

MINIREVIEW

COMPARATIVE ASPECTS OF THE ACCESSORY SEX GLANDS AND SEMINAL BIOCHEMISTRY OF MAMMALS

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Abstract—1. Despite large gaps in the literature of semen biochemistry, especially of wild species, recent studies of the carbohydrate biochemistry of marsupial semen allow an approach to the question of the origin and evolution of mammalian seminal plasma.

2. The marsupials are a very important part of an overall picture of seminal plasma evolution because they are the end product of an alternative line of mammalian evolution genetically separated from the eutherians for over 100 million years.

3. The present paper discusses the accessory sex glands and seminal sugars of mammals from a comparative point of view in the light of present knowledge of evolutionary relationships and suggests possible schemes of evolution of mammalian seminal plasma.

ACCESSORY SEX GLANDS OF MARSUPIALS AND MONOTREMES

A considerable body of knowledge has been collected of reproduction in marsupials, especially the oestrous cycle, gestation and embryonic diapause and this has been the subject of a number of reviews (Sharman 1959, 1970; Waring *et al.* 1966; Tyndale-Biscoe 1973). Although there has been great interest in the female, the male and events in the female prior to fertilization (e.g. coitus and gamete transport) have received scant attention. Due to the paucity of information on the male marsupial, Rodger & Hughes (1973) began a reappraisal of the anatomy, histology and histochemistry of the accessory sex glands of a number of Australian marsupials intended to form a basis for further studies of the physiology and biochemistry of marsupial semen. They examined eight species; which included representatives of the three orders recognised by Ride (1964, 1968) from families, Phalangeridae, Macropodidae, Peramelidae and Dasyuridae and found that the prostate gland, the major accessory gland in all species, was disseminate and divided into distinct segments. Four basic patterns of prostatic segmentation were recognized. The gross anatomy of the accessory glands is similar in all marsupials in that they lack ampullary glands, seminal vesicles, coagulating glands and a lobed prostate, commonly found in Eutheria, but possess a disseminate prostate gland and from one to three pairs of bulbourethral (Cowper's) glands. The shape of the prostate gland is carrot or turnip-like in all species examined by Rodger & Hughes (1973) and recorded in the quite extensive literature, except the bandicoots and koala which have a heart-shaped prostate gland.

Despite the uncertainty expressed in the literature with regard to the presence of urethral accessory sex glands in monotremes (e.g. Price & Williams-Ashman 1961) and the neglect of many workers to discuss or

examine the histology of the anterior portion of the urethra of monotremes (Mackenzie & Owen 1919; Griffiths 1968), Oudemans as early as 1892, clearly depicts and describes a glandular area which, although small, is very similar in position and microanatomy to the disseminate prostate gland of marsupials. That this area was not recognized as a prostate gland is in accord with the lengthy debate over the identity of the urethral glands of marsupials, which were not generally recognized as a true prostate until the work of Chase (1939).

Recent re-examination of the male reproductive tract of the platypus (Temple-Smith 1974) has shown the glandular region of the anterior urethra to be probably larger than described by Oudemans, forming a visible swelling. This disseminate urethral tissue appears to remain active outside of the breeding season although there is an increase in the volume of glandular tissue in breeding animals. Temple-Smith remarked on the obvious phylogenetic interest of this tissue which is so similar to the disseminate prostate of marsupials in both gross and microanatomy. However there is no evidence of segmentation of glandular tissue in the platypus "prostate" (Temple-Smith 1974).

EVOLUTION OF ACCESSORY SEX GLANDS OF MALE MAMMALS

The first accessory sex glands appear to have been undifferentiated disseminate urethral glands. Disseminate urethral glands occur in all three groups of modern mammals which suggests they arose early in mammalian evolution possibly in therapsids during the Triassic. The complex accessory glands of modern eutherians and marsupials are probably the result of parallel evolution of these simple structures. Price & Williams-Ashman (1961); Temple-Smith (1974) have suggested that the urethral glands of monotremes illustrate the derivation of the specialized prostate

gland from simpler urethral structures. The development of the urethra in mammals as distinct from a cloaca, as found in birds and reptiles, has been correlated with the appearance of accessory sex glands (Retief 1949). This loss of accessory reproductive function of the kidney in mammal-like reptiles may have resulted in compensatory development of urethral accessory sex glands (Price & Williams-Ashman 1961).

Despite their common origins, it is hardly surprising that in the 100 million years since the marsupial-eutherian dichotomy the accessory sex glands have developed along quite different anatomical lines. Presumably the monotremes are primitive in the anatomy of the "prostate gland" but the characteristics of the secretions of this glandular tissue are only known from histochemical study (Temple-Smith 1974), and thus any speculation as to the possible primitive character of these secretions is quite unjustified. The relatively simple disseminate prostate gland found in the ancestral mammals has developed in the modern marsupial into a complex segmented but still disseminate structure (Rodger & Hughes, 1973). Some modern eutherians have retained evidence of the disseminate origins of the prostate gland, e.g. the bull and ram, but in most of these species there is also a lobed prostate gland which lies outside the confines of the urethral muscle (Eckstein & Zuckerman 1956) which in many eutherian mammals has replaced the disseminate gland entirely. The development of the other common accessory sex glands (e.g. seminal vesicles, ampullary glands, coagulating glands) is unique to eutherians.

SEMEN BIOCHEMISTRY

Semen has attracted the attention of researchers from the earliest beginnings of modern biology. This interest, stimulated by the discovery of spermatozoan motility, was soon extended to include seminal plasma. Human semen and later the semen of external fertilizers, fish and invertebrates, were the subject of studies up to this century. Not until the development of methods of collecting semen from domestic animals for artificial insemination did the semen of non-human mammals come under intensive study. Artificial insemination itself proved a considerable stimulus to the study of the physiology and biochemistry of semen as in more recent years have problems of human fertility and contraception. The development of the field has been well discussed in a number of reviews (Mann 1954a, 1964; Price & Williams-Ashman 1961).

The source of energy for spermatozoa attracted much work in the period between the wars but not until 1946 was fructose positively identified as the reducing sugar of bull seminal plasma by Thaddeus Mann (Mann 1946a, b). Up till this time the reducing sugar of semen was assumed to be glucose. Mann and his colleagues showed that fructose is present in the semen of many domestic species (Table 1) and is consumed by spermatozoa as an energy source (e.g. Mann 1946b; 1948; Mann & Leone 1953). This finding stimulated much activity in semen biochemistry resulting in the discovery of many other compounds characteristic of semen, e.g., citric acid (Humphrey & Mann 1949), ergothioneine (Mann & Leone 1953), in-

ositol (Mann 1954b) and glycerylphosphorylcholine (Dawson *et al.*, 1957). Recently the carbohydrate biochemistry of the accessory sex glands and semen of Australian marsupials has been the subject of investigation (Roger & White 1974a, b; 1975a, 1976).

SEMINAL SUGARS OF MAMMALS

Table 1 presents the current knowledge of sugars of the semen and accessory sex glands of mammals. The characteristic free sugar of the semen of Australian marsupials is N-acetylglucosamine which is produced by the prostate. Glucose is secreted by the prostate gland of some macropod species. The sugars of semen and accessory glands of American marsupials have not received systematic attention. The resorcinol reactive material found in the prostate gland of *Didelphis* (the common opossum) by Mann & Lutwak-Mann (1963) and called fructose is probably the same as or similar to resorcinol reactive material found in the prostate gland of the brush-tailed possum (*Trichosurus vulpecula*) (Roger & White 1974a). Fructose is probably absent or present in only trace amounts in the semen of marsupials.

Although there has been much work done on the seminal sugars of eutherians many orders have not been examined and even in those examined the bulk of attention has, understandably, been given to domestic and laboratory species. Of the diverse orders Rodentia has received the most systematic study, all three suborders being examined; Sciuromorpha, Myomorpha and Hystricomorpha. Artiodactyla comes next, but only those species of economic importance, the boar, bull and ram, have received close attention. The many deer rate only a cursory reference and camels and wild cattle have not been examined at all. The literature has many surprising omissions: non-human primates rate almost no mention despite their availability to many laboratories. Cetacean data are lacking, yet whales are the subject of huge commercial exploitation. Bats, order Chiroptera, the most widely distributed of all mammals, have not been examined perhaps because of their elusive habits. Equally surprising is the absence of information on carnivores other than the dog and only a passing reference to domestic cats.

Interestingly the brief reference to unpublished observations of the prostate gland of the Australian marsupial *Trichosurus vulpecula* (opossum, Humphrey 1950), means that marsupials were amongst the first mammals examined in the dramatic expansion of semen and accessory gland biochemistry of the late 1940's. The absence of information on monotremes is to be expected. The order is restricted to Australia, specimens are difficult to find and the view is commonly found in the literature, that monotremes lack accessory sex glands except bulbo-urethral glands.

In only a limited number of species have definitive analyses been made of sugars in semen and related glands. Almost all examination of material from wild species has relied upon the colorimetric assay of fructose used by Mann (1948), which is based on a method originally devised by Roe (1934). In only a few cases, as indicated in Table 1, have these estimations been coupled with paper chromatography and

Table 1. Carbohydrates of the semen and accessory glands of mammals

CLASSIFICATION	SEMEN	GLANDS	COMMENTS	REFERENCES
<i>COHORT, ORDER species.</i>				
MONOTREMATA			Not examined	
MARSUPIALIA				
Opossum (<i>Didelphis</i>)		Pr I 3 mg fr % (Roe) Pr II 5 mg fr % Pr III 44 mg fr %	American marsupial	Mann & Lutwak-Mann 1963.
Brush-tailed possum (<i>Trichosurus vulpecula</i>)		Pr fr present (Roe)	Australian marsupial	Humphrey & Robertson unpublished data in Humphrey 1950
	150 mg% N-acetylglucosamine (ME) 1-5 mg% gl (GOD) 10-20 mg% anthrone reactive sugar	Central Pr 160 mg% N-acetylglucosamine (ME) Pr fr absent or trace (HK) gl low Pr	Roe reactive material in Post Pr not fr	Rodger & White 1974a, 1976
Ringtail possum (<i>Pseudochetrus peregrinus</i>)		Post Pr 460 mg% N-acetylglucosamine (ME)		Rodger & White 1976
Grey kangaroo (<i>Macropus giganteus</i>)	336 mg% N-acetylglucosamine (ME) 111 mg% gl (GOD) 165 mg% anthrone reactive sugar fr not detected inositol present	Central Pr 465 mg% N-acetylglucosamine (ME) Post Pr 139 mg% gl (HK) Pr fr absent or trace	Paper chromatography of semen 1974b	Rodger & White 1974b, 1975a, 1976
Tammar wallaby (<i>Macropus eugenii</i>)	509 mg% N-acetylglucosamine (ME) 30 mg% gl (GOD) 66 mg% anthrone reactive sugar fr not detected inositol present	Central Pr 580 mg% N-acetylglucosamine (ME) Pr low gl (GOD) Pr fr absent or trace	Paper chromatography of semen 1974b	Rodger & White 1974b, 1975a, 1976
Red kangaroo (<i>Megaleia rufa</i>)	399 mg% N-acetylglucosamine (ME) 82 mg% gl (GOD) 133 mg% anthrone reactive sugar fr not detected inositol present	Central Pr 630 mg% N-acetylglucosamine (ME) Post Pr 92 mg% gl (HK) Pr fr absent or trace	Paper chromatography of semen 1974b	Rodger & White 1974a,b; 1975a, 1976
Long-nosed bandicoot (<i>Perameles nasuta</i>)		Vent Pr 507 mg% N-acetylglucosamine (ME) Dor Pr 258 mg% N-acetylglucosamine Pr moderate gl Pr anthrone reactive material not gl > 120 mg% Pr fr not detected	Vent Pr paper chromatography 1974b	Rodger & White 1974b, 1976
Short-nosed bandicoot (<i>Isaodon macrourus</i>)		Vent Pr 711 mg% N-acetylglucosamine (ME) Dor Pr 278 mg% N-acetylglucosamine (ME) Pr moderate gl Pr anthrone reactive material not gl > 120 mg%		Rodger & White 1976
UNGUICULATA				
INSECTIVORA				
Mole (<i>Talpa</i>)		G prostatica Sec > 300 mg fr % (Roe)		Mann 1956
Hedgehog (<i>Erinaceus</i>)		G prostatica 1 Sec & 2 Sec > 500 mg fr % (Roe) G prostatica 3 Sec very little fr		Mann 1956
PRIMATES				
Man (<i>Homo sapiens</i>)	100-300 mg fr % SP (Roe) 200 mg% orcinol reactive sugar other than fructose, inositol sorbitol, glucose, ribose, sucrose and oligosaccharides	SV Sec 315 mg fr % (Roe)	Mann & Rottenberg paper chromatography	Mann 1946b, Mann 1954a, Mann & Rottenberg 1966
Monkey	semen contains fr		species?	Mann 1964
CHIROPTERA			Not examined	
DERMOPTERA			Not examined	
EDENTATA			Not examined	
PHOLIDOTA			Not examined	
GLIRES				
RODENTIA				
Prairie dog (<i>Cynomys ludovicianus</i>)		SV 130 mg fr % (Roe) Pr 0 mg fr %	glands from one large animal	Mann & Lutwak-Mann 1963

Table 1 continued.

CLASSIFICATION	SEMEN	GLANDS	COMMENTS	REFERENCES
Squirrel (<i>Sciurus</i>)	semen contains fr			Mann 1964
Field Vole (<i>Microtus agrestis</i>)		Cg 410 mg fr % (Roe) 124 mg gl % (GOD) Dor Pr 248 mg fr % 52 mg gl % Lat Pr 54 mg fr %	fr absent SV Sec Vent Pr, Traces sorbitol in Cg, low levels inositol in all glands, paper chromatography	Fouquet 1971
Rat (<i>Rattus norvegicus</i>)	fr present	Cg 130-475 mg fr % (Roe) 85 mg gl % (GOD), Dor Lat Pr 38-200 mg fr % Amp 186 mg fr %	SV trace fr, Vent Pr fr absent, low inositol in all glands. Paper chromatography Fouquet sorbitol 5-10 mg % in Cg, Amp & Dor Lat Pr.	Humphrey & Mann 1948; Mann, L- Mann & Price, 1948; Mann & Parsons 1950; Mann & Lutwak- Mann, 1951; Fouquet, 1971.
Mouse (<i>Mus musculus</i>)	Total ejaculate 0.457 ± 0.224 mg fr	SV 420-470 mg fr % (Roe) Cg 563-705 mg fr % Dor Lat Pr 126 mg fr %	Vent Pr fr not detectable. All glands gl (GOD) & inositol low, paper chroma- tography Fouquet.	Thomas & Straus: 1965; Marchlewska- Koj, 1971; Fouquet 1971
Golden hamster (<i>Mesocricetus auratus</i>)	Devoid fr and sorbitol	Vent Pr 76 mg gl % (GOD) fr absent	small quantity of gl and inositol in all glands. Paper chromatography	Fouquet 1969 Fouquet 1972
Chinese hamster (<i>Cricetus crioetus</i>)	devoid fr and sorbitol	fr, sorbitol absent low levels inositol SV and Dor Lat Pr appreciable quant- ities of unidentified sugars. Moderate levels of gl in all glands except SV	paper chromatography	Fouquet 1971 Fouquet 1972
Guinea pig (<i>Carvia procellus</i>)		SV 63-135 mg fr % (Roe) Cg, Dor & Lat Pr, 20-30 mg fr % appreciable quantities of unidentified sugars in all glands	low inositol in all glands. Paper chromatography Fouquet	Humphrey & Robertson, 1953 Fouquet 1971
Nutria (<i>Myocastor coypus</i>)		Vesicular G (SV) Sec 36-72 mg fr % (Roe) Cg (Pr) 2-4 mg fr %		Mann & Wilson 1962
LAGOMORPHA				
Rabbit (<i>Oryctolagus cuniculus</i>)	318-515 mg fr % SP (yeast fermentable = fr) 97-138 mg % SP non fermentable sugar fr % fr may vary from 40-420 mg %. Semen, negligible to appreciable quantities of gl	G vesicularis seminalis 45 mg fr % (Roe) Pr 120 mg	large amount of sugar other than fructose	Mann 1946b; Mann & Parsons 1950
MUTICA				
CETACEA				
			whales not examined	
FERUNGULATA				
CARNIVORA				
Dog (<i>Canis familiaris</i>)	20.5 mg % reducing substances 2 mg % yeast fermentable 0.5 mg fr % (Roe) 17.5 mg lactate %	Pr Sec almost complete absence of reducing sugar	Dog sperm has high fructolysis index lactate may be natural energy source	Mann 1954 a Bartlett 1962
Cat (<i>Felis catus</i>)	fr levels comp- arable to dog (Mann 1961 in Bartlett)	Pr 35 mg fr % (Roe)		Mann 1946b Bartlett 1962
TUBULIDENTATA				
			Aardvark, not examined	
HYRACOIDEA				
			Hyrax (conies), not examined	
PROBOSCIDEA				
African elephant (<i>Loxodonta africana</i>)		SV Sec 35-147 mg fr % (Roe) also small amounts inositol & sorbitol Pr Sec probably little fr (Roe) Amp Sec probably little fr (Roe)	paper chromatography	Short, Mann & Hay, 1967

Table 1 continued.

CLASSIFICATION	SEMEN	GLANDS	COMMENTS	REFERENCES
Indian elephant (<i>Elephas maximus</i>)		SV produce fr as a major constituent		unpublished data reported by Short, Mann & Hay 1967
SIRENIA			Sea cows, not examined	
PERISSODACTYLA				
Stallion (<i>Equus caballus</i>)	anthrone reactive material 32.7 mg% (Roe) 8.4 mg% yeast fermentable free fr 2.1 mg% lactate 20.6 mg%	Amp Sec total (Roe) 8.7-24.6 mg% yeast fermentable (fr) 0.1-4.8 mg% anthrone 21.0-57.0% SV Sec total (Roe) 3-15 mg%, only small porportion yeast fermentable (fr)	sperm high aerobic fructolysis	Mann, Leone & Polge 1956
Jackass (<i>Equus</i>)	(Roe) 3.0 mg%, yeast fermentable free fr trace only, lactate 44.4 mg%	Lactate in all glands highest in SV Sec 319 mg%	sperm high aerobic fructolysis	Mann, Minotakis & Polge 1963
ARTIODACTYLA				
Boar (<i>Sus domesticus</i>)	9 mg fr% SP (Roe) = yeast fermentable 21 mg% SP residual reducing sugar, inositol 420 mg% semen	SV Sec 52-65 mg fr % (Roe) 3 mg gl% (GOD) 100 mg% anthrone reactive material other than fr, some free amino sugar, lactate 21 mg% inositol 2414 mg%		Mann 1946b; Mann 1954a & b
Bull (<i>Bos taurus</i>)	710 mg fr % SP (Roe) almost all reducing sugar is fr, residue of reducing sugar 16.35 mg%	SV Sec 840-970 mg fr % (Roe) Pr 5 mg fr %	complete chemical characterization of fructose in SP	Mann 1946b
Ram (<i>Ovis aries</i>)	353 mg fr % SP yeast fermentable sugar = fr, residue of reducing sugar 50-100 mg%	SV Sec 570 mg fr % (Roe) Pr 8 mg fr%		Mann 1946b
Goat (<i>Capra</i>)	fr high up to 100 mg %			Mann & Mann 1951
Deer	semen contains fr		species?	Mann 1964

Abbreviations: G, gland; Sec, secretions; SP, seminal plasma; Pr, prostate; SV, seminal vesicles; Cg, coagulating gland; Amp, ampullary gland; Dor, dorsal; Lat, lateral; Vent, ventral; Post, posterior; fr, fructose; gl, glucose; Roe, fructose measured by the colorimetric method of Roe (1934); GOD, glucose measured by an enzymic glucoseoxidase method; HK, glucose and fructose measured by the enzymic method of Klotzsch & Bergemeyer (1963); ME, N-acetylglucosamine measured by the colorimetric method of Reissig *et al.* (1955).

in only one case, the bull, has definitive chemical identification been made.

Sugars are present in the semen and accessory sex glands of all eutherian mammals that have been examined (Table 1), that is, from all cohorts except Mutica. Levels of sugars vary widely between species and even individuals, but levels of the order of 100-500 mg fructose/100 ml semen or 100 g of secretory tissue are common. Two Ferungulate orders depart from this normal pattern. Carnivora and Perissodactyla not only lack "normal" fructose levels in semen but have very low seminal sugar levels generally (20-30 mg%). Discussion of relationships between the various anatomically distinct accessory glands does not seem important here as it has been dealt with elsewhere (Mann 1954a, 1964; Price & Williams-Ashman 1961). It suffices to observe that the production of sugars and especially fructose is a characteristic of eutherian accessory sex glands and that various glands not anatomically and embryologically

homologous can perform this physiologically homologous function. The diversity of the accessory sex glands between species, yet the similarity of the secretory products, is an intriguing problem that poses difficulties in interpretation of the evolution of eutherian sex glands and seminal plasma.

EVOLUTION OF SEMINAL SUGARS

Eutherians: Hypothesis 1

The widespread occurrence of fructose (Table 1) would suggest that the origin of this and other sugars as a major constituent of eutherian seminal plasma dates from early in eutherian evolution before divergence of the three cohorts examined. If this is so, the low levels of sugars and fructose in carnivore and perissodactyl semen are the result of a later loss, convergent in the two orders. The ancestors of both lines probably following the "normal" seminal sugar profile. Similar losses appear to have occurred in some

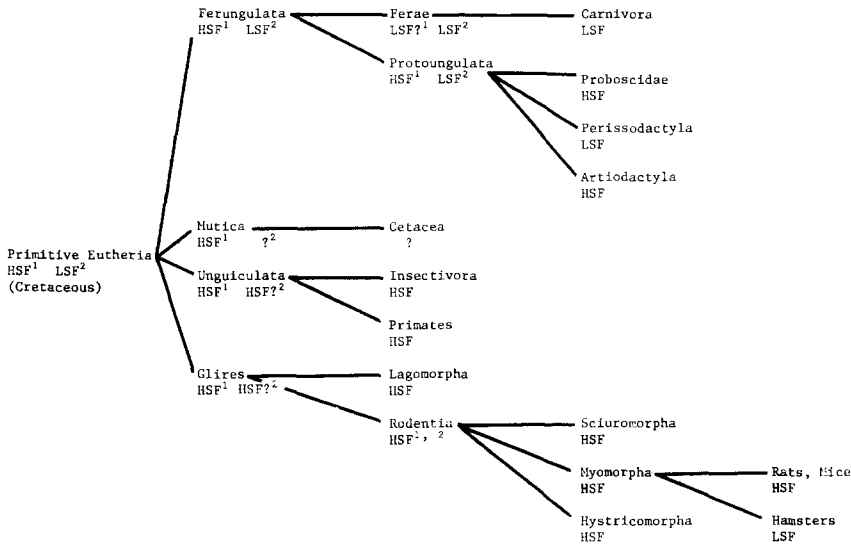


Fig. 1. The evolution of seminal sugars in eutherian mammals

HSF, High levels of sugars including fructose.

LSF, Low levels of sugars including fructose.

¹, Hypothesis 1: Primitive Eutheria possessed seminal sugar regimes similar to the bulk of living Eutheria, i.e. HSF.

², Hypothesis 2: Primitive Eutheria possessed undifferentiated seminal sugar regimes similar to present Carnivora, i.e. LSF.

myomorph rodents, e.g. hamsters, but not in Myomorpha or Rodentia as a whole. This simple scheme is complicated by our knowledge of the diversity of tissues involved in sugar production and the possibility of parallel development of fructose secretion.

Eutherians: Hypothesis 2

Parallelism in evolution of seminal sugars although it may seem perhaps surprising would also be consistent with the data available (Table 1). From those species in which the semen or glands have been examined chromatographically, a large number of various monosaccharides have been discovered. This variety may indicate that the primitive accessory glands produced a number of sugars including fructose, but with none more prominent than the others. If this is the case the present eutherian cohorts arose from an ancestral line with unspecialized accessory gland sugar secretion and only after their divergence and subsequent radiation evolved in parallel the characteristic eutherian seminal sugar profile. Those species who lack high levels of sugars or fructose are thus primitive in this respect. This character would probably be truly primitive and not convergent in Carnivora which is a very ancient line of subordinal status from the beginnings of Ferungulata and also probably true of Perissodactyla which pre dates Artiodactyla. However, the case of the hamsters would almost certainly be a later convergence. These two possible schemes of evolution of the sugar producing accessory glands of eutherians are outlined in Fig. 1.

High semen concentrations of N-acetylaminosugar appear to be unique to marsupials (Rodger & White 1975b), yet present throughout the whole group. Fructose, the characteristic eutherian seminal sugar, is similarly widely spread although lacking in some members. It may well be that some families or species

of marsupial as yet unexamined also diverge from the common pattern. A limiting factor in comparing Marsupialia and Eutheria is uncertainty as to taxonomic levels and their equivalents (e.g. is Marsupialia an order equivalent to a eutherian order or is it a super order? For discussion see Sharman 1974). If Marsupialia is divided into a number of orders, then presumably similar diversity as observed in the eutherians might be expected (e.g. between Carnivora and Perissodactyla as compared with other eutherian orders). The absence of data from American marsupials and from Australian dasyuroid marsupials prevents further discussion on this point. The variation between Australian marsupials and even closely related macropods in the glucose concentration found in seminal plasma indicates that such diversity in seminal constituents does occur, even within a genus.

The distinct differences between the seminal constituents of eutherians and of marsupials tend to suggest that both groups have evolved their own seminal sugar profile independently; probably from common ancestors which possessed an undifferentiated seminal sugar regime (Fig. 2), that is hypothesis two as discussed earlier and illustrated in figure 1. As accessory sex glands are a characteristic feature of male mammals this conclusion adds further weight to the growing body of evidence indicating that therapsids, the common ancestors of the three extant mammalian groups, were actually mammals themselves (Augee 1974). Figure 2 summarizes the proposed scheme for the evolution and radiation of mammalian accessory sex glands.

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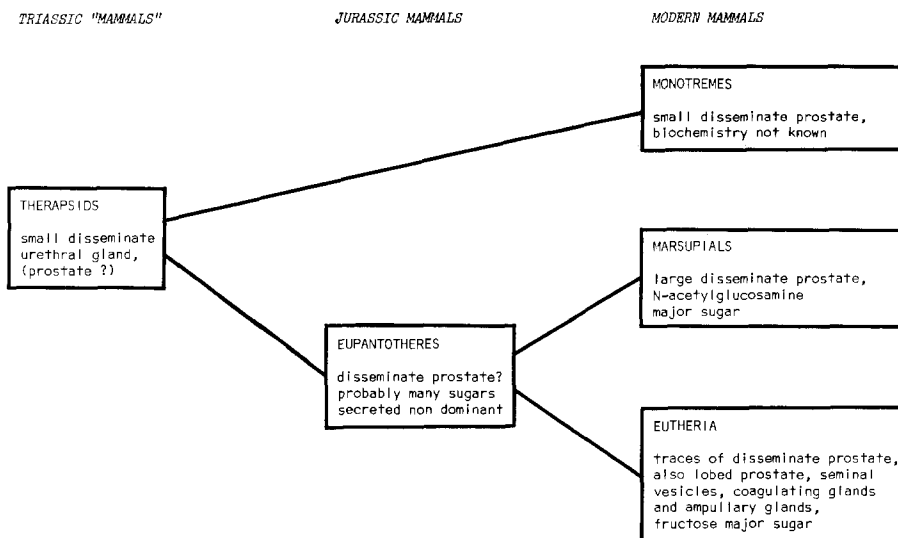


Fig. 2. The evolution of mammalian seminal sugars.

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