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OVERVIEW OF THE MAMMARY GLAND*

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ABSTRACT

The anatomy and development of mammary tissue and the physiology of lactation show many similarities and significant differences among various mammalian species. Although the mammary glands are skin organs whose significance has been recognized for a long time, there is much new information that is reviewed in this paper.

The mammary gland is one of the most important accessory glands of the skin. It is the distinguishing feature of mammals which by definition feed their young with milk secreted by such glands. In this paper, I shall restrict the term *breast* to the human mammary gland since I find it somewhat incongruous to refer to the "breast" tissue of the cow or rat. The mammary gland is part of the reproductive apparatus, lactation being the final phase of the mammalian reproductive cycle. In this overview, I propose to consider in very general terms the structure and functions of the mammary gland and to include some old as well as recent observations since even a little of the historical background gives perspective to progress in this field. I shall omit any reference to certain specialized problems such as malignant transformation and cosmetic surgery since these aspects are fully considered elsewhere in this issue.

ANATOMY OF THE MAMMARY GLAND

The size, shape, and number of mammary glands vary from species to species. Normally the mammary gland becomes functional only in the female, but mammary tissue is present in both sexes except apparently in male marsupials [1]. In most species, the mammary glands are paired: from two in man, goat, and guinea pig to 14-18 in the pig. In some marsupials of the family Didelphidae, there is an odd number because at an early stage of fetal development a pair of nipples fuses [2,3]. The position of the mammary glands is also variable: in the rodent, dog, pig, and rabbit, the glands extend along the ventral thorax and abdomen; in man, bat, and elephant, they are thoracic; in the ruminant, inguinal; in the whale, abdominal; and in the coypu and viscacha, dorsolateral. The shape and form also vary: in the rat and mouse, the mammary glands are flat sheets of tissue enveloping the body wall; in the rabbit and monkey, they are flat and circular; in ruminants, one or two pairs of glands lie in close apposition forming a structure known as the udder. In all female mammals except the monotremes, a nipple or teat is present on each gland; small nipples are present in the males of most species, except the mouse and rat whose mammary ducts end blindly.

Despite these wide external variations, the internal structure of the mature female mammary gland is basically the same in all species from monotremes to man. The glandular or parenchymal tissue, comprising the alveoli and ducts, and the stromal or supporting tissues, in which the glandular tissues lie, are common to all species. Neither light nor electron microscopic studies have revealed any distinctive species differences in the structure of the alveolar cell [4]. Each alveolar cell is a complete milk-secreting unit, synthesizing milk fat, protein, and carbohydrate. Although the cellular processes involved in the secretion of fat and protein appear to be similar in all species, the precise chemical composition of the milk secreted varies considerably.

The disposition of the mammary ducts and the nature of the storage spaces within the mammary gland are variable. The alveolar sectors of the breast, the main ducts of each expanding into a lactiferous sinus, have perhaps never been better illustrated than in the color plates of wax-injected preparations depicted in Sir Astley Cooper's book *On the Anatomy of the Breast* [5] published in 1840 (Fig. 1). The histology and histochemistry of the nipple, areola, terminal milk ducts, and associated glands of the breast are reviewed in detail by Montagna in this issue. The patterns of disposition of the main galactophores in a number of species are illustrated diagrammatically in Figure 2. In rodents, the ducts unite to form a single main duct or galactophore which passes through the nipple. In the rabbit, the circular mammary gland is made up of some six sectors, each with its own separate galactophore. These sectors can be readily demonstrated by injecting a dye or mercury into the openings of the individual galactophores at the tip of the nipple as Cooper showed or by using the equally elegant but more physiologic method, first reported in 1942 by Lyons [6], of injecting a solution of prolactin into a galactophore and inducing localized milk secretion in the alveolar sector served by it. It will be noted that the general layout of ducts in the rabbit mammary gland resembles that in the breast save that in the breast there are some 14 galactophores, each of which expands to form a lactiferous sinus before passing through the

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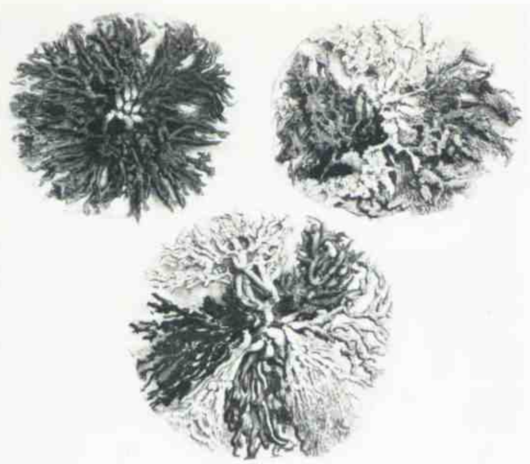

FIG. 1: Sectors of the breast. Part of a colored plate from Cooper's *On the Anatomy of the Breast* (1840). Cooper injected waxes through the galactophores into the duct system and the ducts were subsequently displayed by repeated maceration and dissection. In the preparation on the upper right, lobules of alveoli have also been injected and are clearly displayed.

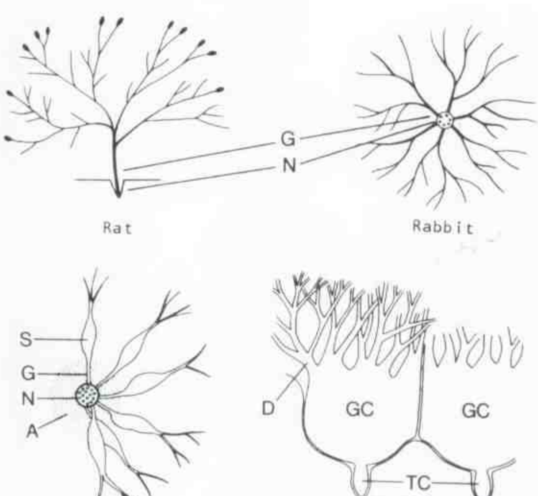

FIG. 2: Diagram showing different arrangements of the mammary duct system. A = areola; D = duct; G = galactophore; GC = gland cistern; N = nipple; S = sinus; TC = teat cistern; TCL = teat canal.

nipple. In ruminants, the larger ducts from each gland open into a large cistern, the gland cistern, which in turn opens directly into the teat cistern which communicates with the exterior through the single teat or streak canal at the tip of the teat. In the monotremes, the mammary gland is composed of some 100–200 lobules, each being drained by a duct which opens directly onto the skin surface in a special area, the areola; there is thus no nipple or teat, the milk pouring out on the surface of the skin when milk ejection is induced. As Griffiths and his colleagues [4] have pointed out, this system is wholly suited to the young platypus whose beak is well adapted to sucking milk off the skin but not for retaining a nipple and drawing milk from it.

Mammary Stroma

In rodents, the pad in which the glandular elements lie is composed mainly of fatty tissue; in the cow the stroma is a mixture of connective tissue and adipose tissue, and in the breast the stroma is mainly connective tissue. The fibrous septa within the stroma connect with a series of mammary ligaments which support the mammary gland, the fully lactating gland being a relatively heavy structure. Again Cooper has provided the classical description of how the fascia from the sternum forms superficial and deep layers to envelop the glandular tissues of the breast, connecting with the mammary stroma and with the aponeurosis of the pectoral muscles so that "the breast is slung upon the fore-part of the chest." Other species have similar ligamentous suspensory systems for the mammary gland; that for the udder of the cow performs no light task in anchoring the mammary glands both directly and indirectly to the bony pelvis [7], for in a high-yielding cow, the udder, including milk and blood, weighs 40 kg or more.

Blood and Nerve Supply

Because the mammary gland is of cutaneous origin, its vascular supply and innervation are that of the contiguous skin and vary with the species according to the position of the gland. In the ruminant and rat and presumably other species, marked increases in the rate of blood flow through the mammary gland occur at the time of parturition and during lactation [8,9]. The mammary gland receives somatic sensory and sympathetic motor nerve fibers, but parasympathetic innervation has never been convincingly demonstrated. The sensory innervation is confined mainly to the region of the nipple or teat. Cathcart, Gairns, and Garven [10] regard the nipple as one of the most highly innervated tissues of the human body; the precise distribution of nerves in the nipple and areolar region is described in this issue by Montagna and Macpherson. Less is known about the distribution of nerves within the substances of the gland; there is no evidence of innervation of the alveolar or myoepithelial cells, and Linzell [11] concludes that innervation of mammary tissue consists only of sympathetic fibers to the arteries with a small number of sensory fibers to the large ducts which seem to be of slow-conducting unmyelinated type (c fibers). Such a distribution would accord with the clinical evidence that the degree of filling of the mammary gland can be detected by the central nervous system.

DEVELOPMENT OF THE MAMMARY GLAND

Fetal Growth

Considerable information exists on the stages of embryologic and fetal growth of the mammary gland in a number of species. The pattern common to all species involves thickening of the ectoderm to form milk lines, reduction and interruption of the milk lines with the formation of mammary buds, and sprouting of the mammary buds to give rise to the mammary cords which penetrate into the mesenchyme and form the primordia of the duct system. There are clear indications that the initial differentiation of the epidermis is controlled by the mesenchyme which exerts an instructive function through organ-specific factors whose nature is not yet known [8]. Sex differences become apparent in the pattern of mammary growth in the fetal rat and mouse; in the male, this growth is affected by androgens from the fetal testis which inhibit the growth of the nipple (Fig. 3). In these two species, excessive estrogenic hormones can induce mammary malformations in the fetus; in the female fetus, androgens induce male-pattern growth. Such observations in rodents should alert us to the possibility that congenital mammary abnormalities in other species are associated with hormonal therapy or hormonal abnormalities in the mother during pregnancy (for references see [8].

Postnatal Growth

Postnatally, the growth of the mammary gland is regulated by a complex interaction of anterior pituitary, ovarian, and, in some species, placental hormones. There is much evidence to suggest that the anterior pituitary and placental hormones are directly responsible, the ovarian hormones mainly by sensitizing the mammary cells to the growth-stimulating action of the pituitary and placental hormones. Recently, however, the direct mitogenic activity of these hormones has been questioned, and it has been suggested that they in turn sensitize the mammary cells to the mitogenic action of insulin [12]. Whatever the precise mode of hormonal action, the administration of ovarian hormones to intact animals, in which anterior pituitary hormones and insulin mammary growth. Details of the complexities of the hormonal control of mammary development are given in other papers in this volume.

The degree of growth of the male mammary gland is usually slight. In some species (e.g., ruminants), the male gland scarcely responds to administered ovarian hormone, whereas in others (e.g., guinea pig, man), a marked growth response sometimes occurs. This is of some clinical significance. Bishop [13] relates how he prescribed an estrogen-progestagen ointment to be applied locally by a patient who consulted him because her husband had become dissatisfied with her "miserable little breasts." Unfortunately, she did not thoroughly inunct the ointment and 60 days later Bishop was confronted by an irate husband complaining of gynecomastia.

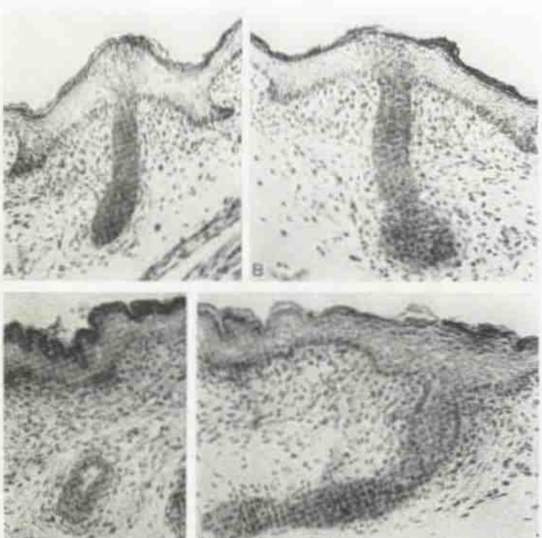

FIG. 3: The development of the mammary rudiments of the fetal mouse (18 days) after fetal gonadectomy on day 13 (from Raynaud, [58]). A. Mammary rudiment of a normal female fetus. B. Mammary rudiment of a female fetus whose ovaries were destroyed by x-ray. C. Mammary rudiment of normal male fetus—mammary bud has become separated from epidermis. D. Mammary rudiment of male fetus whose testes were destroyed by x-ray—bud remains attached to epidermis.

LACTATION

It is convenient to recognize two phases in lactation: (1) milk secretion, in which the constituents of milk are synthesized in the alveolar cells and passed out of the cells to be stored as milk in the lumen of the alveolus; (2) milk removal, which in most species requires the activation of the milk-ejection reflex whereby the milk stored in the alveoli is transferred into the large ducts and cisterns to become available to the suckling or milker. Lactation is also associated with certain behavioral patterns which vary greatly from species to species [14–16].

Milk Secretion

The time of onset of milk secretion varies. In the rat, it begins about 24 hr before parturition, in the goat at midpregnancy [17]. Normally, however, the onset of copious lactation in most species does not occur until after parturition. (The term *lactogenesis* was at one time mainly used to refer to the onset of copious lactation; now it often denotes the first signs of secretory activity. Since this can give rise to confusion, I am avoiding the term.)

Only in the rat have the precise hormonal mechanisms that control the initiation of milk secretion been determined. A fall in the level of blood progesterone enables prolactin and placental lactogen to exert their lactogenic effects on the mammary cells. In a few species, the hormonal requirements for lactation have been determined. Generally a complex of hormones is required, of which prolactin is an important component. Prolactin was isolated in a relatively pure state from ruminant pituitaries some 35 years ago but only in the last few years has its presence in human and subhuman primate pituitaries been confirmed. Indeed, the existence of a human prolactin was doubted, for it was discovered that human growth hormone possessed lactogenic activities and was believed to serve a dual role. However, human prolactin has now been isolated and evidence, reviewed by Forsyth and Edwards [18], suggests that it plays an important role in the maintenance of milk secretion. I know of no evidence to suggest that human growth hormone has a similar role. On the other hand, ruminant growth hormone gives no lactogenic or pigeon-crop response, yet it seems to play a role just as important as or even more important than prolactin in the maintenance of milk secretion in ruminants [8].

Over the last five years, much information on the hormonal responses to the suckling or milking stimulus has been obtained, thanks to new bioassay and radioimmunoassay techniques. Since Meites discusses neuroendocrine interactions elsewhere in this volume, I will merely stress that the natural stimulus to continued milk secretion is the regular and efficient removal of milk from the gland.

Milk Removal

In most species, the milk stored in the alveoli and fine ducts is not available to the suckling or milker until it has been moved into the larger ducts and cisterns. This transfer is brought about by a contraction of the myoepithelial cells surrounding the alveoli in response to the reflex release of oxytocin into the blood effected by the stimulus of suckling or milking. The milk is thus forcefully ejected from the alveoli and distends the large ducts and sinuses or cisterns where it is sometimes contained under considerable pressure. The importance of this milk-ejection reflex to the efficient removal of milk varies with the species: failure of the reflex in the rat, rabbit, and woman leads to a rapid inhibition of milk secretion since little or no milk can be removed from the gland. In the cow about half the milk contained in the udder can be milked out, while in the goat most or all of the milk can be obtained (for references see [8]). The existence of this reflex has long been recognized, but the sudden filling up of the storage spaces and the increase in intramammary pressure were ascribed to the onset of a phase of rapid milk secretion. The phenomenon was known as the "let down" of milk in the cow and the "draught" in the woman. The true nature of the phenomenon in ruminants was first demonstrated by Gaines [19] in 1915 who stated that "milk secretion, in the sense of the formation of the milk constituents, is one thing; the ejection of milk from the gland after it is formed is quite another thing. The one is probably continuous, the other, certainly discontinuous." He actually demonstrated that milk ejection could be induced by injections of posterior pituitary extract. He believed, however, that this was essentially a pharmacologic action and that the milk ejection was a typical neural reflex. Not until 1941 was it postulated by Ely and Petersen [20] that in the cow the reflex was neuroendocrine, involving the release of oxytocin. This view has since been extensively investigated and is now fully accepted [8]. Ely and Petersen also concluded that the reflex could become conditioned to signals associated by the cow with the act of milking. Cooper [5], writing some 50 years before the studies of Pavlov, also noted conditioning of the draught in women: ". . . even the sight of the child will produce this draught, as the thought or sight of food occasions an abundant secretion of saliva." Indeed the "draught" in women was fully described by Cooper although he ascribed it to the onset of rapid secretion. "The secretion of milk may be said to be constant or occasional; by the first the milk tubes or reservoirs are *constantly* supplied by means of a slow and continued production . . . by the *occasional* is understood that secretion which is called by mothers and nurses, the draught of the breast - during which the milk is so abundantly secreted, that if the nipple be not immediately caught by the child, the milk escapes from it, and the child when it receives the nipple is almost choked by the rapid and abundant flow of fluid; if it lets go its hold, the milk spurts into the infant's eyes." The draught reflex was rediscovered and described a century later by Waller [21,22] who wrote: "For within a second or two the child is greeted by an outrush of milk which may be so sudden and copious that he chokes and is compelled to break off feeding to take breath." The wide recognition of the milk ejection reflex, its depiction in art, and its exploitation by primitive peoples have been reviewed by Amoroso and Jewell [23] and Folley [24]. Time does not allow detailed comment, but I shall just mention that "sympathy" between the mammary gland and the reproductive tract has been recognized for several millenia and that at least from the time of Herodotus agricultural peoples have used vaginal stimulation in their milch animals to ensure the "let-down" of milk although some 2400 years were to pass before it was appreciated that vaginal stimulation could release oxytocin into the blood [25]. The milk-ejection reflex of the modern "mechanized" dairy cow, an animal selectively bred over generations for high yields and ease of milking, operates in response to the sight or sound of the milking apparatus.

Duration of Lactation

Lactation can be rapidly inhibited by ceasing to remove milk from the gland. Within a day or so, the storage capacity of the gland becomes inadequate, and the increasing intra-alveolar pressure brings about a rapid degeneration and regression of the secretory epithelium [8]. Normally, however, the decline of lactation and mammary regression are slow processes. As the sucklings grow and begin to eat other food, less milk is withdrawn and less stimulus is applied to the gland. In some species, such as the cow, the onset of a new pregnancy creates a hormonal milieu detrimental to the secretory activity of the mammary gland; in other species (e.g., man), lactation tends to inhibit the sex cycle and thus delays the onset of a new pregnancy. In dairy ruminants, if regular milking is continued and if the animals are not again impregnated, lactation may continue for years and the yields may vary cyclically with the season [26]. Lactations of 10–14 years have been recorded in cows and of 4 years in goats [27].

Milk Yield

The milk yield, in general, is related to body weight. Moreover, when related to the weight of the mammary tissue, the yield is remarkably similar across species, about 1 gm of milk being produced by 1 gm of mammary tissue [28].

The frequency of suckling varies greatly from species to species; rats nurse their young 50–80 times per day [29] whereas at the other extreme the tree shrew (Tupaia), one of the most primitive members of the order Primates, visits her offspring once every 48 hr [30].

Mechanics of Suckling

How do young actually obtain milk? The usual assumption is that milk is sucked from the nipple or teat. This, however, is very much an oversimplification and basically incorrect. Cineradiographic studies on babies and young animals have clearly demonstrated that while "sucking," the suckling actually expresses the milk by movements of the tongue. The young kid, lamb, or calf grasps the teat, the lower jaw is raised to compress the neck of the teat between the tongue and the palate, and the milk so trapped in the teat cistern is then expressed into the back of the mouth by a movement of the tongue which spreads from before backwards [31]. The human child uses a similar procedure: the nipple and the areola are drawn into the mouth to form a "teat," the tip of the nipple reaching the back of the mouth; when the lower jaw is raised, the base of the "teat" is compressed between the upper gum and the tip of the tongue resting on the lower gum; the tongue is then applied to the lower surface of the "teat" from before backwards expressing milk trapped in the sinuses. Suction probably aids the process by widening the pressure differential [32].

Biochemical and Immunologic Aspects

Many are the interesting problems of comparative lactation such as the ability of the kangaroo to secrete simultaneously from adjacent mammary glands milks of entirely different compositions, one for the tiny joey within the pouch, the other for the joey running at heel; and of the monotremes to secrete in quantity milk sugars other than lactose. The biosynthesis and composition of milk are discussed by Jenness in this issue. Again, in many species, immunologic protection to the young is provided by the colostrum and milk, a topic fully discussed by Beer, Billingham, and Head in this issue.

Functions of the Breast

From these general comparative aspects of the mammary gland, we now turn to the breast. As with other mammals, the human mammary gland functions at the end of the reproductive cycle by secreting milk for sustenance of the young. The breast, however, has other functions that, so far as I can ascertain, are not performed by the mammary glands of any other mammal. These functions, moreover, concern the earlier stages of the reproductive cycle. The protruding breast is part of the human sexual signaling apparatus and with its highly innervated nipple is an important receptor organ in the precopulatory phase of sexual behavior. These functions, probably because they are so much part of common knowledge, are generally overlooked when the physiology of the breast is discussed. In 1778, von Haller [33] in his classical text book, *Elementa Physiologiae Corporis Humani*, wrote: "Alia denique est mammarum cum utero nervosa symphatia. Contactus papillarum libidinosus insuetis puellis igniculos movet veneros." ("Moreover there is a certain nervous sympathy between the breasts and the uterus. Libidinous caressing of the nipples can move lusty passions in inexperienced girls.") More recently, Morris [34] in his book, *The Naked Ape*, discusses in a rather popular fashion, the evolution of these sexual roles of the breast. The breast and red lips are considered to be frontal mimicry to the ancient display of fleshy buttocks and red genital labia by the female naked ape before she walked erect. The male, having been primed to respond to these signals when they emanated posteriorly, has now a built-in susceptibility to this frontal mimicry. Be that as it may, these sexual functions of the female breast appear to exert influences not entirely compatible with its subsequent functioning in the nutrition of the young.

Human Lactation

A problem peculiar to human lactation, the subject of much current discussion, is the rapidity with which so-called "lactation failure" is increasing, particularly in Western cultures [35]. Moreover, even in those cultures where breast feeding is carried out, it has been designated "token" breast feeding [36] since it is "characterized by severe limitation of sucking by social customs from the day of birth to the day of eventual total weaning, which usually occurs within a few weeks." (In contrast "unrestricted" breast feeding proceeds without "rules" that materially restrict suckling, no bottle feeds being given.) Even in non-European peoples, the duration of lactation varies greatly. Ploss, Bartels, and Bartels [37] give a long list of peoples with average lactation ranging from less than 1 year (e.g., Samoans, Hottentots) up to 15 years (Eskimos). As a result, in some cultures a mother breast feeds 2 or even 3 children of different ages (there is no evidence, however, that milks of different compositions are secreted as by the more "sophisticated" glands of the kangaroo). In some Eskimo communities in the 19th century, it was apparently not uncommon for a youth of 14 to drink from his mother's breast on his return from a hunting expedition [5,37], but a more recent study reports lactations lasting only 3–4 years in Eskimo communities [38]. Ploss et al [37] also picture a 4-year-old suckling from Central Java smoking a cigarette between breast feeds.

The term lactational failure in connection with the present problem is somewhat misleading because in many instances there is no real evidence of physiologic failure of lactation but rather of the mother suppressing her lactation. In short, many mothers opt out of breast feeding and a more appropriate term would be "failure to breast feed." To what extent physiologic failure to lactate occurs is far from certain, but it seems unlikely that it is the primary cause of many failures to breast feed. The problem, however, is complex. Nervous connections between the orbitofrontal cortex and hypothalamus involved in prolactin release have recently been demonstrated by Tindal and Knaggs [39,40] in the rabbit. A cerebral cortical control of lactation is thus clearly possible with the implication that physiologic failure of lactation in man may be willed. Opting out of breast feeding, despite current anxieties, is no new phenomenon as the excellent historical reviews by Still [41] and Wickes [42] clearly show. For the last 3000 years, mothers in European cultures have been opting out in considerable numbers when it was possible to arrange an alternative source of sustenance for the child. Until the beginning of the present century, the employment of a wet nurse was the only satisfactory alternative and the custom of opting out was therefore confined to the upper classes. In Greek society, slaves were used as wet nurses some 1000 years B.C. The custom was still common in Roman society. An extant treatise on gynecology written by Soranus [43], a Greek physician who practiced in Rome early in the 2nd century A.D., discusses in great detail how a wet nurse is to be chosen, the main requirements being: age between 20 and 40; the mother of 2 or 3 children of her own; of good health with breasts and nipples of medium size; in lactation for 2 to 3 weeks; not ill-tempered. Soranus's requirements were copied and plagiarized throughout the centuries, appearing in an English textbook as late as 1853, although Guillemeau in 1612 and Mauriceau in 1673 added a warning against the employment of red-haired wet nurses [42]. In 1472, in the first printed textbook on the diseases of children, *Libellus de Egritudinibus Infantium*, Bagellardo, a teacher of medicine in Padua, stated that for feeding the newborn a wet nurse is to be procured, but if the infant be a child of the poorer classes, let it be fed on its mother's milk [41]. In 18th century England, the wet nurse enjoyed peak popularity amongst the aristocracy. At the birth of the Prince of Wales (later George IV) in 1762, it was officially announced: "Wet nurse, Mrs. Scott, dry nurse, Mrs. Chapman; rockers, Jane Simpson and Catherine Johnson" [42]. From the beginning of the present century, advances in technology and hygiene made it possible to replace the wet nurse with the feeding bottle, previously a somewhat deadly utensil [42], and the opportunity to opt out of breast feeding was no longer the privilege of the rich mother.

The custom of opting out of breast feeding is thus a very old one and we must ask why the human female should often prefer not to perform what in all other mammalian species is an instinctive process. Over the centuries, the main reasons given have a timeless similarity: breast feeding is unfashionable, it may injure the health, it interferes with social duties (and in the present century with work), it is immodest, it is detrimental to the figure. The last two may hold the key to the question. Recent researches on infant care by the Newsons [44] and studies by Newton and Newton [35], in which the attitudes, life experiences, personality, religion, education, and social class of the mother were investigated, strongly suggest that the sexual and nutritional functions of the breast cause conflict in the mind of the mother. The physiologic responses arising from the stimulation of breast feeding and those arising from breast stimulation during precopulatory activities are closely allied, and the mother, consciously or unconsciously, regards breast feeding not as a nutritional but as a sexual process and thereby attaches to it all the inhibitions and taboos she may associate with sexual behavior. The possibility of the loss of figure may give rise to a further dilemma: if the breasts perform their nutritional function, they may lose their value as signals attractive to the male. This ancient and modern custom of failing to breast feed is specific to the human species and it seems unlikely that comparative animal studies can usefully contribute to its elucidation. Indeed, it does not appear to be basically a physiologic matter but one for the psychologist and psychiatrist.

The custom of opting out of breast feeding was, until the present century, a privilege of the rich mother and made little difference to the infant who fed at the breast of another woman with his grim chances of survival perhaps not greatly altered. In 18th century Great Britain, 1 out of every 3, possibly 1 of every 2, children died before the age of

10 [45,46]. In the present century, the situation has dramatically changed in that the infant is now bottle fed with processed or unprocessed cow milk. The chances of survival of the bottle-fed baby are now excellent, thanks largely to the efforts of such pioneers as Dr. H. L. Coit in the U. S. A. and Dr. R. Stenhouse Williams in England, who led campaigns for supplies of clean and safe cow milk [47,48]. Nevertheless, nutritional, immunologic, and psychologic problems are apparent in bottle-fed babies and were recently discussed at a Symposium on the Uniqueness of Human Milk [49]. Is it possible that the time-honored custom of the privileged mother to avoid breast feeding may now be producing underprivileged children—underprivileged nutritionally, immunologically, and psychologically?

The Breast in Art and Folklore

The importance of the breast in the propagation and preservation of the human race has inspired artists and sculptors from the time of Paleolithic man. By studying prehistoric and historic art forms, Claoué and Bernard [50] have reviewed the changing aesthetics of the breast throughout the ages. The iconography of the breast, its artistic, religious, and erotic symbolism have been extensively reviewed by Witkowski in his books *Les Seins dans l'Histoire* [51] and *Les Seins à l'Eglise* [52], and I have already referred to the discussion of the milk-ejection theme in art and myth by Folley [24].

Human milk has had magical properties attributed to it and has been recommended for such diverse maladies as deafness and snakebite [37]. Conversely, there have been widespread beliefs that supernatural forces influenced lactation, and amulets and charms were used by nursing women to increase their milk [37] and by farmers to increase milk yields in their milch animals and to protect them from disease [53,54]. With perhaps more reason, human milk has been regarded as a valuable nutrient and therapeutic agent for the aged, and in some cultures the very old as well as the very young were breast fed [37]. In this connection, considerable information on a breast theme in art, which has aroused the interest of art historians but is perhaps little known to physiologists, was collected but never published by the late Professor S. J. Folley. This is the theme of "Caritas Romana" (Roman Charity) and arises from the legend of the Grecian daughter Pero, who daily visited and breast fed her aged father Micon (or Cimon), who had been condemned to death by starvation in prison. This legend was popular in Imperial Rome and representations of the incident have been found on pottery fragments dating from the 1st century A.D., and in mural paintings and terra-cotta statuettes in Pompeii. Medieval examples are few, but it is pictured in a 13th century manuscript of the works of Solinus (a grammarian and compiler of the 3rd century, A.D.) and later in 1473 in a Boccaccio text. The theme became popular again in the 16th century, appearing on copper engravings by Beham and thereafter in numerous paintings of the scene by various artists, including Rubens and Murillo, some emphasizing the heroic and spiritual aspects of the theme, others the erotic [51,55–57]. A relief of the scene was placed on the facade of the prison in Ghent in 1741; when it suffered the ravages of time, it was recently replaced by a 20th century copy (Fig. 4). (I am indebted to Prof. Georges Peeters of the Ghent Veterinary School for information about this relief.)

FIG. 4: Caritas Romana. The relief on the facade of the city prison in Ghent known as the "Mammelokker" (Breast-Sucker). The original relief dated from 1741 but, being badly weathered, was replaced by a copy in the 1960s.

In sum, the mammary gland is a skin gland whose importance has long been recognized. Most of us become acquainted with it at a very early stage of our existence and develop a relatively enduring interest. The gland indeed merits a place in a Symposium on Biology of Skin and is well worthy of the scientific and clinical considerations given to it in this issue.

REFERENCES

1. Sharman GB: Reproductive physiology of marsupials. Science 167:1221–1228, 1970
2. Bresslau E: Die Entwickelung des Mammarapparates der Monotremen, Marsupialier und einiger Placentalier. Denkschr Med-Naturw Ges Jena 7 (Semon Zool Forschungsreisen 4):647–874, 1912
3. Bresslau E: The Mammary Apparatus of the Mammalia. London, Methuen and Company Limited, 1920
4. Griffiths M, Elliott MA, Leckie RMC, Schoefl GI:

Observations of the comparative anatomy and ultrastructure of mammary glands and on the fatty acids of the triglycerides in platypus and echidna milk fats. J Zool (Lond) 169:255–279, 1973
5. Cooper AP: On the Anatomy of the Breast. London, Longmans, Orme, Green, Brown and Longmans, 1840
6. Lyons WR: The direct mammotrophic action of lactogenic hormone. Proc Soc Exp Biol Med 51:308–311, 1942
7. Swett WW, Underwood PC, Matthews CA, Graves RR: Arrangement of the tissues by which the cow's udder is suspended. J Agric Res 65:19–43, 1942
8. Cowie AT, Tindal JS: The Physiology of Lactation. London, Edward Arnold Limited, 1971
9. Hanwell A, Linzell JL: The time course of cardio-vascular changes in lactation in the rat. J Physiol (Lond) 233:93–109, 1973
10. Cathcart EP, Gairns FW, Garven HSD: The innervation of the human quiescent nipple, with notes on pigmentation, erection, and hyperneury. Transactions of the Royal Society of Edinburgh 61:699–717, 1948
11. Linzell JL: Mammary blood vessels, lymphatics and nerves, Lactation. Edited by IR Falconer. London, Butterworths, 1971, pp 41–50
12. Oka T, Topper YJ: Is prolactin mitogenic for mammary epithelium? Proc Natl Acad Sci USA 69:1693–1696, 1972
13. Bishop PMF: Breasts of inappropriate size. Practitioner 203:171–176, 1969
14. Smith EA: Adoptive suckling in the grey seal. Nature (Lond) 217:762–763, 1968
15. Findlay ALR: Neural and behavioural interactions with lactation, Lactation. Edited by IR Falconer. London, Butterworths, 1971, pp 75–91
16. Klopfer PH: Mother love: what turns it on? Am Sci 59:404–407, 1971
17. Cowie AT: Influence of hormones on mammary growth and milk secretion, Lactation. Edited by IR Falconer. London, Butterworths, 1971, pp 123–140
18. Forsyth IA, Edwards CRW: Human prolactin, its isolation, assay and clinical applications. Clinical Endocrinology 1:293–314, 1972
19. Gaines WL: A contribution to the physiology of lactation. Am J Physiol 38:285–312, 1915
20. Ely F, Petersen WE: Factors involved in the ejection of milk. J Dairy Sci 24:211–223, 1941
21. Waller H: Clinical Studies in Lactation. London, Toronto, William Heinemann Limited, 1938
22. Waller HK: A reflex governing the outflow of milk from the breast. Lancet 1:69–72, 1943
23. Amoroso EC, Jewell PA: The exploitation of the milk-ejection reflex by primitive peoples. Occasional paper number 18 of the Royal Anthropological Institute, London, 1963, pp 126–137
24. Folley SJ: The milk-ejection reflex: a neuroendocrine theme in biology, myth and art. J Endocrinol 44:x–xx, 1969
25. Roberts JS, Share L: Oxytocin in plasma of pregnant, lactating and cycling ewes during vaginal stimulation. Endocrinology 83:272–278, 1968
26. Linzell JL: Innate seasonal oscillations in the rate of milk secretion in goats. J Physiol (Lond) 230:225–233, 1973
27. Linzell JL: The role of the mammary glands in reproduction. Research in Reproduction 3:2–3, 1971
28. Linzell JL: Milk yield, energy loss in milk, and mammary gland weight in different species. Dairy Science Abstracts 34:351–360, 1972
29. Lincoln DW, Hill A, Wakerley JB: The milk-ejection reflex of the rat: an intermittent function not abolished by surgical levels of anaesthesia. J Endocrinol 57:459–476, 1973
30. Martin RD: Tree shrews: unique reproductive mechanism of systematic importance. Science 152:1402–1404, 1966
31. Ardran GM, Cowie AT, Kemp FH: A cineradiographic study of the teat sinus during suckling in the goat. Vet Rec 69:1100–1101, 1957; 70:808–809, 1958
32. Ardran GM, Kemp FH, Lind J: A cineradiographic study of breast feeding. Br J Radiol 31:156–162, 1958
33. Haller A von: Elementa Physiologiae Corporis Humani. Second Edition, tomus 7, pars 2, liber 28, sectio 1. Lausanna, Societas Typographica, 1778
34. Morris D: The Naked Ape. London, Jonathan Cape Limited, 1967
35. Newton N, Newton M: Psychologic aspects of lactation. N Engl J Med 277:1179–1188, 1967
36. Newton N: Psychologic differences between breast and bottle feeding. Am J Clin Nutr 24:993–1004, 1971
37. Ploss HH, Bartels M, Bartels P: Woman—An Historical Gynaecological and Anthropological Compendium. Vol 3. London, William Heinemann (Medical Books) Limited, 1935
38. Oswalt W: Napaskiak: An Alaskan Eskimo Community. Tuscon, University of Arizona Press, 1963 (quoted by Berman et al, Am J Obstet Gynecol 114:524, 1972)
39. Tindal JS, Knaggs GS: Pathways in the forebrain of the rabbit concerned with the release of prolactin. J Endocrinol 52:253–262, 1972
40. Tindal JS: Hypothalamic control of secretion and release of prolactin. J. Reprod Fertil, 1974 (In press)
41. Still GF: The History of Paediatrics. Oxford, Oxford University Press, 1931
42. Wickes IG: A history of infant feeding. Arch Dis Child 28: 151–158, 232–240, 332–340, 416–422, 495–502, 1953
43. Soranus' Gynecology, translated by O Temkin. Baltimore, The Johns Hopkins Press, 1956
44. Newson J, Newson E: Infant Care in an Urban Community. London, George Allen and Unwin Limited, 1963
45. Buchan W: Domestic Medicine. London, 1772, quoted by TC Smout (46)
46. Smout TC: A History of the Scottish People, 1560–1830. London, William Collins Sons and Company Limited, 1969
47. Burgess HF: Robert Stenhouse Williams and the origin and early development of the National Institute for Research in Dairying. Br Med Bull 5:222–225, 1947
48. Waserman MJ: Henry L. Coit and the certified milk movement in the development of modern pediatrics. Bull Hist Med 46:359–390, 1972
49. Symposium on the Uniqueness of Human Milk. Edited by DB Jelliffe, EFP Jelliffe. Am J Clin Nutr 24:967–1024, 1971.
50. Claoué C, Bernard I: L'Esthétique Mammaire à travers l'Histoire. Paris, Librairie Maloine, 1936
51. Witkowski G-J: Les Seins dans l'Histoire. Paris, A. Maloine, 1903
52. Witkowski G-J: Les Seins à l'Eglise. Paris, A. Maloine, 1907
53. Davidson T: Animal treatment in eighteenth-century Scotland. Scottish Studies 4:134–149, 1960
54. Davidson T: The amuletic and transfer charm cure of cattle and horses. Br Vet J 116:205–218, 1960
55. Pigler A: Valère Maxime et l'iconographie des temps modernes. Hommage à Alexius Petrovics, Budapest, 1934, pp 213–216
56. Knauer ER: Caritas Romana. Jahrbuch der Berliner Museen 4:9–23, 1964
57. Harris E: A Caritas Romana by Murillo. J Warburg and Courtauld Inst 27:337–339, 1964
58. Raynaud A: Morphogenesis of the mammary gland, Milk: The Mammary Gland and its Secretion. Edited by SK Kon, AT Cowie. New York, London, Academic Press, 1961, vol 1, pp 3–46