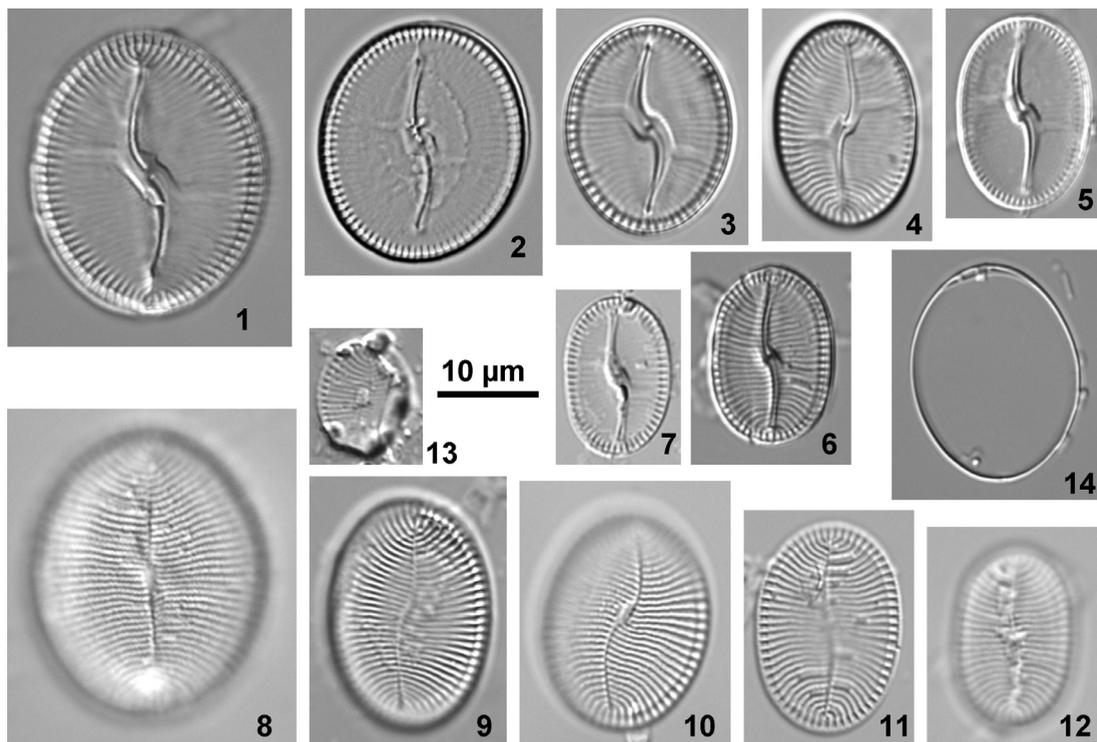
RESULTS

Besides some benthic and planktonic taxa of marine and even brackish-freshwater origin which occur as contaminants or occasional dwellers, a single species from a genus endemic on cetaceans, *Epipellis* Holmes (Holmes 1985), was observed in samples from four specimens (Figs 1–23). *Epipellis* is a heterovalvar monoraphid genus, reminiscent of *Cocconeis* Ehr. in general morphology but differing by having double-layered valves which both present alveolate striae with internal fenestrae at their margin and a particular raphe structure. It is represented by only two very similar taxa: *E. oiketis* Holmes (synonym *Cocconeis orcii* Kliashorin) and *E. heptunei* Denys & Van Bonn, both occurring in the Pacific.

The valves in the North Sea material vary from suborbicular to oval in outline (Figs 1–13 & 15–18). The number of marginal fenestrae ranges from 10.5 to 16 in 10 µm on the raphe valve (RV) and from 10 to 15 in 10 µm on the sternum valve (SV), whereas striae density is 14 to 20 in 10 µm on the RV and 16 to 22 in 10 µm on the SV. These values agree most closely with those of *E. oiketis*, which is more coarsely structured than its sibling species (Holmes 1985; Denys & Van Bonn 2001). Nevertheless, some valves are considerably smaller than reported so far for *E. oiketis* (length 17–47 µm, width 16–42 µm; Denys & Van Bonn 2001), with the smallest measuring only 12.2 by 9.9 µm (Fig. 13). In very small valves the density of marginal fenestrae and striae approaches or even overlaps with the range considered typical

for *E. heptunei* (17–18 fenestrae in 10 µm on the RV and ca 13 in 10 µm on the SV, ca 22 striae in 10 µm on both RV and SV; Denys & Van Bonn 2001). However, larger valves consistently present a coarser structure, suggesting that all specimens can be attributed to *E. oiketis*.

SEM observations of the exterior of the RV (Figs 15 & 19–21) reveal two rows of poroids on the slope of the marginal crest towards the mantle, and not 3 or 4 as in *E. heptunei*. The slightly irregular decussate arrangement of these perforations is not always continuous. In some valves the double row is reduced to only one or two pores opposite to the interstriae (Fig. 19). These isolated pores appear to be slightly larger. Also, some additional isolated or aligned poroids may occur in the apical region, even producing a third row over a short distance (Figs 15, 20 & 21). At some distance from the double row of poroids, the narrow RV mantle presents a single row of more elongated perforations (Figs 15 & 19–21). The absence of a crescent-shaped embossment distally from the polar raphe endings on the external valve surface (Figs 15, 20 & 21) further corroborates its identification as *E. oiketis*. A narrow and irregularly outlined interruption of the biseriate striae occurs close to the valve margin, separating a 2–3-areolae-wide band adjacent to the inner slope band of the marginal crest (Figs 19–21). The sigmoid raphe widens slightly towards the central endings, which are coaxial and separated by a thickened silica bridge (Fig. 15). The droplet-shaped polar terminations are slightly deflected to opposite sides and situ-



Figs 1–14. *Epipellis oiketis* Holmes from the North Sea (LM). 1–7 – RV. 8–13 – SV. 14 – Closed pleura.

ated within a small transversely expanded depression (Figs 15, 20 & 21).

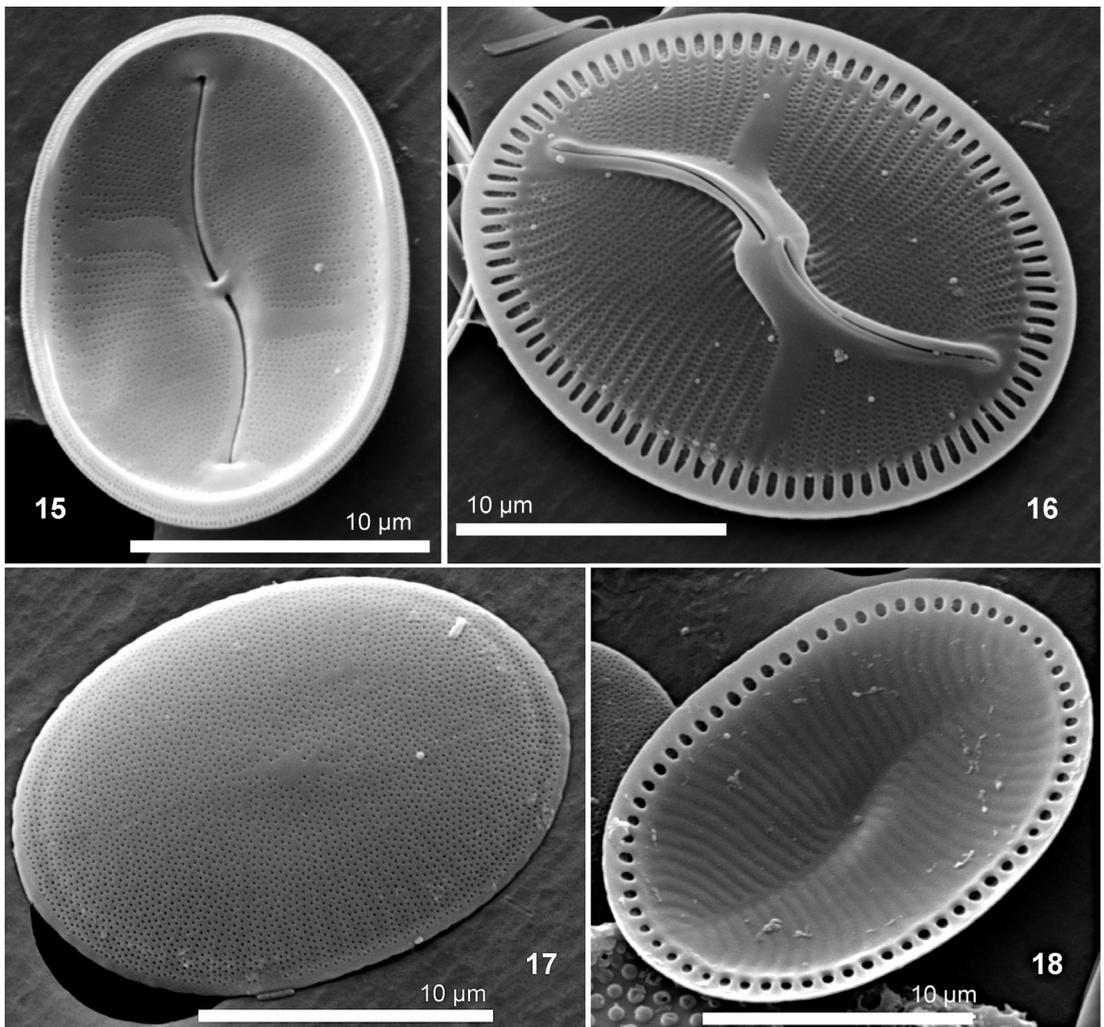
The RV interior shows largely biseriata striae separated by slightly raised interstriae (Fig. 16). The interstriae thicken near the margin, separating somewhat elongated fenestrae which continue along the entire margin. The raphe is situated on a raised sternum which expands into a roof-like central nodule. This overhang gradually expands on the concave side of each raphe slit, starting close to the polar termination. Just before it becomes broader and bilateral near the middle of the valve, one arm of a slightly protruding stauros-like structure extends towards the margin on the opposite side. The interior central raphe terminations widen slightly and bend in opposite directions. They are not aligned and almost juxtaposed, whereas the polar endings are only very slightly deflected. The terminal part of the raphe sternum is slightly more developed but lacks a helictoglossa (Fig. 24). It is set within a semicircular imperforate area.

The exterior of the SV presents a very narrow sigmoid axial area with at the most only a slight lanceolate, transverse or linear enlargement in the middle (Figs 8–10 & 17). Small \pm equidistantly placed round areolae are arranged in wavy to curved radial rows which gradually increase in number towards the circumference of the valve. In contrast to the RV, the valve passes into the imperforate mantle without a marked change in slope (Fig. 17). Its interior surface is smooth (Fig. 18). The inner layer of the valve presents thickened ribs which gradually become stronger towards the valve margin, where they fuse with a heavily silicified rim and then continue, leaving oval to circular fenestrae between them before joining close to the mantle edge (Figs 18 & 25). The inner layer of the SV is considerably thicker than the perforate outer membrane, and the walls separating the transapical alveoli are more delicate than the ribs of the inner layer from which they extend (Fig. 25). Holmes (1985, p. 54–55, figures

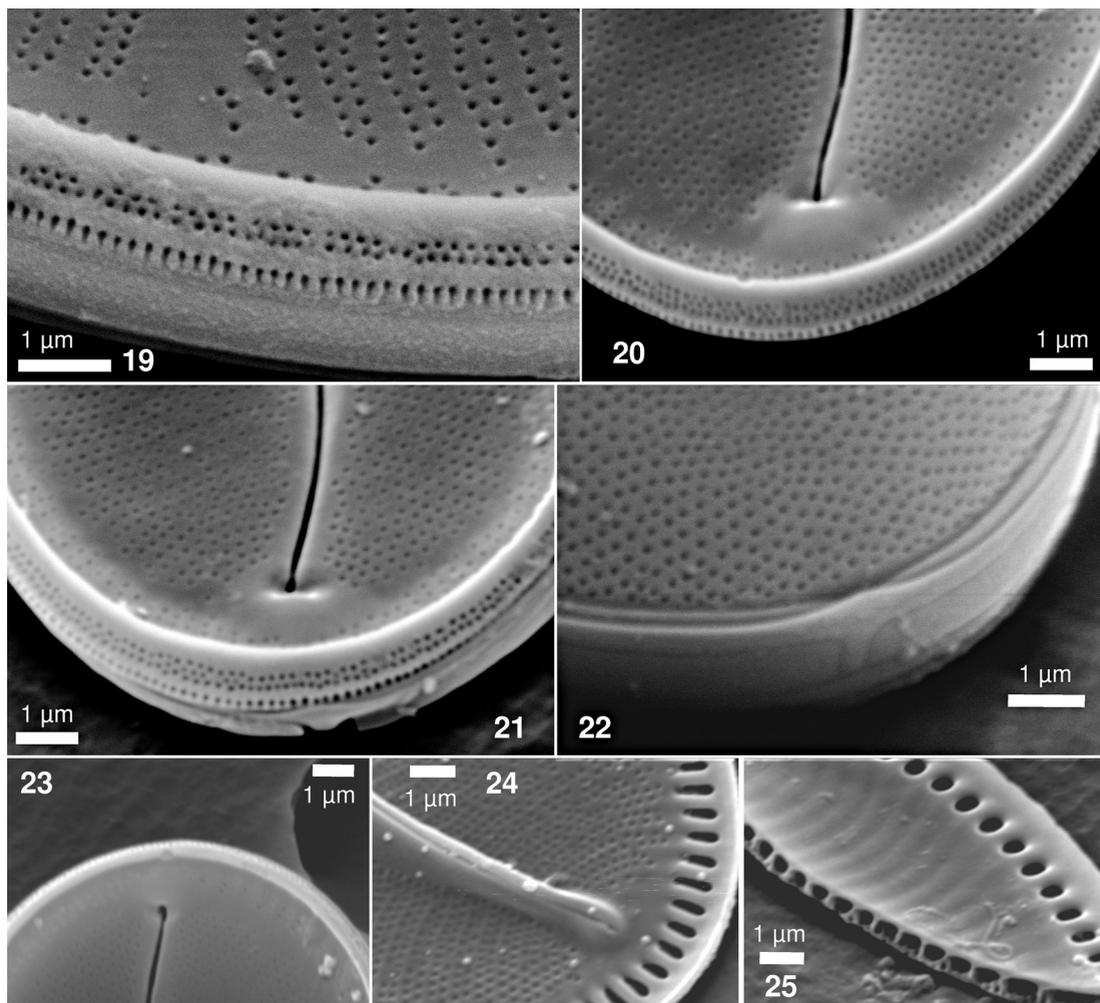
43 & 44) indicates that the ragged or wavy appearance of the interstriae results from short lateral cross-extensions. These extensions appear to be simple or branched struts extending sideways from the separating walls, providing additional support for the thin external layer and enhancing its mechanical strength (Fig. 25). We did not examine the structure of the pore membranes, but Holmes *et al.* (1989, 1993) showed that they consist of simple rotae with 7–9 radial struts.

Holmes (1985) presents no details on the cin-

gulum of *E. oiketis*, and Denys and Van Bonn (2001) only observed open bands in *E. heptunei*. From our present observations it appears that the number and structure of the connecting elements are similar to those in *Bennettella* Holmes, although the width of the cingulum is considerably smaller (Figs 19, 21 & 22). In *Epipellis* all three cingular bands are narrow and imperforate. The valvocopulae are open and lack fimbriae. The single pleural band in between is closed and presents a ligula *ca* 0.5 μm wide. Its antiligula is



Figs 15–18. *Epipellis oiketis* Holmes from the North Sea (SEM). 15 – Exterior of the RV. 16 – Interior of the RV. 17 – Exterior of the SV. 18 – Interior of the SV.



Figs 19–25. *Epipellis oiketis* Holmes from the North Sea (SEM). 19 – Margin and mantle of a RV with part of the cingulum. 20 & 21 – Details of the distal part of the RV. Note the flat \pm semicircular imperforate area surrounding the raphe terminations, and the double row of perforations on the outer slope of the valve with isolated or \pm aligned pores in between. In Figure 21 the closed pleura band with ligula and antiligula and the underlying valvocopula of the SV are visible. 22 – Detail of the distal part of a SV with cingulum. 23 – External view of the distal part of a RV with the polar raphe termination. 24 – Internal view of the distal part of a RV with the polar raphe termination. 25 – Longitudinally fractured SV with internal layer facing upwards.

about as wide but less strongly developed (Figs 14, 21 & 22).

DISCUSSION

Most of the structural features characterizing *Epipellis*, such as a SV with transapical alveoli and biseriate external pores, a marginal crest on the RV, a sigmoid raphe, the absence of helictoglossae or

valvocopula lacking fimbriae, are observed in certain marine members of *Cocconeis* (e.g., Navarro 1982; Poulin *et al.* 1984; Kobayasi & Nagumo 1985; De Stefano *et al.* 2000; De Stefano & Marino 2001; De Stefano & Romero 2005; Riaux-Gobin & Compère 2008). Perhaps the most striking similarity is observed in *Cocconeis costata* Greg., and especially so in *C. costata* var. *subantarctica* (Riaux-Gobin *et al.* 2009) and *C. costata* var.

pacifica (Grun.) Grun. (Romero & Rivera 1996), the last of which Morejohn (1979) reported from a harbor porpoise. These taxa present an alveolate SV with an extensive internal axial plate and large marginal openings, a RV with multiseriata striae, deflected internal raphe terminations and narrow stauros, as well as a rather similar cingulum. More significantly, connecting bars between the mantle and an imperforate thickening of the RV alongside a *crista marginalis* create a peripheral ring of compartments. This structure strongly resembles that of *Epipellis*, although the chambers have not developed into true alveoli (Riaux-Gobin *et al.* 2009). Moreover, the stauros is symmetric and the sternum more simple in these *Cocconeis*. The strongly sigmoid raphe sternum with non-coaxial lateral extensions and a roof-like expanded central nodule are prominent features of *Epipellis* which further enhance the structural stability of its frustule. These are shared only by *Bennettella*, a genus that lives in the same habitat and essentially appears to differ only by having bifurcate external polar raphe endings (Holmes 1985; Holmes & Nagasawa 1995).

Our observations on the morphology of *E. oiketis* from the North Sea indicate that certain features tend to intergrade somewhat with those of *E. heptunei*. Although morphometric observations of several collections of *E. oiketis* from the Pacific Ocean have been made, these have not revealed the reduced cell size and finer structure attained in the North Sea populations. This shows that it may not be enough to rely on LM for identification in some cases. Additional SEM observations are also necessary to elucidate the variation of the perforation pattern of the *crista marginalis* occurring in this species. Although the present observations suggest even greater similarity between the two taxa than recognized so far, we nevertheless consider that the remaining differences in the structure of the marginal crest and valve surface at the distal raphe endings, combined with the disparity in the density of the marginal fenestrae and in the modal striation pattern, are still sufficient to separate both at the species level. As with many other diatom taxa that have been separated lately from close relatives based on observations from single locations, fur-

ther details on the morphological plasticity of both *E. oiketis* and *E. heptunei* are warranted.

The geographic distribution of *Epipellis* seems of particular interest. *E. oiketis* has been collected from a killer whale, *Orcinus orca* (L.) shipped to a whaling station on the Kuril Islands, Dall's porpoises *Phocoenoides dalli* (True) in the Bering Sea and north Pacific as southward as Monterey Bay, as well as two harbor porpoises and a sperm whale *Physeter macrocephalus* (L.) from nearby San Francisco (Kliashtorin 1962; Morejohn 1979; Holmes 1985; Holmes *et al.* 1989, 1993; Nagasawa *et al.* 1989). Nagasawa *et al.* (1989) retrieved it from sediments close to a Japanese fishing harbor where porpoises are marketed. These records define its reported distribution to latitudes above 36.5°N in the Pacific Ocean. *E. heptunei* was collected from captive bottlenose dolphins *Tursiops truncatus* (Montague) in San Diego Bay (32.7°N). Morejohn and Hansen (unpublished ms. cited by Morejohn 1979) examined the diatoms on several cetaceans in Monterey Bay, California. Re-examination of their material by R. W. Holmes (Holmes *et al.* 1993) revealed at least four obligate epizoics on *Phocoena phocoena*: *Bennettella ceticola* (Nelson) Holmes on four specimens, *Epipellis oiketis* and *Epiphallina aleutica* (Nemoto) Holmes, Nagasawa & Takano on two individuals, and *Cocconeis ceticola* f. *subconstricta* Nemoto on one. The *Cocconeis ceticola* f. *ovalis* mentioned by Morejohn (1979) for four animals represents large cells of *B. ceticola* (Holmes 1985). The same taxa except for *Epiphallina aleutica*, and also *Bennettella constricta* (Nemoto) Holmes, were found on Dall's porpoise, a species closely related and sometimes hybridizing with harbor porpoise (Rosel *et al.* 1995; Fajardo-Mellor *et al.* 2006; Jefferson 2009). Holmes *et al.* (1993) suggest that the different diatom flora on Dall's porpoises from the Bering Sea, Japan and Monterey Bay indicates that the subpopulations from these areas do not intermingle. Our observations and those presented by Morejohn (1979) indicate that Pacific harbor porpoises support a more diverse diatom flora than their peers from the North Sea.

Atlantic and Pacific populations of the harbor porpoise represent different subspecies (Bjørge

& Tolley 2009), whereas the more oceanic Dall's porpoise is restricted to the northern Pacific. These small cetaceans do not migrate or move over vast distances. Killer and sperm whales, however, are cosmopolitan, and some may travel over much larger distances. Assuming that transfer of epizoic diatoms requires physical contact or at the least close proximity of individuals, the presence of *E. oiketis* on harbor porpoises in both oceans could simply date to before the biogeographic divide arose. Alternatively, the disjunct distribution of *Epipellis* might also be explained by continuing interspecific transfer, primarily between Atlantic and Pacific individuals of migrating large whales in (sub)Antarctic waters, followed by secondary infestation of porpoises in northern areas. Both attacks by killer whales and 'play' provide the opportunity for transmission of epizoic diatoms between cetacean species, and the fact that there are few indications of any host-specificity suggests that such transfers effectively take place. In this case, migrating cetaceans and transient killer whales might present the highest diatom diversity, and the northern Atlantic flora could turn out to be quite similar to those of other world seas. All cetacean diatoms reported from the North Atlantic so far occur in the Pacific Ocean as well. Nevertheless, further studies of this poorly known aspect of biodiversity are definitely needed to confirm any generalizations.

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