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Review article

Epidermal lipid in several cetacean species: ultrastructural observations

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Abstract. The ultrastructure of the skin of four cetacean species, bottlenose dolphin (*Tursiops truncatus*) long-finned pilot whale (*Globicephala melaena*), humpback whale (*Megaptera novaeangliae*), and fin whale (*Balaenoptera physalus*) was investigated with particular reference to epidermal lipid. It has already been established that massive lipid reservoirs exist in whales, that the biochemical structures of cetacean lipids are unique, and that unusual intracellular lipid droplets appear in the epidermis. We report here some novel findings on scanning electron microscopic morphology of epidermal lipid, and on its ultrastructural morphology in general and specialized integumentary sites, including species not previously investigated. The intracellular epidermal lipid droplets were more extensive than lamellar body-derived intercellular lipid which is within the interstices of stratum externum cells. The intracellular droplets were spherical, highly variable in size ranging from 0.24 μm to 3.0 μm in diameter, appeared singly or were aggregated in cytoplasmic cavitations, and often were closely associated with epidermal cell nuclei. Evidence for exocytosis of the intracellular droplets was not observed. Significant numbers of intracellular lipid droplets are not observed in the epidermis of terrestrial mammals, so their presence is one of several aquatic specializations of the cetacean integument. Its full significance remains obscure, but it is more probably associated with epidermal cell metabolism than with secretion of lipid.

Key words: Epidermis – Integument – Cetacean – Ultrastructure – Lipid

Introduction

The function and metabolism of lipids have assumed unique importance in whales, since these diving mammals have evolved atypical and widespread deposits of fat which are biochemically distinct from those of terrestrial mammals, and which vary biochemically amongst the cetacea. Also, the large reservoirs of lipid, such as blubber and intracellular deposits in the skin and elsewhere in cetaceans are aquatic adaptations that are not so extensively developed in terrestrial mammals. In whales the stored lipid may serve as an energy source during months of migration and breeding when food intake ceases, as a source of insulation, e.g., blubber, in cold seawater, as a medium for sound transmission and reception during echolocation, or as a possible buoyancy-control mechanism. The rorqual whales store fat largely as triacylglycerols within muscle, around viscera and in blubber. In contrast, sperm whales store little fat in muscle and viscera, but retain considerable lipid as in the blubber or spermaceti organ (Lockyer 1991). Another massive, subdermal reservoir of oil, described by Howell (1930) in the narwhal (*Monodon monoceros*), was a veritable circulatory system for oil, occurring largely subjacent to the blubber layer. This system has also been observed in other species (Howell 1930) but has not been subsequently described. The biochemical nature of cetacean lipids has been extensively studied by Litchfield and associates (Litchfield et al. 1973; Ackman et al. 1973; Litchfield and Greenberg 1974, 1979) and others (Varanasi and Malins 1970; Blomberg 1974; Downing et al. 1983). Two main lipid classes, triacylglycerols and wax esters, have been identified in cetaceans, and they vary among the family groups, according to evolutionary lines.

Epidermal structure and function of both toothed and baleen whales has been a subject of investigation for many years as this tissue, generally void of hair and glands, has undergone many aquatic adaptations (Sokolov 1960; Palmer and Weddell 1964; Williams 1968; Sokolov et al. 1969; Spearman 1972; Viale 1979; St. Aubin and Geraci 1980; Brown et al. 1983; Liu Renjun et al. 1986; Ridgeway and Carder 1990). Subdermal blubber, the major lipid store for cetaceans, may constitute 25–40 percent of the body weight. Lipid content of the epidermis has been quantitatively assessed by Menon and coworkers (1986) only for the harbor porpoise (*Phocena*

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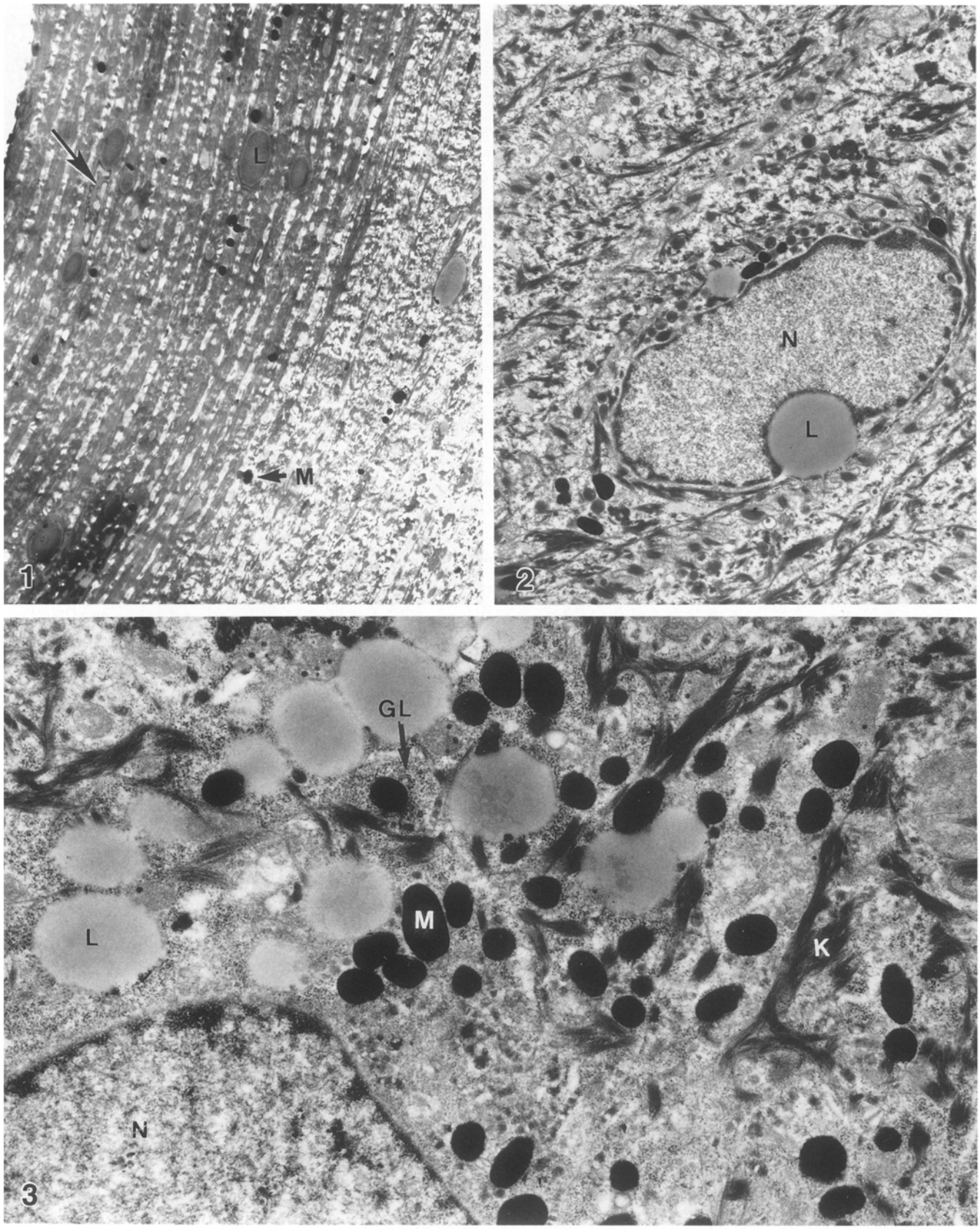


Fig. 1. Low-power transmission electron micrograph of bottlenose dolphin (lateral trunk) epidermis. About 19 layers of squamous cells comprise the electron-dense stratum externum. Note retained parakeratotic nucleus (*arrow*), intracellular lipid droplets (*L*), and melanosomes (*M*). ×4750

Fig. 2. In this higher-power electron micrograph of dolphin epidermis the close association of intracellular lipid (*L*) with the nucleus (*N*) is shown. ×9520

Fig. 3. Transmission electron micrograph of portion of epidermal cell of bottlenose dolphin, lateral aspect of the trunk. Several non-membrane bound intracellular, lipid droplets (*L*) are depicted, as well as part of the nucleus (*N*), melanosomes (*M*), glycogen (*GL*), and keratin fibrils (*K*). ×19700

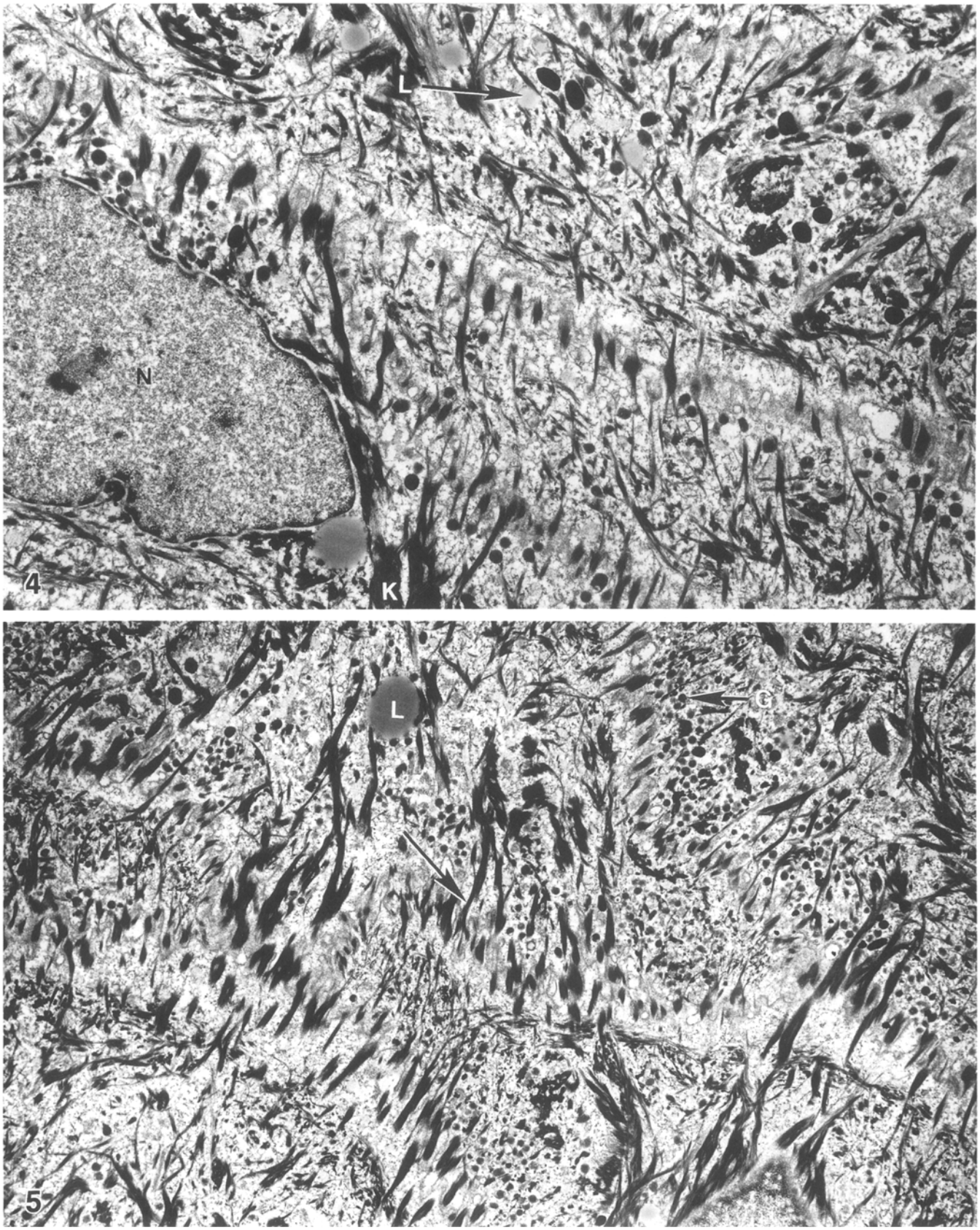


Fig. 4. Electron micrograph of parts of several epidermal cells from the stratum spinosum of the bottlenose dolphin, illustrating very small intracellular lipid droplets (*L*), keratin fibrils (*K*) and nucleus (*N*). ×8700

Fig. 5. Numerous intracellular lamellar granules (*G*) can be seen, as well as a single lipid droplet (*L*). Note the attachment of some of the keratin fibrils to desmosomes between adjacent cells (*arrow*) in this sample from bottlenose dolphin stratum spinosum. ×7100

phocena). It has previously been observed in droplet form intracellularly and in diffuse or droplet form intercellularly (Sokolov and Kalashnikova 1971; Tinyakov et al. 1973; Harrison and Thurley 1974; Stromberg 1985; Geraci et al. 1986; Menon et al. 1986). While quantitatively small compared to cetacean lipid stores elsewhere, such intracellular epidermal lipid deposits are not observed in terrestrial mammals but are common in birds and snakes (Varicak 1938; Ahern and Downing 1974; Landmann 1980; Menon and Aggarwal 1982; Stromberg et al. 1990). The function of this significant intracellular lipid content of cetacean epidermis remains obscure. Its hypothetical roles in providing insulation, producing an external layer of lubricant (Geraci et al. 1986), or reducing permeability to water transport does not seem readily apparent. The layered intercellular lipid present in the interstices of the epidermal stratum externum is generally considered to function as a water barrier (Elias 1983). Accordingly, in the course of our long-term comparative study of cetacean integument we have observed with particular interest the anatomical disposition of epidermal lipid stores. The present communication describes some of our recent ultrastructural findings of cetacean epidermal lipid, including the first scanning electron microscopic perspective of this reservoir.

Materials and methods

Skin samples were obtained directly from a variety of adult cetacean species which had been stranded along the Atlantic shore of North America. These included several individuals of each of the following species: bottlenose dolphin, *Tursiops truncatus*, the long-finned pilot whale, *Globicephala melaena*, the fin whale, *Balaenoptera physalus*, and the humpback whale, *Megaptera novaeangliae*. Data described in this paper were obtained only from fresh or good-quality specimens. Our experience has shown that in recently stranded animals the skin is one of the more resistant tissues to post-mortem changes. In our routine procedure we collect skin specimens from the mid-dorsal, ventral and lateral aspects of the body, from dorsal and ventral aspects of the fin or fluke, from standardized sites around the urogenital slit area, and from various sites within the oral cavity and the blowhole. This communication will describe the epidermis from several of these sites, as well as from the penis skin.

Specimens measuring 3 mm × 1 mm for transmission electron microscopy (TEM) and 4 mm × 4 mm for scanning electron microscopy (SEM) were placed in cold 5% glutaraldehyde/3% formaldehyde in 0.1 M Na cacodylate buffer at pH 7.4 for initial fixation. Other larger samples were fixed in 10% buffered formaldehyde for light microscopy. After fixation for a minimum of 12 h in the glutaraldehyde solution, specimens were washed in 0.1 M cacodylate buffer, post-fixed in 1% osmium tetroxide in 0.1 M Na cacodylate for 1 h, washed in buffer again, and dehydrated in graded alcohols. SEM specimens were critical point dried, mounted and coated with gold (approximately 1500 Å) in a SPI sputter coater for 5 min, and examined in a JEOL JSM 35C scanning electron microscope (JEOL, USA, Medford, Massachusetts) operating at 10 KV. Other specimens were embedded in Poly/Bed 812 resin (Polysciences, Warrington, Pennsylvania) sectioned at 1 μm for light microscopy and stained with 1% toluidine blue in 1% sodium borate for 30 s, followed by 0.5% safranin in 0.5% sodium borate for 10 s by standard procedures (Pfeiffer et al. 1974; Pfeiffer and Kinkead 1990). Intracellular lipid treated in this way is stained green. Further histochemical analyses of epidermal lipid were not undertaken, as these have been reported elsewhere (Stromberg 1985; Menon et al. 1986). Ultrathin sections were doubly stained with lead citrate and uranyl acetate and studied with a JEOL 100 CX-11 transmission electron microscope operating at 80 KV.

There is some variability in the literature over the terminology and number of cellular strata in the cetacean epidermis. In this report we conform to the terminology of Geraci and co-workers (1986), i.e., three layers, strata germinativum, spinosum, and externum (corneum).

Results

We have observed, as others before us, that cetacean epidermal lipid is found as intracellular droplets as well as intercellularly. However, we did not find the latter reservoir conspicuous in most cases, nor did we observe stages in which intracellular droplets were being exocytosed into intercellular spaces.

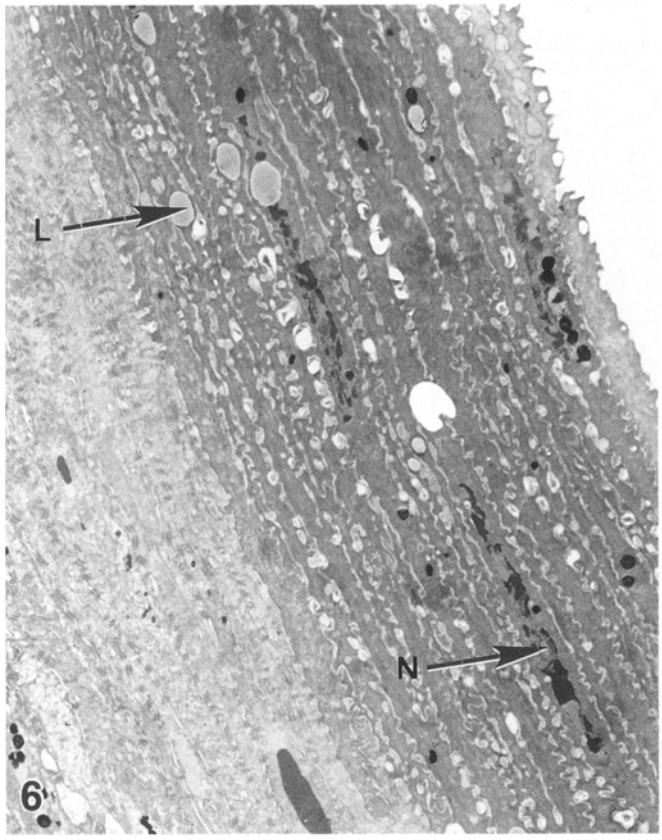
In the bottlenose dolphin epidermis (from the lateral surface), large intracellular droplets of lipid were seen in the stratum externum and deeper (Fig. 1). In epidermal cells of this region the lipid droplets were accompanied by occasional melanosomes as well as retained, degenerating cellular nuclei. In the deeper stratum spinosum the intracellular lipid droplets frequently occurred clustered in the perinuclear region, and sometimes rested within nuclear indentations (Fig. 2) but some were also isolated more peripherally throughout the cytoplasm. The intracellular lipid droplets were not membrane-bound and appeared distributed around melanosomes, extensive pools of cytoplasmic glycogen, and strands of intracellular keratin fibrils (Fig. 3). The droplets were spherical and of variable size, ranging from 0.24 μm to 1.6 μm (Figs. 3, 4). Spherical lamellar granules of high electron density and approximately 0.2 μm in diameter were numerous within the epidermal cell cytoplasm (Figs. 4, 5). These granules were readily differentiated from the melanosomes due to the greater electron density and more ovoid shape of the melanosomes. In some regions the stratum spinosum cells showed few intracellular lipid droplets or none (Fig. 5). Lipid droplets were absent in the stratum germinativum.

Fig. 6. This epidermis, showing mostly the denser stratum externum, is from the integument lining the blowhole of the bottlenose dolphin. Note the conspicuous intracellular lipid droplets (*L*) and retained nuclei (*N*). The lighter region on the left is part of the stratum spinosum. ×4600

Fig. 7. Stratum germinativum of bottlenose dolphin blowhole epithelium. This figure shows centrally a cross section of the base of an epidermal peg surrounded by more electron-lucent collagenous tissue of the dermal papillae. Lipid droplets are absent. Note the prominent melanocyte (*M*). ×2700

Fig. 8. Outermost epidermal cells of stratum externum of skin on penis of the pilot whale. Note the large and smaller intracellular lipid droplets (*L*). Separation between the layers reflects the process of sloughing of these cells. ×15300

Fig. 9. In the fin whale epidermal stratum spinosum, intracellular lipid droplets (*L*) were prevalent and were observed, as is frequently seen in other cetacean species, clustered near the nucleus (*N*). ×4500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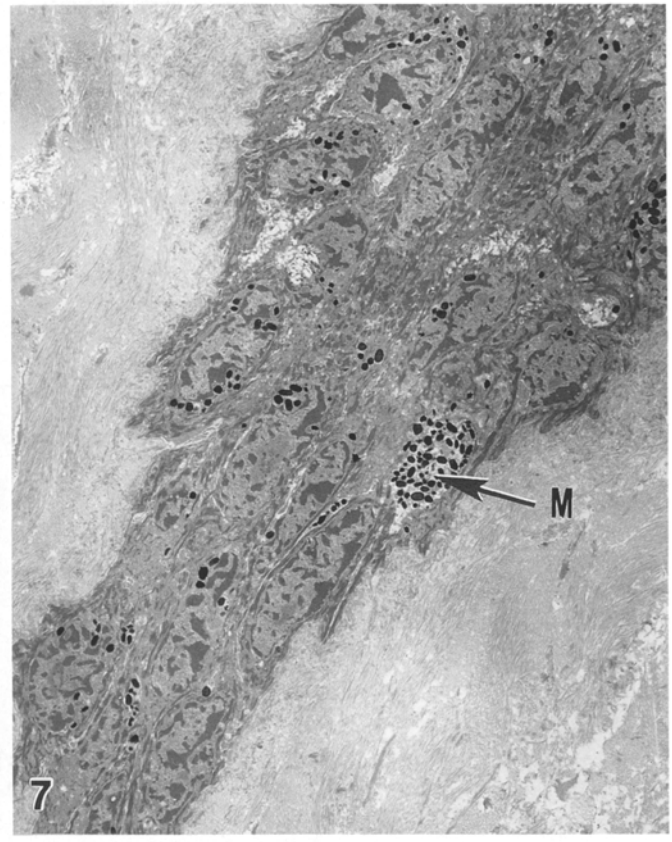
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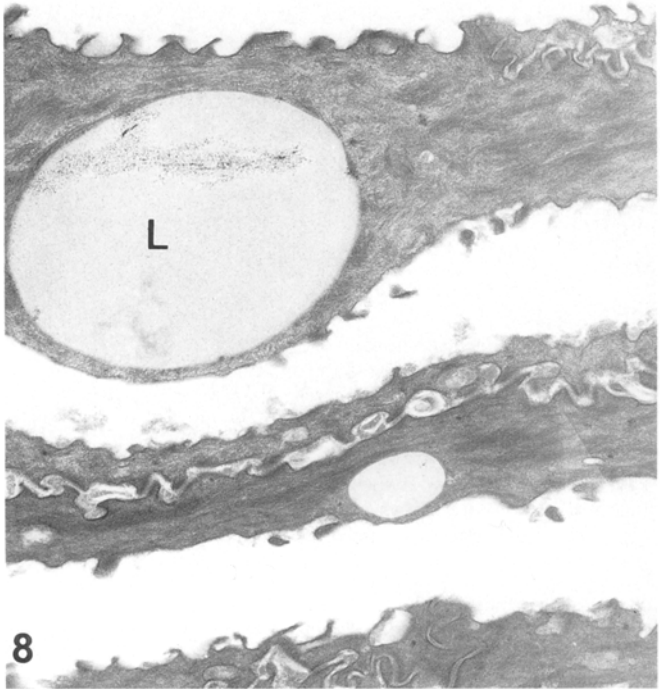
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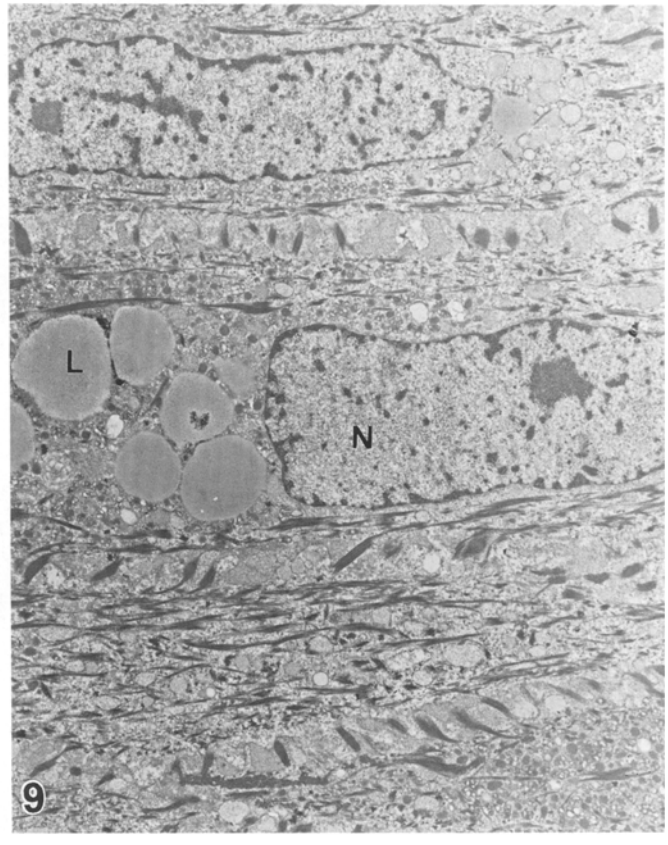
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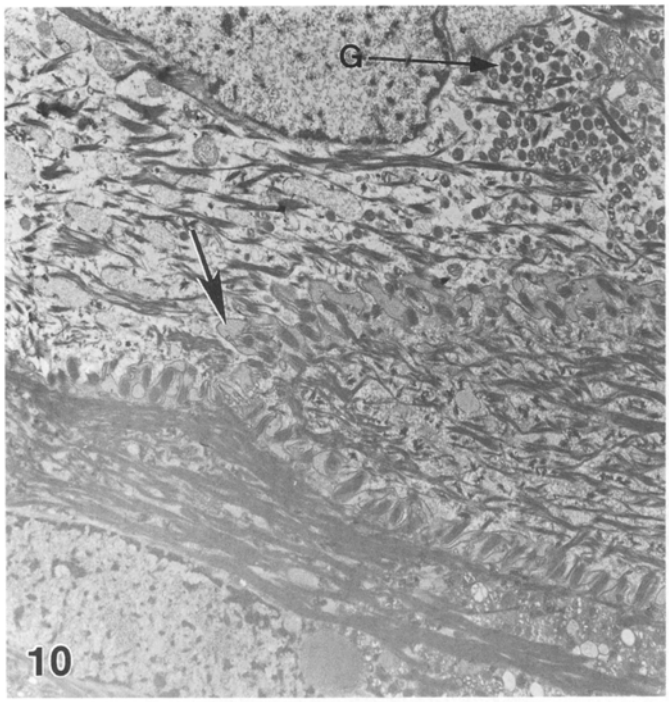
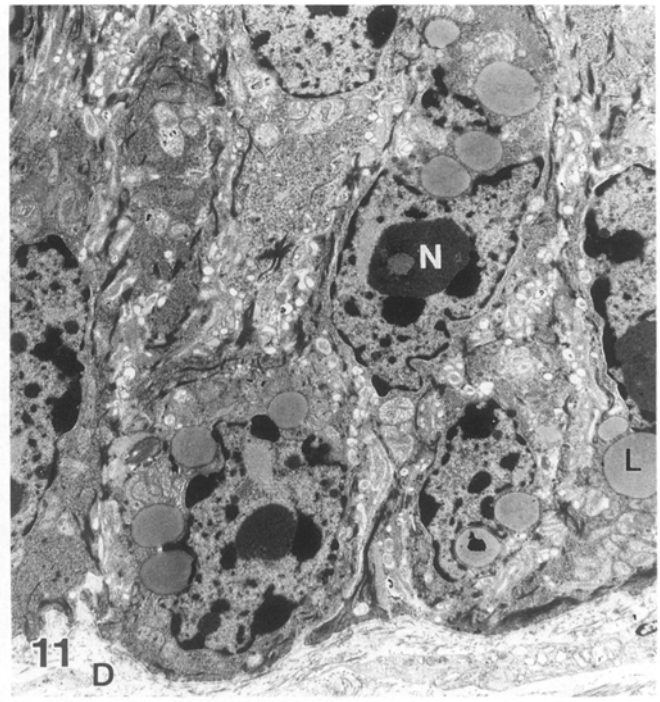
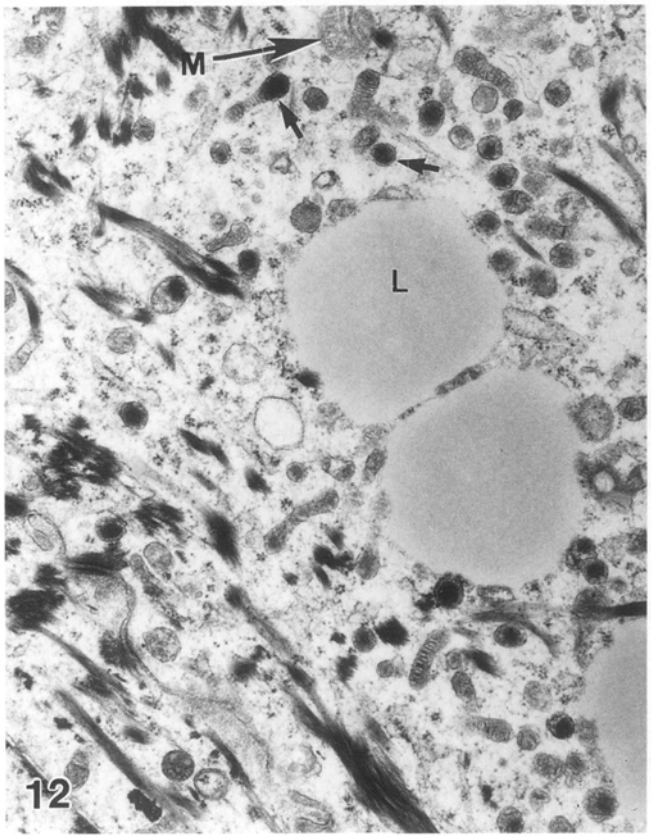






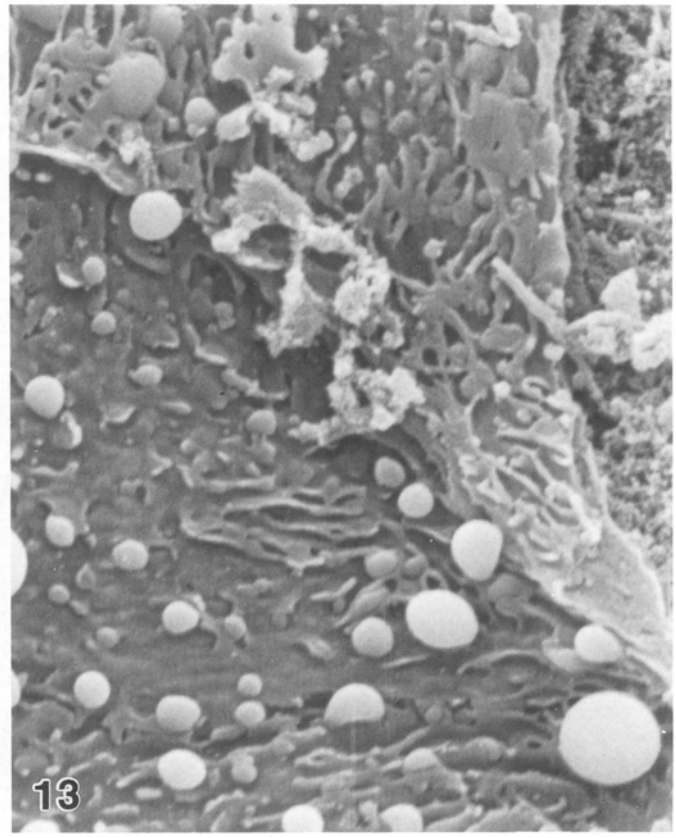
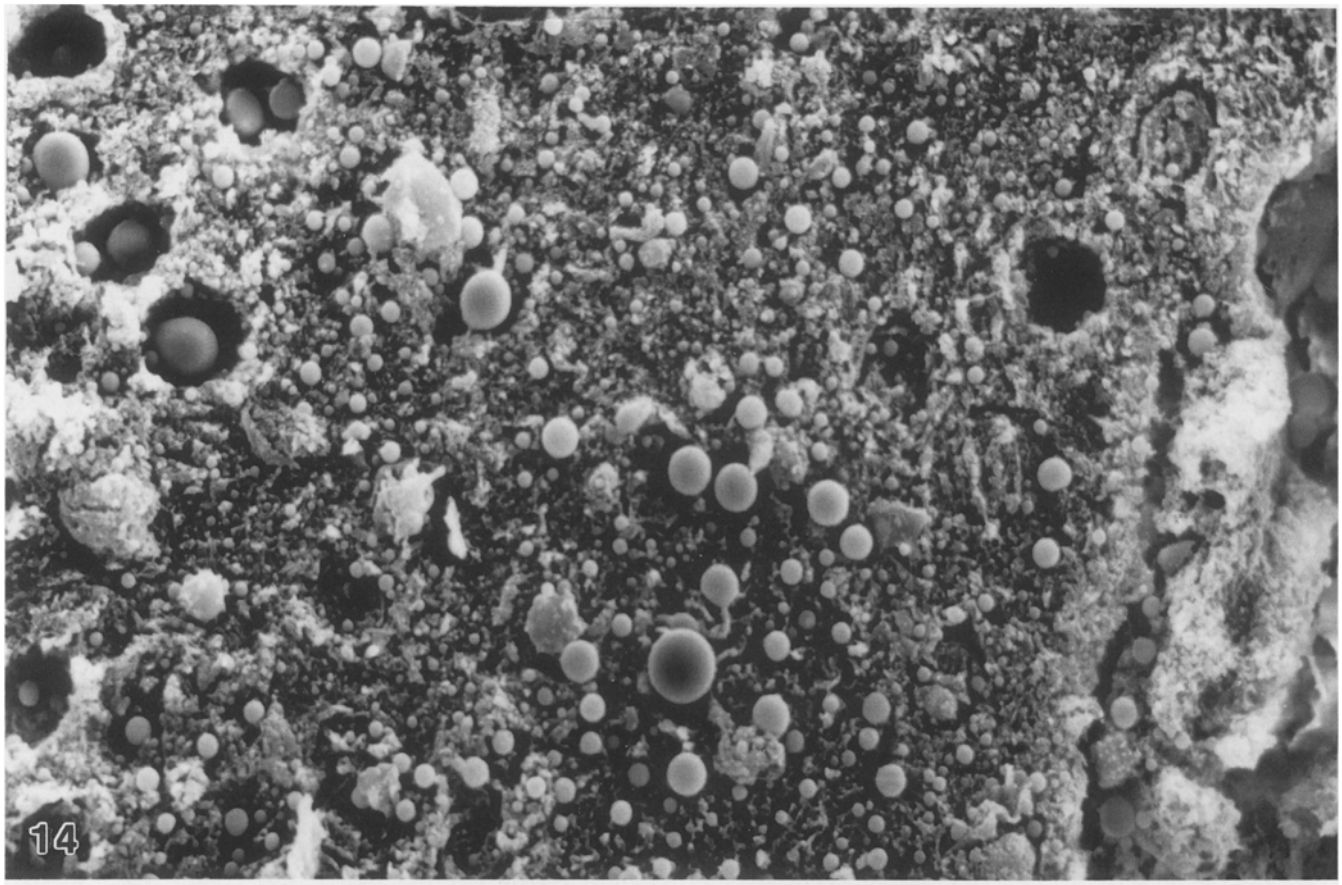


Fig. 10. An area of fin whale epidermis that has only a single intracellular lipid droplet (bottom of figure), but contains extensive keratin fibrils in the stratum spinosum. Note the amorphous intercellular lipid (*arrow*) and lamellar granules (*G*). ×7000

Fig. 11. Epidermal cells and dermal connective tissue (*D*) from skin of the urogenital region of the humpback whale. Note the intracellular lipid droplets (*L*), and prominent nucleoli (*N*) of stratum germinativum cells

Fig. 12. Intracellular lipid droplets (*L*) in stratum spinosum cells from the urogenital region of the humpback whale. Note the membrane-bound lamellar granules. (*arrows*), mitochondrion (*M*) and keratin fibrils. ×17500

Fig. 13. Scanning electron microscopy revealed spherical lipid droplets on epidermal cellular surfaces between the stratified layers in the stratum externum in the bottlenose dolphin. ×8140



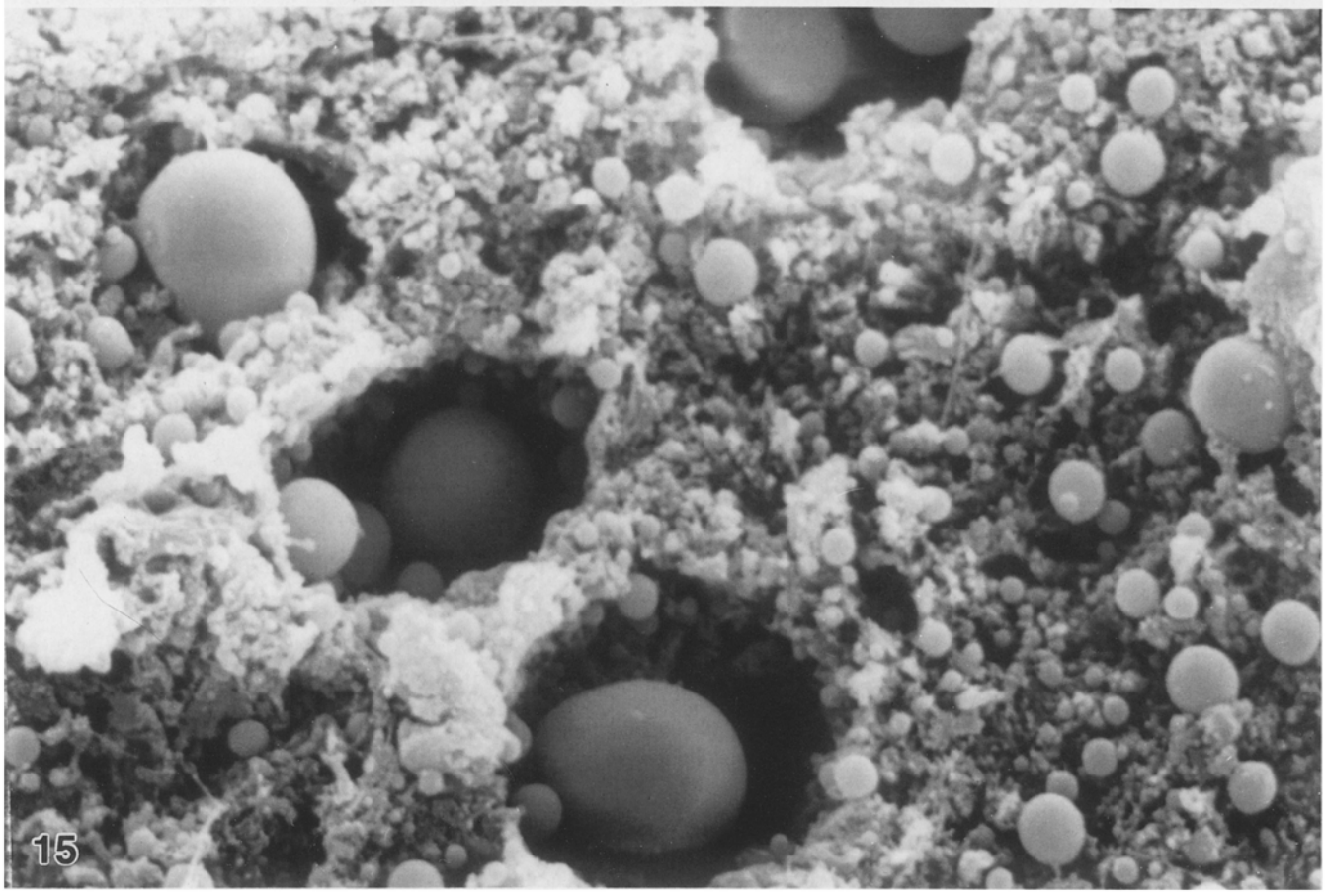


Fig. 14. Scanning electron micrograph of fractured bottlenose dolphin epidermis revealing numerous spherical intracellular lipid droplets of various sizes. ×1960

Fig. 15. This scanning electron micrograph depicts the epidermal cytoplasmic cavitations in which several lipid droplets of various size aggregate together. Other free, smaller lipid droplets are also present. ×6700

Examination of the epidermis of the bottlenose dolphin taken from the integument lining the blowhole (Fig. 6), about 3 cm deep within the cavity, also revealed the presence of intracellular lipid deposits. These were similar in size and number to those found on the exterior of the dolphin. Parakeratotic nuclei were also observed within the stratum externum of the epidermis of this region. Epithelial cells in the stratum germinativum of the epidermis of blowhole integument did not contain intracellular lipid droplets (Fig. 7). Epidermal stratum externum of the vestibular sac (portion of nasal sinus) integument also contained intracellular lipid droplets. The integument of other specialized regions, such as the skin of the penis of the pilot whale was also investigated. The skin of this organ, like that of the blowhole, is usually not exposed to the aquatic environment. The epidermis of pilot whale penile skin also revealed prominent intracellular lipid droplets (Fig. 8) which in some cases were considerably larger (up to 3.0 μm) than those seen in various sites on the bottlenose dolphin.

Epidermal cellular structure of the fin whale was remarkably similar to that of the toothed whales described above, in view of the evolutionarily distinct lines separating mysticete from odontocete whales. Intracellular lipid deposits were also conspicuous in the fin whale epidermis (Fig. 9). As in the toothed whale epidermis, the lipid droplets of the fin whale were sometimes clustered near the nucleus (Fig. 9), and in other regions were sometimes scarce (Fig. 10). Lamellar granules and keratin fibrils (Fig. 10) were also evident. Amorphous material in the intercellular interstices had the electron density of lipid seen intracellularly (Fig. 10).

In the humpback whale epidermis, intracellular lipid deposits were also conspicuous, as shown in samples taken near the urogenital slit area (Figs. 11, 12). In contrast to blowhole integument of the bottlenose dolphin, cells of the stratum germinativum contained prominent intracellular lipid droplets (Fig. 11) in the humpback-whale. Lamellar granules and keratin fibrils were notable in the cytoplasm of stratum spinosum cells, along with the non-membrane bound lipid droplets (Fig. 12).

A new perspective on the lipid deposits in the epidermis was provided by scanning electron microscopy of fractured epidermal cells of the bottlenose dolphin. This was of interest because the highly variable size of lipid droplets and their varying depth could be visualized by this technique (Figs. 3–15). When lipid droplets were viewed only by planar sections with transmission electron microscopy, it was impossible to conclude whether cross sections of various sizes represented droplets of different size or only off-center sections of larger lipid droplets. Observation by SEM of intracellular lipid droplets revealed that aggregates of non-membrane bound droplets of various sizes resided in some cases in cytoplasmic cavitations (Figs. 14, 15). A view of the non-fractured surface of epidermal cells, which probably represents an interstitial zone between layers of stratum externum cells, revealed lipid droplets in the intercellular region (Fig. 13).

Discussion

The skin of cetaceans, which is generally devoid of hair, sweat and sebaceous glands, consists of a thick epidermis (1.0–3.5 mm, depending upon species) that is keratinized minimally or not at all, a dermis, and an exceptionally thick hypodermis. The epidermis is parakeratotic, unlike normal terrestrial mammalian epidermis, and has an outermost stratum externum (corneum), a deeper stratum spinosum, and a stratum germinativum (basale). Since the epidermal ridges which interdigitate with the dermal papillae are very deep, the numbers of stratum germinativum cells are large relative to those of most terrestrial mammalian epidermal tissues, and the quantity of epidermis produced is therefore relatively high (Brown et al. 1983; Hicks et al. 1985). In the bottlenose dolphin, the epidermal turnover time is relatively slow, and the sloughing rate is relatively much higher than in human epidermis (Hicks et al. 1985). Although some general differences between the integument of toothed whales and baleen whales have been reported (Sokolov 1960), the epidermis is similar in both suborders. In the largest baleen whales such as fin whales (Giacometti 1967) and bowhead whales (Haldiman et al. 1985) the epidermis is significantly thicker than in small toothed whales (Harrison and Thurley 1974).

Although three earlier reports have depicted the scanning electron microscopic perspective of cetacean skin (Harrison and Thurley 1974; Haldiman et al. 1985; Liu Renjun et al. 1986), these previous accounts showed only the epidermal surface and thus could not reveal the internal lipid reservoir. The most detailed earlier account of cetacean epidermal lipid was that of Menon and associates (1986) in which histochemical and chromatographic analyses were undertaken. Their studies revealed that for the harbor porpoise, *Phocena phocena*, novel, non-polar acylglucosylceramides were sequestered extracellularily between stratum externum cells. The intracellular, triglyceride lipid droplets, at least in the harbor porpoise, were not the source of released intercellular lipid, which is derived from the intracellular lamellar granules. The barrier function of cetacean epidermis is probably regulated by the lipid within the intercellular interstices. This function appears to be osmotically disrupted, as manifested by epidermal degeneration and sloughing, when "saltwater" cetaceans are placed in freshwater (Simpson and Gardner 1972). In the present investigation, epidermal lamellar granules, i.e., the keratinocyte small granules or membrane-coating granules described by earlier writers (Matoltsy and Parakkal 1965; Landmann 1980), were observed, but neither these organelles nor intercellular lipid deposits in the interstices were extensively developed. They were structurally similar to this type of granule reported by Elias and associates (1987) in harbor porpoise skin.

The function of cetacean epidermal lipid stores, shown in this study as primarily intracellular reservoirs, remains open to speculation. Many of the functions of epidermal lipid of terrestrial, non-aquatic species, or previously alleged functions for cetaceans, do not seem likely, or are not supported by evidence. In non-aquatic

species, epidermal lipid provides a barrier to water loss (Elias et al. 1977) and evaporation, but in cetaceans evaporation is not a factor. It has recently been demonstrated that a high lipid content of tissue enhances the rate of oxygen diffusion and may compensate for reduced diffusion in fish muscle at the low temperatures of sea water (Desaulniers and Sidell 1992). However, in cetacean epidermis the most active proliferative zone, stratum germinativum, contains the least concentration of lipid droplets, and also many cetaceans reside in warm water near the surface.

The notion that for some cetaceans fast movement in water is facilitated by reduced frictional drag, due in part to excreted intracellular epidermal surface lipid is not supported by evidence (Sokolov et al. 1969). Geraci and associates (1986) questioned whether intercellular lipid exposed by desquamated layers of stratum externum cells could serve as a drag-reducing material. This does not seem plausible, especially in view of the rough surface contour provided by cellular microridges present at the surface boundary area. The very extensive subdermal blubber layer of cetaceans serves as an important energy store (Lockyer et al. 1984) and has an insulating function in cetaceans, but the proportionally much smaller epidermal lipid deposits do not seem to have this role. The cetacean skin has a degree of compliance which might be actively controlled to facilitate rapid movement by reducing frictional hydrostatic drag forces (Surkina 1971), or in any case would respond to whole-body bending. However, intracellular lipid deposits in the epidermis do not seem to have evolved to enhance compliance, because many terrestrial mammals which manifest far greater bodily contortions do not show similar epidermal lipid deposits. Perhaps the most likely function of cetacean epidermal intracellular lipid droplets is as a metabolic requirement of the epidermis itself. Cetacean skin has been found to have an exceptionally high capacity for the production of epidermis (Geraci et al. 1986) and, at least in man, fatty acids in the epidermis have been shown to be the principal source of energy (Yardley and Summerly 1981). Stromberg (1985) has also given particular attention to the fat distribution in bottlenose dolphin skin, and reported that extracellular fat was deposited in the dermis, and lipid particles were even observed within the lumen of blood vessels in the reticular dermis. In addition, we have reported within the cardiac tissue of the bowhead whale, *Balaena mysticetus*, a unique spongiosum which probably harbors extensive lipid deposits (Pfeiffer 1990), and have observed the presence of intracellular integumentary lipid droplets in terminal baleen bristles of the humpback whale, *Megaptera novaengliae* (Pfeiffer 1993). Cetaceans have, therefore, many unusual sites for fat storage, but further study will indeed be necessary in order to elucidate the functional roles of their epidermal lipid, which is so conspicuous from the morphological perspective.

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