THE COPULATION PLUG AND THE ACCESSORY GENITAL GLANDS OF MAMMALS

By Earl Theron Engle

The existence of a rigid plug which completely fills the lumen of the vagina of certain mammals after completed ejaculation has been known for nearly seventy-five years. During this period it has been observed to be a constant phenomenon in eleven genera among four mammalian orders.

The first recorded observation of the plug is that of Leuckart (1847) with the guinea-pig. He suggested that it was formed by the secretion from "a pair of contorted tubes," undoubtedly meaning the seminal vesicles. Later (1853) Leuckart concluded that the plug was formed by the mixing of the prostatic secretion with that of the seminal vesicles. The same year Bischoff (1853) confirmed the observations of Leuckart. Later Lataste (1882 and 1883) investigated the occurrence of the "bouchon vaginale" in several genera of rodents including *Pachyuromys duprasi*, *Dipodillus simoni*, *Meriones shawi*, *Cavia cobaya*, and *Mus musculus*. He concluded that the formation of the copulation plug was due entirely to the secretion of the seminal vesicles. Camus and Gley (1896–1900) carried the work further, and concluded that the coagulation was caused by the action of an enzyme present in the prostatic secretion. This they called "vesiculase." Recently (1922, a, b) these authors have observed plug formation in the jerboa (*Dipus* sp.) and in an Argentine rodent, *Viscacia viscacia*. A more extended historical summary is found in Stockard and Papanicalou (1919).

Walker (1910, a, b) advanced the view that the entire prostate in the rat and the guinea-pig is not concerned in secreting the ferment which coagulates the vesicular secretion, but that this enzyme is derived from paired prostatic lobes lying in the same fascial sheath as the vesiculae seminales.

The experiments of Walker, together with further experiments, were repeated on the guinea-pig by the writer (Engle, 1926) and confirm the view that the proximal pair of the three pairs of lobes of the prostate is the only source of the activating substance which coagulates the vesicular secretion. On the basis of histological differences between the proximal and the distal and the intermediate lobes, Walker regarded the proximal lobe as a distinct organ, the "coagulating gland."

The embryological evidence found by the writer does not confirm this position. The so-called "coagulatory gland," more properly the proxi-

TABLE 1

	SEMINAL VESICLE	PROSTATE	BULBO-URETHRAL GLANDS	AUTHORITY
Monotremata:				
Ornithorhynchus	Absent	Lacking	One pair	Home, 1802
Echidna	Lacking	Lacking	One pair	Home, 1802
Marsupialia:				
Macropus sp.	Lacking	Numerous glands in urethral bulb	Three pairs	Broek, 1910
Caenolestes obscurus	Lacking	Very large single	Three pairs	Osgood, 1921
Didelphis v. virginiana	Lacking	Disseminata	Three pairs	Engle, unpubl.
Other marsupials	Lacking	Unknown	One to three pairs	Disselhorst, 1904b
Insectivora:				
Erinaceus europæus	Lacking	Three large pairs	Two pairs	Rauther, 1903a
Tupaia ferruginaea	One pair	One pair		Wood-Jones, 1917b
Talpa europæa	Lacking	One large pair	One pair	Rauther, 1903a
Chiroptera:				
Pteropus edwardsi	One pair	One pair	One pair	Oudemans, 1892
Vesperugo pipistrellus	"glandula ampullarum"	One pair	One pair	Rauther, 1903b. See also Disselhorst, 1904a
Carnivora:				
Canis familiaris	Lacking	Unpaired gland	Lacking	Sisson, 1911
Felis domestica	Lacking	Two pairs	One pair	Schmaltz, 1911
Felis leo	Lacking	One pair	One pair	Oudemans, 1892
all Mustelidae	Lacking	Present	Lacking	Oudemans, 1892
Pinnipedia:				
Trichechus rosmarus	Lacking	Present	Lacking	Murie, 1872
Otaria jubata	Lacking	Present	Lacking	Murie, 1872
Phoca vitulina	Lacking	Present	Lacking	Oudemans, 1892

*Primates:**				
Lemuroidea	One pair	One body	One pair	Oudemans, 1892
Chiromys madagascariensis	Lacking	One body	One pair	Oudemans, 1892
Aye-aye	Lacking	One body	One pair	Owen, 1862
Lemur vapi	One pair	One body	One pair	Oudemans, 1892
Anthropoidea:				
Macacus nemestrinus	One pair	Two parts	One pair	Oudemans, 1892
Other Anthropoids	One pair	Two lobes	One pair	Oudemans, 1892
Homo	One pair	Two lateral, one middle	One pair	
Pan	One pair	Two lateral, one middle	One pair	Sonntag, 1923
Rodentia:				
Mus, all species	One pair	Three pairs	One pair	Rauther, 1903a
Rattus norvegicus	One pair	Three pairs	One pair	Rauther, 1903a
Cavia cobaya	One pair	Three pairs	One pair	Rauther, 1903a
Sciurus vulgaris	One pair	Lacking	One pair	Grosz, 1905
Lagomorpha:				
Lepus cuniculus	Lacking	"Paraprostate"	At least three glands	Rauther, 1903a
Artiodactyla:				
Sus scrofa	One large pair	Two parts	One pair	Sisson, 1911
Dicotyles torquatus	One pair	One body	One pair	Oudemans, 1892
Ovis aries	One pair	Disseminata	One pair	Schmaltz, 1911
Bos taurus	One pair	Two parts	One pair	Sisson, 1911
Nubian giraffe	Not stated	Two glands	Not stated	Owen, 1868
Hippopotamus amphibius	One pair	Disseminata	One pair	Hofmann, 1923
Auchenia lama	Absent	Present	One pair	Oudemans, 1892

*For additional data the papers of Klaar and Krasa, 1921, and Mijsberg, 1923, may be consulted.

TABLE 1—*Concluded*

	SEMINAL VESICLE	PROSTATE	BULBO-URETHRAL GLANDS	AUTHORITY
Perissodactyla:				
Equus caballus	One pair	"Two lateral lobes, isthmus"	One pair	Sisson, 1911
Rhinoceros indicus	One pair	Present	Not stated	Owen, 1862
Ceratorhinus sumatraensis	One pair	One body (?)	Not stated	Forbes, 1881
Tapirus americanus	Paired	Two pairs	Present	Hofmann, 1923
Xenarthra:				
Manis javanica	One pair	Two pairs	Absent (?)	Oudemans, 1892
Bradypus tridactylus	Rudimentary	"disseminata"	One pair	Klinkowström, 1895
Dasypus sps	Absent	One large gland	One pair	Klinkowström, 1895
Myrmecophaga jubata	Rudimentary	Present	One pair	Klinkowström, 1895
Proboscidia:				
Elephas indicus	One pair	Two pairs	One pair	Watson, 1872
E. africanus	One pair	One pair	One pair	Hofmann, 1923
Sirenia:				
Halicore dugong	One pair	One body	Lacking	Riha, 1911
Hyracoidea:				
Hyrax capensis	One pair	Several lobes	One pair	Oudemans, 1892
Cetacea:				
Phocaena phocaena	Lacking	Paired	Lacking	Daudt, 1898
Beluga leucas	Lacking	Present	Lacking	Daudt, 1898
Sibbaldus musculus	Lacking	Present	Lacking	Daudt, 1898

mal prostate, develops in the same manner and from the same anlage as the remaining two lobes; its duct is continuous with that of the intermediate lobe until shortly before birth. From this embryological evidence it is evident that the "coagulating gland" of Walker should be considered as a morphological unit of the prostate gland.

The occurrence of a copulation plug is not confined to rodents for it is present in several widely separated orders. Hartman (1924) records the occurrence of the plug in the opossum (*Didelphis virginiana virginiana*) but offers a different opinion as to its formation, saying that "the plug is not derived entirely from the male organs, but consists rather of the fluid of the lateral vaginal canals, coagulated under the influence of the seminal fluid." Hartman added that "the plug represents the contents of the lateral vaginal canals plus semen." In the guinea-pig, however, the secretion of the female genital tract has no part in the formation of the copulation plug. A vaginal plug apparently occurs also in the Chiroptera for Wood Jones (1917) wrote: "The cervical secretion (of the uterus), possibly under the influence of the prostatic secretion in the seminal fluid, entirely plugs the female genital passage with a mucous 'bouchon'."

A plug also has been found in the hedgehog, *Erinaceus europaeus*, by Gley (1899) although the glands concerned in producing the coagulation are still undetermined owing to the confused state of both the nomenclature and the homology of the accessory genital glands. Gley stated that Cowper's glands in the hedgehog elaborate the ferment which causes coagulation of the secretion of the seminal vesicles.

Rauther (1903) and Disselhorst (1904a) made careful studies of the accessory genital glands, and agree as to structural details. Rauther concluded that there are no vesiculae seminales in *Erinaceus* but three pairs of prostatic lobes. Disselhorst (p. 181) says regarding this matter "Denn die sogenannte Samenblase des Igels mündet nicht in den Samenleiter (und das ist die morphologische Voraussetzung zu dieser Bezeichnung), sondern in den Canalis Urogenitalis." Linton (1907) considered these glands to be neither bulbo-urethral (Cowper's) nor prostatic, and held that they should be considered *sui generis* until embryological evidence is obtained. However, that an entirely new structure should appear in this genus is not in accord with present concepts of morphology, although it may be said that there is some evidence that the Cowper's glands of the opossum, and perhaps of all the Marsupialia, are not true bulbo-urethral glands.

The copulation plug is not known to occur in other animals than the

ones cited above, but it is reasonable to surmise its occurrence in some other mammals. Since plug-formation is dependent upon one or more of the accessory genital glands, a summary of the literature dealing with these glands is given in Table I. Since I have not covered all the literature, these organs may be mentioned in other works. The arrangement of orders in the table follows that of Miller (1923). The genus and species is that of the author quoted, without correction in regard to synonymy.

The seminal vesicles occur in eight of the sixteen orders listed here. The insectivores are not included in the eight, although Wood Jones (1917b) records *Tupaia* as possessing seminal vesicles. In his description he states that it is difficult to distinguish the seminal vesicles from the paired prostate gland in a gross examination. Since he does not publish figures of the microscopic anatomy of the glands in question, and since other insectivores have been shown by Rauther (1903a) to have no seminal vesicles, it would seem better to regard the matter as undecided.

With a few exceptions the prostate has been found in all of the species above the monotremes. One noticeable exception is that of *Sciurus vulgaris*, which is stated by Grosz (1905) to possess seminal vesicles but no prostate. Such an exception occurring in an order in which many species are known to possess a compound prostate is very unusual. In his discussion of the Cervidae, Oudemans (1892) states that the prostate is lacking in this family. His diagrams of the urogenital tract in this group, and our knowledge of the Bovidae, suggest the possibility that the prostate, as in the buck and the ram, is of the disseminate type, and is not immediately apparent on dissection.

That these accessory genital glands and the copulation plug are of some significance for systematic mammalogy, as well as for life history studies, is scarcely to be doubted. It is to be hoped that more complete observations on American mammals will supply the present lack in this regard.

This paper represents a portion of a study of the prostate gland of the guinea-pig undertaken at the suggestion of Doctor Meyer, and under his direction. I am greatly indebted to him also for a reading of the manuscript.

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