FORAGING BEHAVIOUR, FOOD SELECTION AND DIET DIGESTION
of
Babyrousa babyrussa
(SUIDAE, MAMMALIA)

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Thesis presented for the degree of
Doctor of Phylosophy
The University of Edinburgh
May 1994

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ACKNOWLEDGEMENTS

I gratefully acknowledge the financial support of the Commision of the European Communities for this study. The Development Trust of The University of Edinburgh provided me with the portable computer on which most of this thesis was written, and supported an introductory visit to most of the European zoos housing babirusa in preparation for this thesis. I received a travel scholarship from the Faculty of Veterinary Medicine to present my work on the diet of babirusa in captivity at an international meeting.

I would like to thank my supervisor, Dr Alastair Macdonald, for the caring and sharing, for being an excellent teacher and colleague, for the never ending enthusiasm and good spirit and for his striving for postgraduate "customer-care"; it was a pleasure to be your customer. Grateful thanks also go to my co-supervisor Prof. Colin Whittemore for the support and sincere interest in my progress and welfare. Dr Ilias Kyriazakis and Dr Colin Morgan have been excellent teachers in animal nutrition, digestion and food selection. Working with them was a constant stimulus. Many thanks for your help, guidance and concern.
I have had the pleasure to receive excellent technical assistance and teaching from a large number of people. I would specifically like to thank Mr David Anderson, Mr Terry McHale and Mr Jim Fraser for their help with the food selection study and digestibility study with the domestic pigs, Mr Jack McGowan, Mr Bill Kerr, Mr John Swaney and Ms Sheila Smith for teaching me the methods for biochemical analyses of food and faeces, and Mr Gordon Goodall, Ms Judith Watson and Ms Kate Rennie for making the histological slides. The food bowls for the food selection study with the babirusa were made by Mr Jimmy Brown and Mr Graham Moodie for which my sincere thanks. Mr Colin Warwick provided professional assistance with photography and computer graphics for the thesis and questions for help were always answered with "geen probleem". The secretarial support of Ms Suzanne Sellar, Ms Ann Stirling-Whyte and Ms Elaine Chalmers over the three years of this study was greatly appreciated. All of these people, and more, have helped to turn work into a real pleasure. Special thanks also to the lab of plant physiology of the Department of Biology at the Universitaire Instelling

Antwerpen, Belgium, who put up with the smell of pig faeces drying in their ovens.

This thesis would not have been possible without the co-operation of the zoos housing babirusa worldwide. I am very grateful for the many signs of confidence and support and for the many practical contributions of the international zoo community to my studies. Specific thanks go to Mr Bruno Van Puijenbroeck, Dr Walter de Meurichy, Ms Helga de Bois, Ms Linda Van Elsacker, Mr Paul Vercammen, Mr Patrick Immens, Ms Carina Pols, Mr Ronny Lorentsen, Mr Filip Nahooy, Ms Pascale Henneco and the entire staff of The Royal Zoological Society of Antwerp who have supported me in every aspect of my studies from the very beginning. The diets for the food selection study with the babirusa were supplied and prepared by Antwerp Zoo and specific thanks go to Mr Roland Van Bocxstaele and Steven Herreygers who took excellent care of that. The entire staff of Wilhelma Zoo, Stuttgart and specifically Dr Lutz Plasa, Mr Marcus Gehring and Berndt Jungman and colleagues are thanked for their full co-operation in the babirusa food selection study. My sincere thanks also to Dr Walter de Meurichy of Antwerp Zoo, Dr Willem Schaftenaar of Rotterdam Zoo, Dr Gisela Von Hegel of Munich Zoo, Dr Klaus Eulenberger of Leipzig Zoo, Dr Goltenboth of Berlin Zoo, Dr Bernd Matern of Frankfurt Zoo and Dr Thomas Kauffels of Wuppertal Zoo, for collecting the gastrointestinal tracts of babirusa that died in their institiutions and in some instances for notifying me in advance so that histological samples could be taken as soon as possible. In conclusion, I would like to thank the many zoos that have sent me detailed replies to the babirusa diet questionnaire which allowed detailed analyses of the diets fed to babirusa in captivity.

Finally, I would like to thank my fellow PhD students and "office-mates" at the Dick Vet, Ms Katharine Leach, Ms Alison Murray and Mr John Reilly for sharing the ups and downs of PhD life and for their honest support and understanding during the writing-up period. Thanks also to Nathalie Van Moeffaert for the practical help with the final stages of the writing and the excellent meals she provided when time for cooking was short, to my flatmate Letty for her care and concern and to Jacky who sacrificed a sunny day in Scotland to help me format the appendix.

ABSTRACT

A population of 79 babirusa distributed over 19 zoos in Europe and the United States were the subject of a study of the foraging behaviour, food selection, and digestion of the babirusa (*Babyrousa babyrussa*).

Stomachs of six adult babirusa and one twelve month old animal were collected from zoological gardens. Gross anatomical and microscopic examination revealed the large size of the stomach (approximately 3000cm^2 for adults) and the very large area covered by its cardiac glands (more than 70% of the total stomach's mucosal surface area compared to about 33% in the domestic pig (*Sus scrofa*)). Mucus was produced in the cardiac glands and micro-organisms were found both in the mucus-gel adhering to the stomach surface and within the stomach lumen. The pH in the lumen of the cardiac gland area of the stomach was between 5.3 and 6.4 which is suitable for the survival of microorganisms. Gastric glands were confined to a small region occupying the distal end of the corpus ventriculi which was named the "gastric unit".

A comparative study of the digestibility of the dry matter, organic matter and fibre in a basal barley-soya diet supplemented with different amounts of dried grass was carried out with eight babirusa, eight Large White x Landrace and eight Chinese Meishan pigs using the chromic oxide indicator ratio technique. The digestibility of the Acid Detergent Fibre (= cellulose + lignin) component of grass was less in the babirusa than in the domestic pigs. However, babirusa were able to digest Neutral Detergent Fibre (= hemicellulose + cellulose + lignin) and Organic Matter from the total diet better than the domestic pigs.

The foraging and other behaviour of a male and female babirusa when given access to a semi-natural enclosure was recorded using one-minute time scans for six hours per day during five consecutive days. Foraging mainly took the form of walking around with the nose close to or on the ground surface while sniffing. Rooting only took place in that part of the enclosure with very loose sand and was never observed in regions with more compact soil. The two most important food items consumed by the babirusa (in addition to the food that was offered to them by the zoo staff) were bramble leaves and cherry fruits. The animals also demonstrated their ability to carefully select certain plant parts when eating herbs and grasses.

The results of these three studies suggested that the babirusa was a non-ruminant foregut fermenting frugivore/concentrate selector, specialised in the fermentation of plant solubles and more easily digestible fibres and was able to select those plants and plant parts which are more easily digestible.

Information on the diet being fed to babirusa in the 19 zoos indicated that fruits were the items most favoured in captivity. The animals also readily consumed a wide variety of leaves, buds and twigs from branches. The range between zoos in the amounts of total food, dry matter, crude protein, fat, fibre and digestible energy being fed was extremely large. Using prediction equations for domestic pig breeds the energy requirements for the babirusa were estimated to be 11.3 MJ/day for males and 8.5 MJ/day for females and the protein requirements were estimated to be 88g CP/day for males and 59g CP/day for females.

These results together with other information gathered from the literature support the view that the main items in the diet of wild babirusa are likely to be fruits and leaves supplemented with smaller amounts of herbs, grass, roots and animal matter.

CHAPTER 1: GENERAL INTRODUCTION

1. The babirusa

Taxonomy and distribution

The babirusa (*Babyrousa babyrussa*)* is a unique member of the family of the Suidae (pigs) (Artiodactyla - Mammalia) (Groves, 1980; Groves and Grubb, 1993) (Fig. 1.1). They are the only members of the subfamily Babyrousinae and belong to a single genus *Babyrousa.* The most obviously peculiar features of this extraordinary pig are the oddly shaped tusks of the males which can grow to enormous lengths (Fig. 1.2). The alveoli of the maxillary canines are directed vertically upwards which is a unique feature among mammals. As the canines grow upwards from these alveoli they pierce through the skin of the upper jaw and curve backwards over the front of the forehead. The canines of the mandible also grow upwards in a curved fashion but run alongside the sides of the snout. The canines of the female do not grow out as tusks although the upper canines can sometimes be present, and are seen as white dots piercing through the skin.

The babirusa is endemic to the Indonesian islands of Sulawesi, Buru and the smaller Sula and Togian islands. The three living subspecies recognised at present are confined to different islands (Fig. 1.3) (Groves, 1980; Groves and Grubb, 1993):

Babyrousa babyrussa babyrussa (Linnaeus, 1758):
Present on Buru and the islands of Mangole, Taliabu and formerly Sulabesi of the Sula island group (Fig. 1.3). This smallest of the three subspecies is characterised by its dense hair cover composed of both light, golden hairs and dark, black hairs distributed in various patterns over the body. Because of its hair cover this subspecies is often called the "golden" or "hairy" babirusa. The males have shorter and more slender canines than those of the other two subspecies.

Fig. 1.1 Group of young male babirusa in a water pool at Jakarta Zoo, Indonesia.

Fig. 1.2 Photograph of the skull of an adult male babirusa. Note the large size of the canines and the vertically upward direction of the alveolus of the maxillary canine.

Babyrousa babyrussa togeanensis (Sody, 1949):
Present on the islands of Togian, Malenge, Batu Daka, Talatakoh, Batone and formerly (?) Pangenpan of the Togian group (Groves and Grubb, 1993; Vercammen, pers. comm.) (Fig. 1.3). This largest of the three subspecies possesses a shorter and less dense hair cover which is paler on the underparts. The canines are also fairly short and slender.

Babyrousa babyrussa celebensis (Deninger, 1910):
Present on the island of Sulawesi and the offshore island of Lembeh (Fig. 1.3). This subspecies is intermediate in size to the two former subspecies but possesses the longest and most robust canines. Its body hair is usually very short and sparse, giving the impression of the animal having a naked skin (Fig. 1.1). This is the only subspecies currently held in captivity and as a consequence is the best known. The babirusa studied for this thesis were all of this subspecies.

A fourth subspecies *Babyrousa babyrussa bolabatuensis* Hooijer, 1950 was described from a Holocene skull found in the Bola batu caves of southern Sulawesi (Hooijer, 1950). It is not known whether there are still living representatives of this sub-fossil subspecies present in southern or central Sulawesi (Groves and Grubb, 1993). Fossil (Pleistocene) material from southern Sulawesi gave rise to the description of a fifth subspecies *Babyrousa babyrussa beruensis* Hooijer, 1948 which is likely to have been distinctly larger than any of the living subspecies (Hooijer, 1948; Groves, 1980; Groves and Grubb, 1993).

Evolution

The babirusa have experienced a long geographic isolation and evolutionary divergence from the other pigs. Geological evidence suggests that western Sulawesi has been separated from Borneo by the Makassar strait at least from the Eocene onwards (about 55-40 million years ago), although there is a chance that some land connection(s) across the Makassar strait were present during the mid-Miocene (about 20 million years ago) (Audley-Charles, 1981). Whichever may be the case, the present geological evidence indicates that the babirusa on Sulawesi have known a long period of isolation. This concept fits well with the

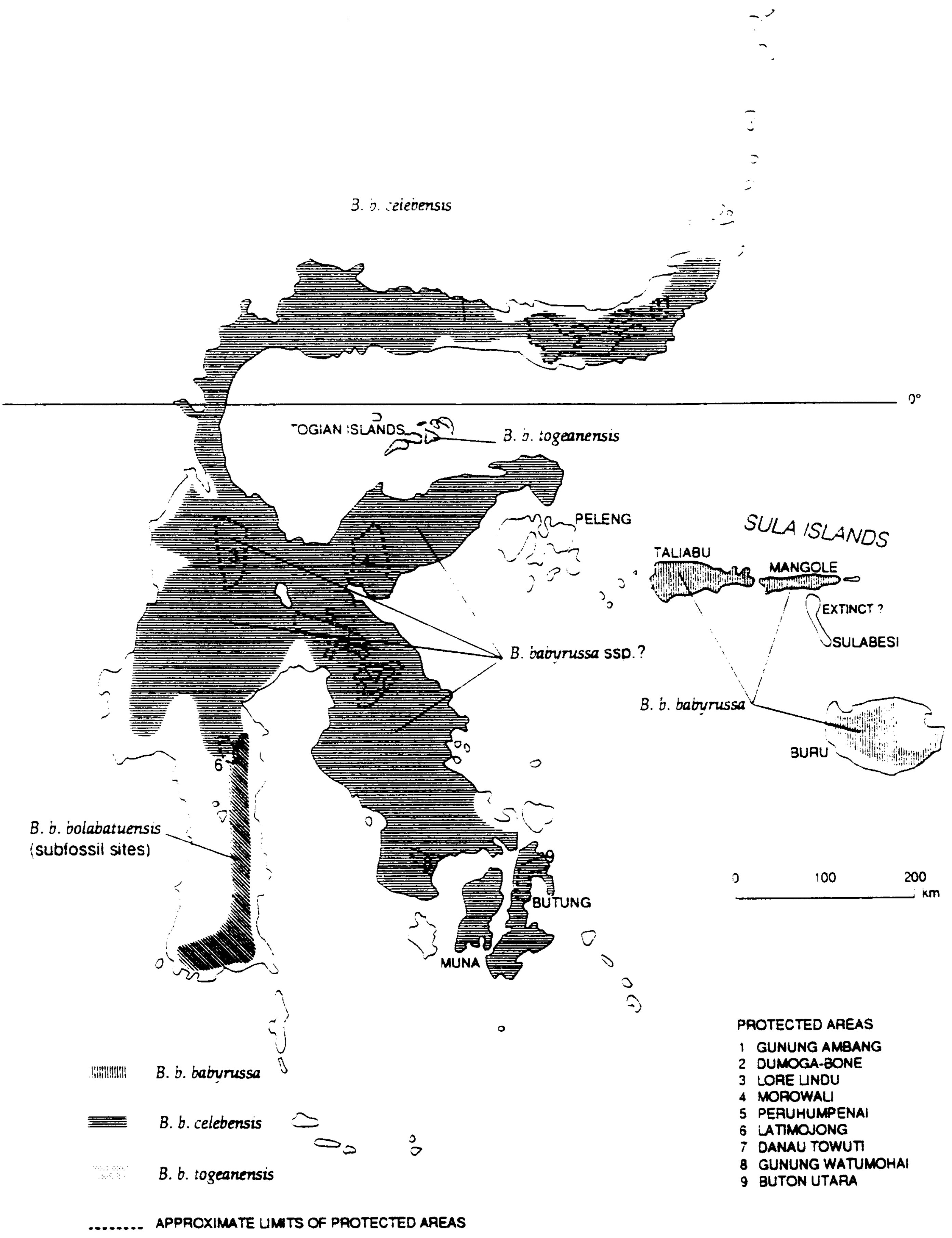

Fig. 1.3 Approximate distribution of the babirusa. From Macdonald (1993).

results of a study on the phylogeny of the Suidae which was based on paleontological and anatomical evidence (Thenius, 1970). Thenius concluded that the Babyrousinae must have split away from the European pig-parent group *Palaeochoerus* as early as the Oligocene (40-30 million years ago) and to have experienced a long evolutionary divergence from the other pigs (Thenius, 1970). At what stage in their evolution and at what time the babirusa first reached Sulawesi is not known. Study of this question is further complicated by the relative lack of fossil material; the only paleontological evidence from babirusa is of relatively young (Pleistocene and Holocene) material from southern Sulawesi (see above) (Hooijer, 1948, 1950). The theory of long evolutionary divergence was supported by the characteristics of the babirusa karyotype when compared with those of the genera *Sus* and *Phacochoerus*. Five pairs of babirusa autosomes were found to have no direct equivalents in domestic or wild *Sus scrofa* or in *Phacochoerus* and another two chromosomes showed signs of having been involved in Robertsonian translocations (Bosma, 1980; Bosma and de Haan, 1981; Bosma et al., 1991).

Biological aspects

Adult male *B.b. celebensis* can grow to about 100kg in weight whereas adult females tend to be 30% smaller and reach about 60-70kg (Macdonald, 1991a). Recent video recordings of babirusa in northern Sulawesi suggest that these animals live in small social groups of up to eight individuals composed of mainly females with offspring of various ages. Large adult males seem to be more often solitary (Patry and Capois, 1989; Patry, pers. comm.). No detailed information is presently known about their social structure and territoriality in the wild.

Compared to other pigs, the babirusa has an unusually small litter size and a long gestation length. Normally 1-2 and sometimes 3 piglets are produced after a gestation of about 155-158 days, which is six weeks longer than that of the domestic pig (114 days) (Vercammen, 1991; Macdonald, 1993). Like warthog piglets (*Phacochoerus* spp.) and unlike the piglets of all the other wild pigs, babirusa piglets are not striped but are uniformly brown in colour (Macdonald, 1991a). Additional information on the

reproduction and reproductive behaviour of the babirusa lies outwith the scope of this study and the reader is thus referred to the papers by Selmier (1983), Bowles (1986), Macdonald (1991b), Plasa (1991), Vercammen (1991), Leus et al. (1992) and Macdonald (1994) for further details.
From early times it has been noted that the babirusa was not able to root in hard compact ground in the way that most other pigs can (Valentijn, 1726; Stehlin, 1900). This inability has been confirmed several times in recent years (Selmier, 1978; Macdonald et al., 1989, 1993; Leus et al., 1992; Leus, 1993) and has been associated with the animal's lack of a rostral bone in the nose (Stehlin, 1900; Macdonald, 1993). Information on the diet of babirusa in the wild is scarce and largely anecdotal, but observations from the wild, together with those from captivity, suggest that the babirusa, like other pigs, is omnivorous; it will consume a variety of herbs, leaves, roots, fruits, invertebrates, small mammals and birds. It was one of the aims of this study to examine the foraging behaviour of and the diet fed to babirusa in captivity, and to investigate further the nature of the possible diet of babirusa in the wild.

Babirusa demonstrate several differences from other pigs in a number of aspects of their soft tissue anatomy such as their limb musculature (Kneepkens et al., 1989; Macdonald and Kneepkens, 1994) and more importantly for this study, the anatomy of their stomach. The fundus region of the babirusa stomach is said to be much enlarged compared to that of the other pigs and to be provided with a well-developed diverticulum (Vrolik, 1843; Davis, 1940; Langer 1973a, 1988). As a consequence of these differences, it has often been suggested in the popular press that the babirusa could be a ruminating pig, a misunderstanding for which there is no supporting evidence (Macdonald, 1991b). However, the question remains, what is the function of this enlarged stomach area? The functional aspects of its gross anatomy and histology, and the ability of the babirusa to digest fibre will also form areas of investigation within this thesis. For more information on the anatomy of the babirusa which lies outwith the scope of this study the reader is referred to the papers by Davis (1940), Macdonald et al. (1984, 1985), Macdonald (1988), Kneepkens et al. (1989), Macdonald (1991b, 1994) and Macdonald and Kneepkens (1994).

Habitat

The tropical forests of the Far East can be categorised into a number of forest types according to the soil type, drainage conditions and altitude of the terrain (van Steenis, 1950; Whitmore, 1975, 1984a, b). Most reports of babirusa are from lowland forest areas, from 0-1000m altitude, but they have also been recorded in hill forests (Bloembergen, 1940), forests on limestone (Bloembergen, 1940), fresh water swamp forest and riverine forest (Lesson and Garnot, 1826; Patry and Capois, 1989; Patry, 1990) and peat swamp forest (Zwahlen, 1992). No detailed information is available on which of those forest types are most favoured by the babirusa. Recent investigations have indicated that babirusa tend to disappear from a region as soon as the forest is cleared (Whitten et al, 1987). The distribution map of the babirusa (Fig. 1.3) was therefore largely based on the total forest cover map of the region recently published by Collins et al. (1991) with additional information gathered from first hand accounts of people who live in a number of the areas represented (Macdonald pers. comm). Until further information has been gathered, it was assumed for the purposes of this thesis that babirusa are present, at least to some extent, in every forest type. The characteristics of the different forest types will be discussed in more detail in chapter 6 where hypotheses are made about the nature of potential ingredients in the diet of wild babirusa according to the results of the studies presented in the other chapters.

Conservation and status in the wild

The only natural predators of the babirusa are pythons (*Python reticulatus* and *Python molurus*) and the endemic Sulawesi civet (*Macrogalidea musschenbroeckii*) which will sometimes predate on the piglets (Wemmer and Watling, 1986; Whitten et al., 1987). The impact of hunting and forest clearance by people constitute a much more serious threat to the survival of the babirusa (Blouch, 1989; Macdonald, 1993). These threats were recognised by the Indonesian government as early as 1931 when the babirusa was accorded full protection under Indonesian law (Dammerman, 1950). At present, a number of protected areas in Sulawesi have already been gazetted and a number of others are under consideration (Macdonald, 1993). The babirusa is listed as "vulnerable" in the IUCN Red Data Book (IUCN, 1978) and is included on appendix 1 of CITES (Convention of International Trade in Endangered Species) which means that neither the live animal nor any parts of it may be traded without prior consent. Considering the smaller geographical distribution of *B.b. togeanensis* and *B.b. babyrussa* the above mentioned threats are of a much more acute nature for these subspecies. As a consequence they were awarded the conservation status "seriously threatened" or "endangered" in the recently published Status Survey and Conservation Action Plan for Pigs Peccaries and Hippos (Oliver, 1993); *B.b.celebensis* was awarded the status "known to be at risk" or "vulnerable". The only subspecies currently kept in captivity, *Babyrousa babyrussa celebensis,* is the subject of an international captive breeding program whereby the details of all animals kept in zoological collections are recorded in an international studbook (Plasa, 1991, 1992, 1993). Throughout the remainder of the thesis, individual babirusa used for the studies will be referred to by their studbook number.

2. Aims

The aims within this thesis are:

1. To investigate the gross and microscopic anatomy of the babirusa stomach and to discuss the possible functional implications of these anatomical characteristics.

2. To compare the digestion of dry matter, organic matter and fibre by the babirusa with that of *Sus scrofa* as represented by two breeds of domestic pig.

3. To investigate the manner of foraging, the nature of food items selected and the general behaviour of the babirusa when given access to a semi-natural enclosure, and to discuss these results in the light of the hypothesis made in section 1 and the results obtained in section 2 of the thesis.

4. To analyse the diet fed to babirusa in captivity with regard to the nature of the ingredients, the amounts of each ingredient offered, the

preferences and dislikes of the animals for particular ingredients, and the nutritional composition of the diet in terms of dry matter, crude protein, fat, fibre and digestible energy. The nature of the ingredients offered and the preferences and dislikes of the animals will be discussed in the light of the results of aims 1-3. The nutritional composition of the diet fed to the babirusa will be discussed with respect to the estimated crude protein and energy requirements of the babirusa as calculated from prediction equations used for commercial pig breeds. The feasibility of application to the babirusa of a recently developed method for measuring crude protein requirements of pigs by dietary self selection will be investigated.

5. To gather all available information on the diet of babirusa in its natural habitat, to formulate hypotheses on the nature of potential ingredients in the diet derived from results in preceding sections of the thesis, and from these hypotheses present a detailed analysis of potential sources of food available to babirusa in Sulawesi.

* The systematic classification and the scientific names for the pigs, peccaries and hippos mentioned throughout the thesis will be those presented in the Status Survey and Conservation Action Plan for Pigs, Peccaries and Hippos (Oliver, 1993). The names of other animal species will be those used by Corbett and Hill (1991). The names of European plant species will be those published by Stace (1991). The sources of the names of plants from Sulawesi will be indicated in the relevant sections of the thesis.

CHAPTER 2: STOMACH ANATOMY OF THE BABIRUSA.

1. Introduction

The anatomy of the babirusa stomach was studied on three separate occasions in the past (Vrolik, 1843; Davis, 1940; Langer, 1973a, 1988). All other accounts in the literature are based on these original pieces of research (Flower, 1872; National Research Council, 1983; Stevens, 1988). It was obvious from these studies that the anatomy of the babirusa stomach was substantially different from that of the other pigs. The intestines of the babirusa were described by Mitchell (1916) who indicated that these were very similar to those of *Sus scrofa*. The latter was confirmed by my personal observations and it was therefore decided to concentrate on the anatomy of the stomach for the purpose of this thesis.

Vrolik (1843) recognised two areas in the stomach, a cardiac part with a well delineated "appendice en capuchon" (i.e. the corpus ventriculi and the fundus ventriculi with its diverticulum ventriculi (Langer, 1988)) and a pyloric part (i.e. the pars pylorica (Langer, 1988)). The babirusa stomach was considered to be very complex and to represent a transitional form between the simple stomach of *Sus scrofa* and the composite stomach of the ruminants (Vrolik, 1843). Like Vrolik, Davis (1940) considered the stomach of the babirusa to be much more complex than that of domestic pig, the main differences being the enormous size of the diverticulum, the clear external constrictions delineating the three main stomach parts and the size and complexity of the cardia (i.e. the fundus ventriculi (Langer, 1988)). Davis also followed Vrolik (1843) in considering the babirusa stomach to be a transitional form between the simple stomach of the pig and the composite stomach of the ruminant, and even recognised all the chambers of the ruminant stomach, except the omasum, in the stomach of the babirusa.

The most recent and most extensive study of the babirusa stomach was carried out by Langer (1973a, 1988). Langer also stressed the large relative size of the fundus and diverticulum and agreed that the stomach of the babirusa was more complex than that of *Sus scrofa* but concluded that the comparison of the babirusa stomach to a ruminant stomach was not justified (Langer, 1973a, b, 1988). Nevertheless, the shape of the babirusa stomach still catches the public imagination and even in recent times several references have been made to the possibility of the babirusa being a "kosher" pig (Anon, 1985, 1991). Babirusa have never been observed to ruminate and are therefore certainly not "kosher" pigs (Macdonald, 1991b). The true function of the stomach and the digestive mechanism of the babirusa, however, remains unknown.

One of the problems often experienced when trying to interpret the earlier descriptions of stomach anatomy is the lack of uniformity in the nomenclature of the different anatomical parts of the stomach. With respect to the babirusa, this problem was addressed by Langer (1973a, 1988); he provided a translation of the older anatomical terms used by Vrolik (1849) and Davis (1940) into the modern Nomina Anatomica Veterinaria terms in his 1988 work. The Nomina Anatomica Veterinaria (NAV, 1983) is an internationally recognised list of anatomical terms for the anatomy of domestic animals which also gives short descriptions of the structure implied by each name.

In 1992 the first Illustrated Veterinary Anatomy Nomenclature (IVAN) was published (Schaller, 1992). However, two fundamental problems remain in the IVAN with respect to the descriptions of the anatomical parts of the stomach such as the fundus ventriculi, corpus ventriculi and pars pylorica (Schaller, 1992). The first is that although the IVAN provides clear and objective demarcation points between the different stomach regions on the lesser curvature, those between the stomach regions on the greater curvature are less well defined and leave room for speculation. Secondly, the IVAN descriptions of the gross anatomical stomach parts include reference to the type of mucosal lining. Comparative studies have indicated that the internal lining of the stomach is so variable among different species that for clarity of description, it would be essential to make as many exceptions to the definitions as there are variations (Edelman, 1889; Oppel, 1896; Bensely, 1902; Haane, 1905; Pernkopf and Lehner, 1939; Schultz 1962; Langer, 1973a; Sheahan and Jervis, 1976; Langer, 1988). It appears that there is a need for clear, objective and uniform definitions of the gross anatomical stomach parts which are independent of their mucosal lining and which can be used throughout the range of mammals.

The studies of the muscle coat of the vertebrate stomach by Pernkopf (1930) provide a possible solution to the above problems. The muscle coat of the mammalian stomach has, like the rest of the intestinal tract, an outer longitudinal and an inner circular muscle layer (Brade, 1883; Oppel; 1896; Pernkopf, 1930; Nickel et al., 1973). Unlike the rest of the mammalian tract however, the mammalian stomach shows a third, inner layer of oblique muscle fibres, the fibrae obliquae internae (Pernkopf, 1930; Nickel et al., 1973; Schaller, 1992). Each of the stomach parts (corpus ventriculi, fundus ventriculi and pars pylorica) is delineated by a different combination of two of these three muscle layers (Pernkopf, 1930). This organisation of muscle layers not only follows a similar pattern among those animals with a unilocular stomach but can also be found in bilocular and even multilocular stomachs such as those of the ruminants (Pernkopf, 1930). Furthermore, these descriptions of the different stomach parts respect the borders on the lesser curvature given by IVAN (Schaller, 1992) and provide objective and uniform demarcation points for the stomach parts on the greater curvature. In the present study, the babirusa stomach will be divided in its different gross anatomical parts according to the course of the muscle layers. The description of the spread of the different types of mucosal linings will then be made with reference to these borders. This will eliminate the existing inconsistencies between the external gross anatomical parts, the course of the muscle layers and the internal lining of the stomach.

The only reference to the histology of the babirusa stomach is an indication of the distribution of the different types of gastric glands over the surface of the stomach (Langer, 1973a, 1988). No histological description of the different gland types in the babirusa stomach is available in the literature. In the present study the histological structure of the different gland types in the babirusa stomach will be described and histochemical techniques employed to identify the sites of mucus production in these glands.

Finally, the results of both the gross anatomical and histological studies will be discussed with regard to possible mechanism of digestion in the babirusa.

2. Materials and methods

Specimens

The stomachs of the following babirusa were used for this study (studbook data from Plasa (1992, 1993)). The cause of death of the animals was unrelated to the gastrointestinal system unless indicated otherwise.

Adult female: studbook number 0004
Born: Antwerp 05.04.1975
Died: Antwerp 11.11.1991
Stomach was modelled in plasticine to preserve the way it was positioned in the abdomen of the animal. This plasticine model formed the basis for the orientation of all the gross anatomical drawings. The stomach was opened, emptied and fixed in 10% formalin about 90 min. after death.

One year old male: studbook number 0156
Born: Antwerp 18.07.1991
Died: Munchen 21.08.1992
Stomach was collected and fixed unopened in 10% formalin approximately 12 hours after death. The animal had been stored in a cold-room until that time.

Adult male: studbook number 0012
Born: Stuttgart 29.07.1976
Died: Frankfurt 17.09.1992
Stomach was collected and fixed approximately 90 minutes after death. The stomach was opened and emptied completely (except for the diverticulum which remained closed and filled) before it was fixed in Klotz fixative.

Adult male: studbook number 0015
Born: Surabaya ca. 1975
Died: Rotterdam 29.10.1992
Stomach was fixed unopened in 10% formalin.

Adult male: studbook number 0020
Born: Stuttgart 04.01.1979
Died: Leipzig 09.01.1993
Animal suffered from chronic diarrhoea over a period of about 6 weeks; it died during the night and was autopsied the next day (Eulenberger, pers. comm.). Stomach was fixed unopened in 10% formalin. The autopsy revealed gastric mycosis (Eulenberger, pers. comm.). This stomach was only used for gross anatomical purposes.

Adult male: studbook number 0030
Born: Frankfurt 26.02.1981
Died: Leipzig 17.03.1993
Animal was autopsied several hours after death. The stomach was fixed unopened in 10% formalin.

Adult female: studbook number 0048
Birth date unknown, arrived from Jakarta in Antwerp 28.04.1984
Died: Antwerp 02.05.1993
Animal died from an abdominal malignant leiomysome cancer not associated with the gastro-intestinal tract (De Meurichy, pers. comm.). The stomach was collected and fixed opened and emptied between 60 and 90 minutes after death. The fixative used was Bouin's.

Stomachs were opened by cutting along the greater curvature leaving the region of the diverticulum intact in order not to damage the spiral fold at its entrance. Whether or not stomachs were opened and emptied before fixation was mainly governed by the time span between death of the animal and collection of the stomach. In those cases where stomachs could be collected during autopsies which were carried out immediately after death, it was chosen to open up and empty the stomachs in order to obtain histological samples of good quality. If stomachs could not be collected soon after death, it was assumed that the histological structure of the mucosa would already be damaged. It was therefore decided to fix the organ when still filled with its contents so that the natural shape would be more or less preserved. Table 2.1 indicates which specimens were used for which aspects of the anatomical study

Table 2.1 Use made of individual stomach specimens. The animals were identified by their studbook number according to Plasa (1992, 1993). (+ = used for that aspect of the study, - = not used for that aspect of the study)

Animal number	Topographical drawings	Muscle layers	Surface area	Histology
0004	+	-	+	+
0156	-	+	+	+
0012	-	-	+	+
0015	+	+	+	-
0020	+	-	+	-
0030	+	-	-	-
0048	-	-	-	+

Gross anatomy

The division of the stomach into its gross anatomical parts (fundus ventriculi, diverticulum ventriculi, corpus ventriculi and pars pylorica) was carried out according to the descriptions published by Pernkopf (1930). Each of the stomach parts is delineated by a different combination of two of the three muscle layers in the stomach wall.

The fundus ventriculi is built up of the external stratum longitudinale (longitudinal muscle layer) and the internal fibrae obliquae internae (internal oblique fibres) and stretches from the incisura cardiaca on the lesser curvature to the place on the greater curvature where the circular muscle layer of the corpus ventriculi starts. The corpus ventriculi is mainly constructed out of the stratum circulare (circular muscle layer) externally and the internal oblique fibres internally with some external longitudinal fibres on its lesser and greater curvature. It extends on the lesser curvature from the oesophagus to the incisura angularis and on the greater curvature from the place where the circular muscle layer starts (because that is the border with the fundus) to the place where the internal oblique fibres stop. The pars pylorica is made up of the external longitudinal and internal circular muscle layer and stretches from the incisura angularis on the lesser curvature to the place on the greater curvature where the internal oblique fibres of the corpus ventriculi stop. The orientation of the internal muscle layers across the stomach was studied by removal of the tunica mucosa. The orientation of the outer layers was often clear from external examination; the serosa was only removed in doubtful regions.

Stomach luminal surface measurements were carried out on the mucosal lining of the stomach, except for the unopened diverticulum the surface area of which was estimated from the outside. Pieces of paper were fitted against the internal surface of the stomach, care being taken to follow the major sacculations and muscular folds. The method did not allow incorporation of the smaller mucosal folds, especially in those stomachs which were very contracted as a result of fixation after emptying of the stomach contents. These pieces of paper were dried to constant weight in a drying oven at 45°C together with 3 papers with a known surface area of 25cm^2 and 3 with a surface area of 100cm^2. After drying, the papers were weighed and the unknown surface areas were calculated from the weight of the papers with known surface areas. The 3 papers of 100cm^2 had a weight of 0.502 ± 0.008g and those of 25cm^2 weighed 0.126 ± 0.001g. These results confirmed that the 100cm^2 papers were indeed four times heavier than the 25cm^2 papers and that there were no large variations in the paper thickness and quality. The value of 0.126 g per 25cm^2 was used for the calculations of the unknown surfaces.

Histology

Samples were taken from the different regions of the stomach. Photographs of the sample sites allowed retrospective identification of the sites sampled at all times. All samples from stomach 0048 were fixed in Bouin's fluid. Most samples from stomach 0004 were taken from the fresh stomach and fixed in Bouin's fluid, some additional samples were later taken from the formalin (10%) fixed stomach. Samples of stomach 0012 were taken after the stomach had been stored in Klotz fluid for one day and were then fixed in Bouin's fluid. All samples from stomach 0156 were fixed in 10% formalin. All samples fixed in Bouin's fluid were kept in the fluid for 24 hours only, after which they were stored in 70%

alcohol. Paraffin sections of 6µm thickness were stained with: Ehrlich's haematoxylin and eosin (H&E), H&E/Periodic acid-Schiff (PAS) technique, Alcian blue (pH 2.5) (AB), Alcian blue/PAS technique (AB/PAS) and High iron diamine/Alcian blue (pH 2.5) method (HID/AB) (Culling et al., 1985).

Throughout this study, various terms will be used with reference to mucus. Mucus is the slimy product which is secreted by various cells (Reid and Clamp, 1978). The various substances giving the mucus its typical slimy characteristics are the mucosubstances (Reid and Clamp, 1978; Creeth, 1978). In the case of stomach mucus, these mucosubstances are glycoproteins, also referred to as mucins (Creeth, 1978; Allen and Garner, 1980; Allen et al.,1982). In order to detect all the sites of mucus production in the glands of the stomach, it was necessary to apply staining techniques for the different types of glycoproteins. The PAS technique stains only neutral glycoproteins (deep red colour) (McManus and Mowry, 1960; Drury and Wallington, 1976; Culling et al., 1985). Alcian blue indicates with a blue colour the presence of sulphated and non-sulphated acid glycoproteins (also called sulphomucins and sialomucins respectively) (McManus and Mowry, 1960; Drury and Wallington, 1976; Culling et al., 1985). The AB/PAS technique stains neutral glycoproteins red, acid glycoproteins blue and a mixture of the two types purple to dark blue (McManus and Mowry, 1960; Culling et al., 1985). The HID/AB method allows differentiation between sulphated and non-sulphated acid glycoproteins; the former are coloured grey-purple-black and the latter blue (Spicer, 1965; Culling et al., 1985).

Mast cells also colour blue with AB and grey-purple black with HID because of the presence of heparin, a sulphated and carboxylated mucosubstance (Culling et al., 1985).

Nomenclature

The anatomical nomenclature used in the present study is that found in the Illustrated Veterinary Anatomical Nomenclature which already contains all the changes approved for the 4th edition of the Nomina Anatomica Veterinaria (Schaller, 1992). The names of the gross anatomical parts of the babirusa stomach correspond with those proposed in IVAN and the regions of the stomach identified by these terms are indicated in the text.

3. Results

Gross anatomy

External gross anatomy

In general terms, the babirusa follows the basic plan of the porcine stomach. It is a unilocular, pouched and composite stomach, meaning that it consists of a single chamber provided with a diverticulum and contains areas of both non-glandular and glandular mucosa (Langer, 1988). To the left of the oesophagus a blindsac is found, the fundus ventriculi, separated from the oesophagus by the incisura cardiaca on the lesser curvature. The fundus ventriculi possesses a blind pouch at its extremity, the diverticulum ventriculi. On the lesser curvature, to the right of the oesophagus, another notch can be found, the incisura angularis, separating the central part of the stomach, the corpus ventriculi, from the right part of the stomach, the pars pylorica, which leads distally to the duodenum. As will become clear in the following descriptions, however, the babirusa stomach is a more complex version of this basic porcine stomach plan. For convenience, the corpus ventriculi will be referred to as corpus, the fundus ventriculi as fundus and the diverticulum ventriculi as diverticulum throughout the remainder of the text.

Drawings of the adult babirusa stomach as it was positioned within the abdomen of the animal can be found in Fig 2.1. The fundus was positioned to the left of the corpus and extended dorsally into the diverticulum. The diverticulum itself pointed caudally and to the right. The pars pylorica of the stomach was relatively small, positioned to the right of the corpus and pointed in cranial direction. The division of the stomach into its gross anatomical parts along the greater curvature, as indicated in the drawings, was carried out according to the course of the muscle layers (see introduction). The muscle coat of the babirusa stomach was described in detail by Langer (1973a) the results of which are

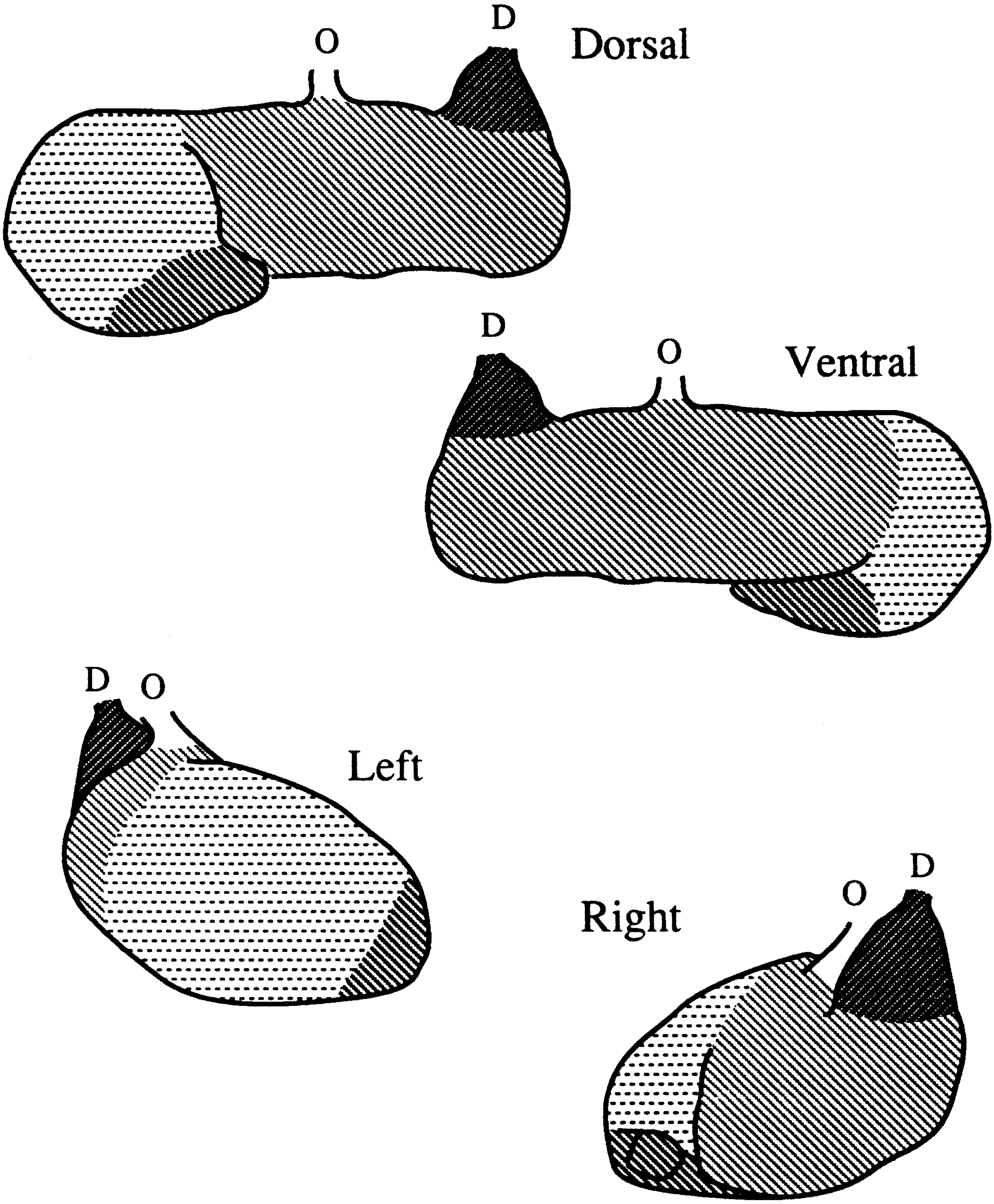

Fig. 2.1 Adult babirusa stomach as it was positioned within the abdomen of the animal. The shadings indicate the delineations of the different external gross anatomical regions of the stomach.

▧ Corpus ventriculi

▤ Fundus ventriculi

▨ Diverticulum ventriculi

■ Pars pylorica

O = Oesophagus

D = Duodenum

indicated in Fig. 2.2a. Personal observation largely confirmed the distribution of these muscle layers but in addition suggested two changes as indicated in Fig. 2.2b.

Both on the parietal and the visceral sides, the fibrae oblique internae extended further towards the end of the stomach thereby including the entire bend of the stomach towards the pylorus. This latter region formed a clearly identifiable entity not described as such by Vrolik (1843), Davis (1940) or Langer (1973a, 1978). The structure was wedge shaped and positioned towards the end of the right half of the babirusa stomach. The narrow end of the wedge was located at about the height of the incisura angularis on the lesser curvature. The wide end of the wedge was found on the greater curvature where the stomach bent in a caudal direction (Fig. 2.3). The area was characterised by a smoothly stretched surface, a non-folded convex border with the greater curvature and a clearly visible and plentiful supply of blood vessels running from the greater curvature towards the lesser curvature in the direction of the point of the wedge. An obvious fan of collagen fibres was visible on its ventral surface towards the lesser curvature. According to the degree of filling of the stomach the impression was sometimes created of two external constrictions on the greater curvature separating this region from the remaining corpus of the stomach on the left side and the pyloric end on the right side. However there were no internal muscular folds corresponding to these external constrictions and it was likely that this impression was created by differences in the characteristics of the stomach wall. The remaining corpus of the stomach had a very thin and much folded wall with haustra-like sacculations which contrasted well with the thicker, smoothly stretched wall of the wedge-like structure. The difference in wall structure between the two regions was certainly clear to the touch, especially if the stomach was filled. Since the outer extent of the fibrae obliquae internae on the greater curvature indicated the border between corpus ventriculi and pars pylorica, the significance of the fibrae obliquae internae completely incorporating the wedge shaped entity was that this structure now definitely belongs to the corpus ventriculi and not to the pars pylorica. This observation proved to be of significance when the internal lining of the stomach was examined.

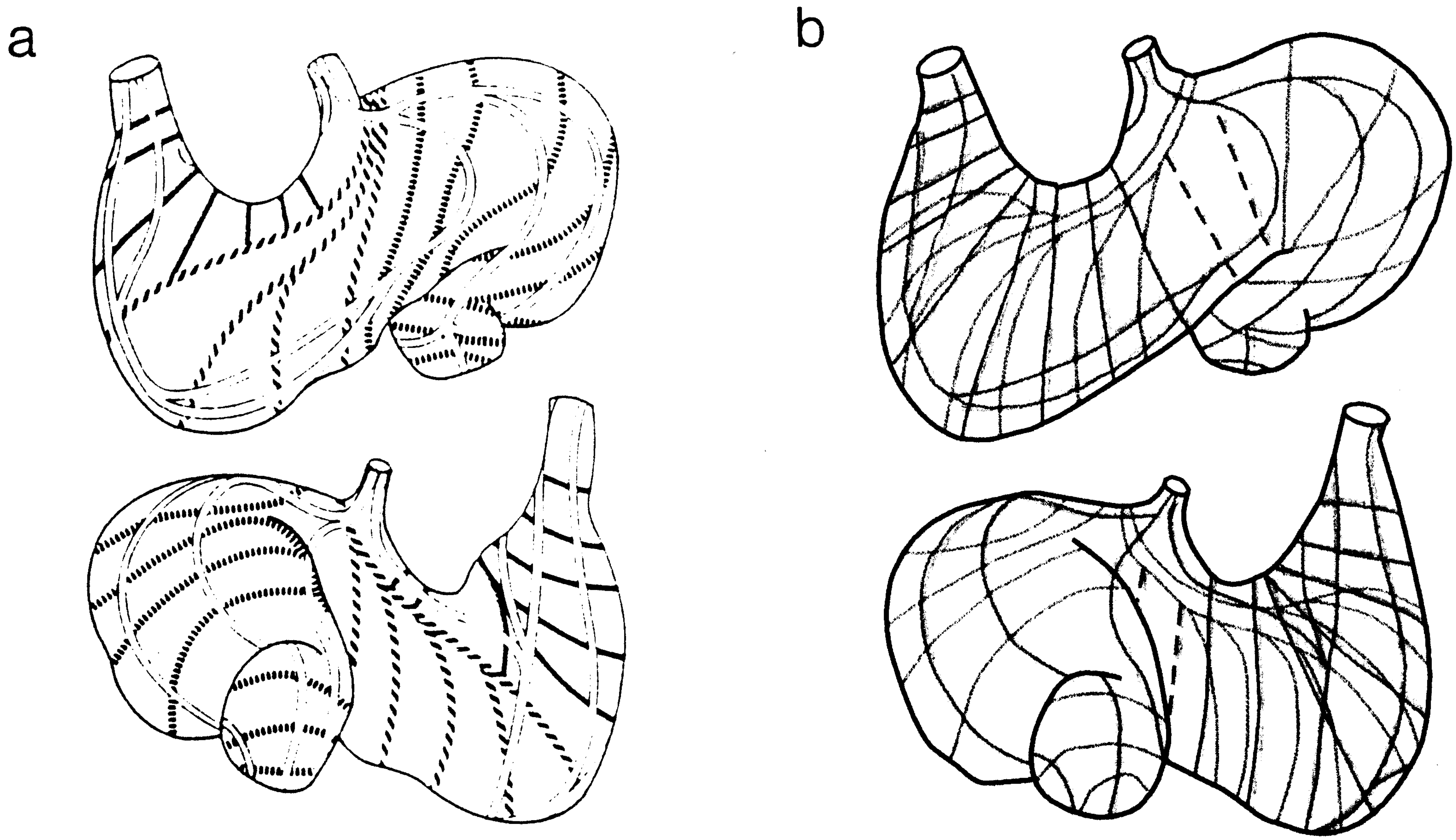

Fig. 2.2 Organisation of the different muscle layers in the babirusa stomach in ventral (top) and dorsal (bottom) view:
a. according to Langer (1973a)
b. corrections made in the present study

═ and blue = fibrae longitudinales; ▬ and full green = fibrae circularis; hatched green = fibers of uncertain origin with a circular orientation; //// and ⦙⦙⦙⦙ and yellow = fibrae obliquae internae

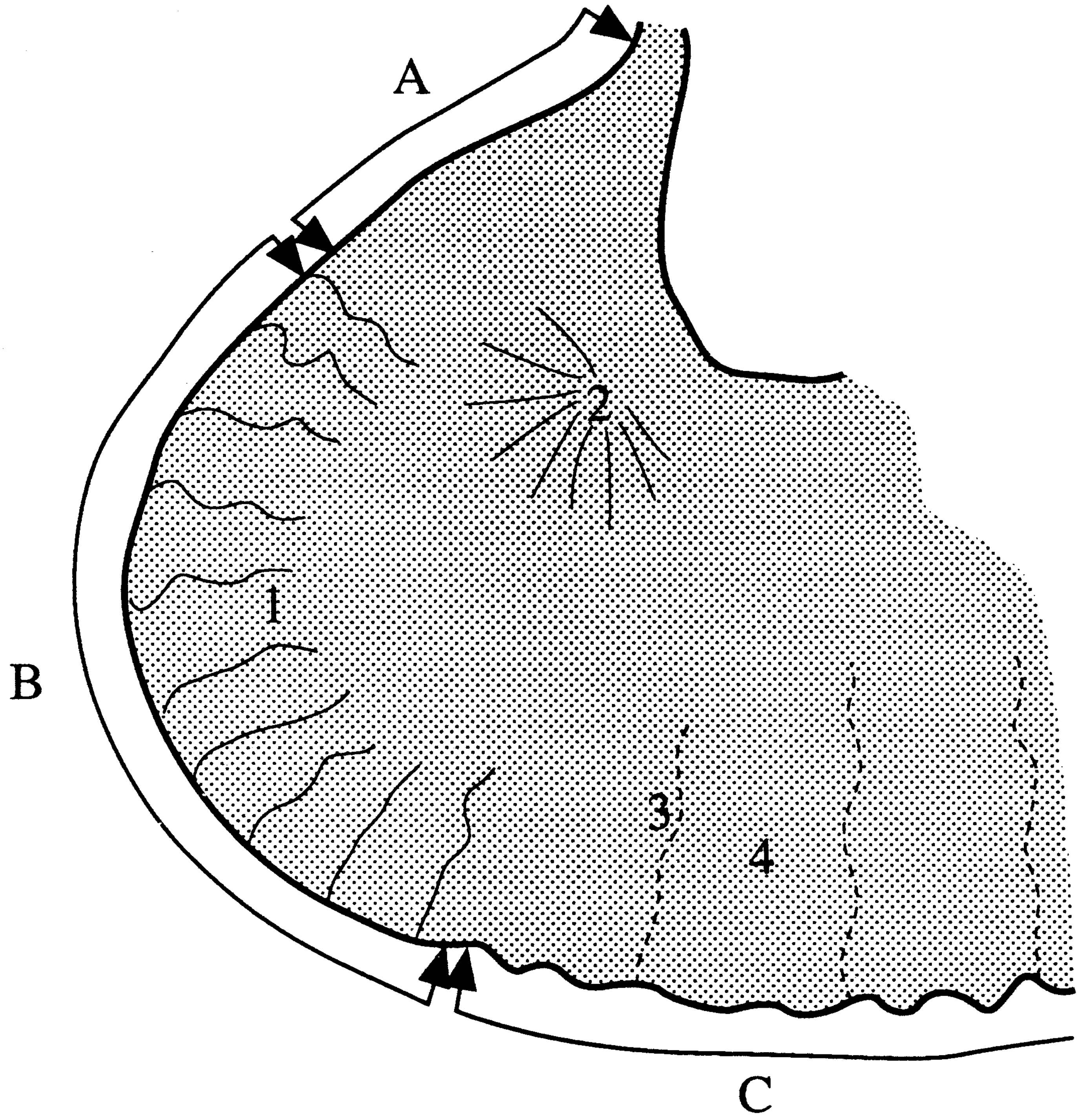

Fig. 2.3 Detail of the visceral pyloric part of the babirusa stomach.
(Drawn from the stomach of the 1 year old animal (studbook number 0156))

A: Pars pylorica
B: Wedge shaped entity representing the right outer part of the corpus ventriculi
C: Remainder of the corpus ventriculi

1: Blood vessels
2: Fan of collagen fibres
3. Tenia-like folds in the corpus ventriculi
4. Haustra-like sacculations of the corpus ventriculi

The second change to be made with regard to the course of the muscle layers concerned the outer circular layer in the corpus ventriculi (Fig. 2.2b). According to Langer (1973a, 1988) this layer was only present for a very short distance on the lesser curvature; the consequence of this assertion was that the haustra-like sacculations of the corpus ventriculi were made up of only one muscle layer, the fibrae obliquae internae, the thickened fibres of which formed taenia-like folds. Personal observations suggested that for the greater part of the corpus ventriculi, the outer circular layer was present over a larger area of the corpus wall, its extent only becoming less clear at the greater curvature. Only the outer left part of the corpus seemed to be composed of only one muscle layer. This ran in a circular fashion but could not be identified with certainty as being either the true circular layer or alternatively the fibrae obliquae internae running in a circular fashion. Since the end of the circular layer of the corpus ventriculi on the greater curvature constituted the border between the corpus and the fundus, the former observation would complicate the positioning of this border. However, two further observations were made in the region with a singular muscle layer. Firstly, an internal muscular fold was present in this region; this appeared to be part of the internal spiral fold at the entrance of the fundus ventriculi described by Langer (1973a, 1988). Secondly, the outer longitudinal muscle layer, which in the corpus region was only present as a narrow strip along the greater curvature, passed onto the side walls of the stomach in this region to form the outer muscle layer covering the fundus and diverticulum. Both of these observations helped to locate the border between corpus and fundus at the end of the small region with a single circular muscle layer.

After the establishment of objective borders between the different parts of the stomach it was possible to measure the surface areas of the mucosa covering each of these parts. The results in Table 2.2 demonstrated that the babirusa stomach was a voluminous organ which had a total luminal surface area of around 3000cm^2 in the fully grown adult animal. The total mucosal surface area of the one year old animal (0156) was about half the size of that of the adult animals. Except for the proportionately larger size of the diverticulum, the percentage of the total stomach surface area taken up by the different stomach parts did not seem to be

Table 2.2 Surface area measurements of the gross anatomical parts of the babirusa stomach. Animals were identified by their studbook number according to Plasa (1992, 1993)

Animal	Fundus Area (cm^2)	%	Diverticulum Area (cm^2)	%	Corpus Area (cm^2)	%	Pars pylorica Area (cm^2)	%	Total Area (cm^2)	%
0015	940	32	208	7	1642	55	192	6	2982	100
0020	1139	36	231	7	1576	49	256	8	3202	100
0156	529	36	205	14	608	42	113	8	1455	100

Table 2.3 Surface area measurements of the different types of internal (mucosal) lining of the babirusa. stomach. Animals were identified by their studbook number according to Plasa (1992, 1993)

Animal	Squamous epith. Area (cm^2)	%	Cardiac glands Area (cm^2)	%	Gastric glands Area (cm^2)	%	Pyloric glands Area (cm^2)	%	Total Area (cm^2)	%
0015	129	4	2438	82	223	8	192	6	2982	100
0020	112	4	2286	71	548	17	256	8	3202	100
0156	86	6	1077	74	179	12	113	8	1455	100

markedly different in the young animal. In all animals the corpus formed the largest part of the stomach closely followed by the fundus. The area covered by fundus and diverticulum together was almost the same as that covered by the corpus alone. The pars pylorica covered less than 10% of the stomach's mucosal surface area.

In addition to the results in Table 2.2 the mucosal surface areas of stomachs from two other adult babirusa were measured. The results from these animals were quite different. The areas covered by the different stomach parts in the animal 0012 were: fundus 224cm^2 (14%), diverticulum 358cm^2 (22%), corpus 707cm^2 (44%), pylorus 322cm^2 (17%) and total stomach area 1611cm^2 (100%); those for the animal 0004 were: fundus+diverticulum: 474cm^2 (39%), corpus 518cm^2 (43%), pars pylorica 210cm^2 (18%), total stomach area 1202cm^2 (100%). Both these stomachs had been fixed after removal of the digesta and the muscular wall had therefore undergone extensive contraction. Because of the thinness of both the tunica muscularis and tunica mucosa in the fundus, diverticulum and corpus (up to the wedge-shaped entity), these regions were especially susceptible to contraction during fixation, resulting in extensive folding and a general decrease in measurable mucosal surface area. The stomach of the animal 0012 was opened up entirely except for the diverticulum which was fixed while full of digesta. As a consequence this latter region of the stomach had retained its large size. The opened stomach of the animal 0004 had contracted to such an extent that it was no longer possible to detect the border of the diverticulum. The fundus and diverticulum were therefore measured together. The pars pylorica seemed to be less affected by shrinkage through fixation, the results for this area in both stomachs being in the same range as those of the stomachs in Table 2.2.

Because of the alteration in total stomach mucosal area, and the differential degrees by which the different parts of the empty stomach contracted during fixation the results from the opened stomachs were excluded from further analyses.

Internal surface differentiation
The muscular differentiation of the internal surface of the stomach was described by Langer (1973a, 1988) and confirmed by personal observations. The fibrae obliquae internae closest to the lesser curvature were strongly developed and formed a loop around the cardiac opening, the crest of which lay in the incisura cardiaca. The legs of this muscular loop were so thick that they formed the bases of two mucosal folds running towards the pars pylorica in the pars nonglandularis, equivalent to the more well developed gastric groove of the ruminant. The floor of this groove was formed by the circular muscle layer of the corpus region. At the base of the diverticulum a spiral fold was formed by the internal oblique fibres which ran counter clockwise into the diverticulum (Langer, 1988). Another spiral fold formed by the internal oblique fibres could be found at the border between the corpus and fundus spiralling into the fundus.

The present study indicated the following with regard to the distribution of the different gland-types over the internal surface of the stomach (Fig. 2.4). Like all pigs, the babirusa showed a small area of nonglandular squamous epithelium or pars nonglandularis on the lesser curvature. This surrounded the oesophagus and extended for a small distance into the fundus, but mainly stretched in the direction of the pars pylorica and ended before the plica angularis. Nonglandular squamous epithelium completely covered the two folds running towards the diverticulum which formed the equivalent of the gastric groove.

The diverticulum, fundus and the largest part of the corpus, up to the wedge-shaped structure discussed above, were covered by the glandulae cardiacae or cardiac glands. The border between the pars nonglandularis and the cardiac gland area was always abrupt. The glandulae gastricae or gastric glands were mainly confined to the wedge-shaped structure at the end of the corpus. This structure will from now on be referred to in the thesis as the "gastric unit". The terms gastric pouch or gastric chamber were avoided because of the wide internal connections between the gastric unit and both the remainder of the corpus and the pars pylorica. The gastric gland area did not reach as far as the incisura angularis region of the lesser curvature but was separated from it by a thin strap of cardiac glands. The internal border between the gastric unit and the remainder

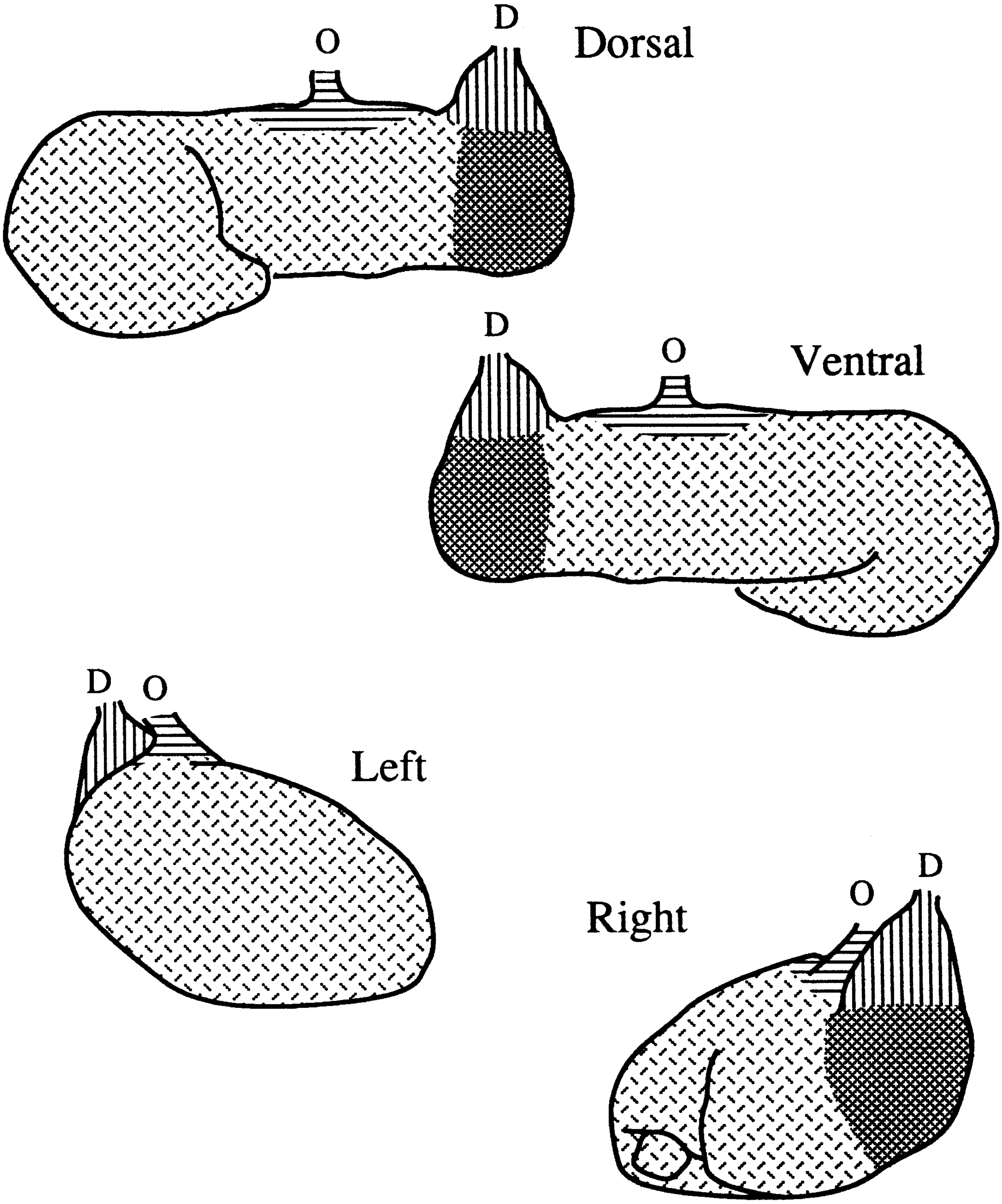

Fig. 2.4 Adult babirusa stomach as it was positioned within the abdomen of the animal. The shadings demonstrate the distributions of the different types of mucosal lining within the stomach.

≡ Stratified squamous epithelium

⁘ Cardiac glands

▦ Gastric glands

||||| Pyloric glands

O = Oesophagus

D = Duodenum

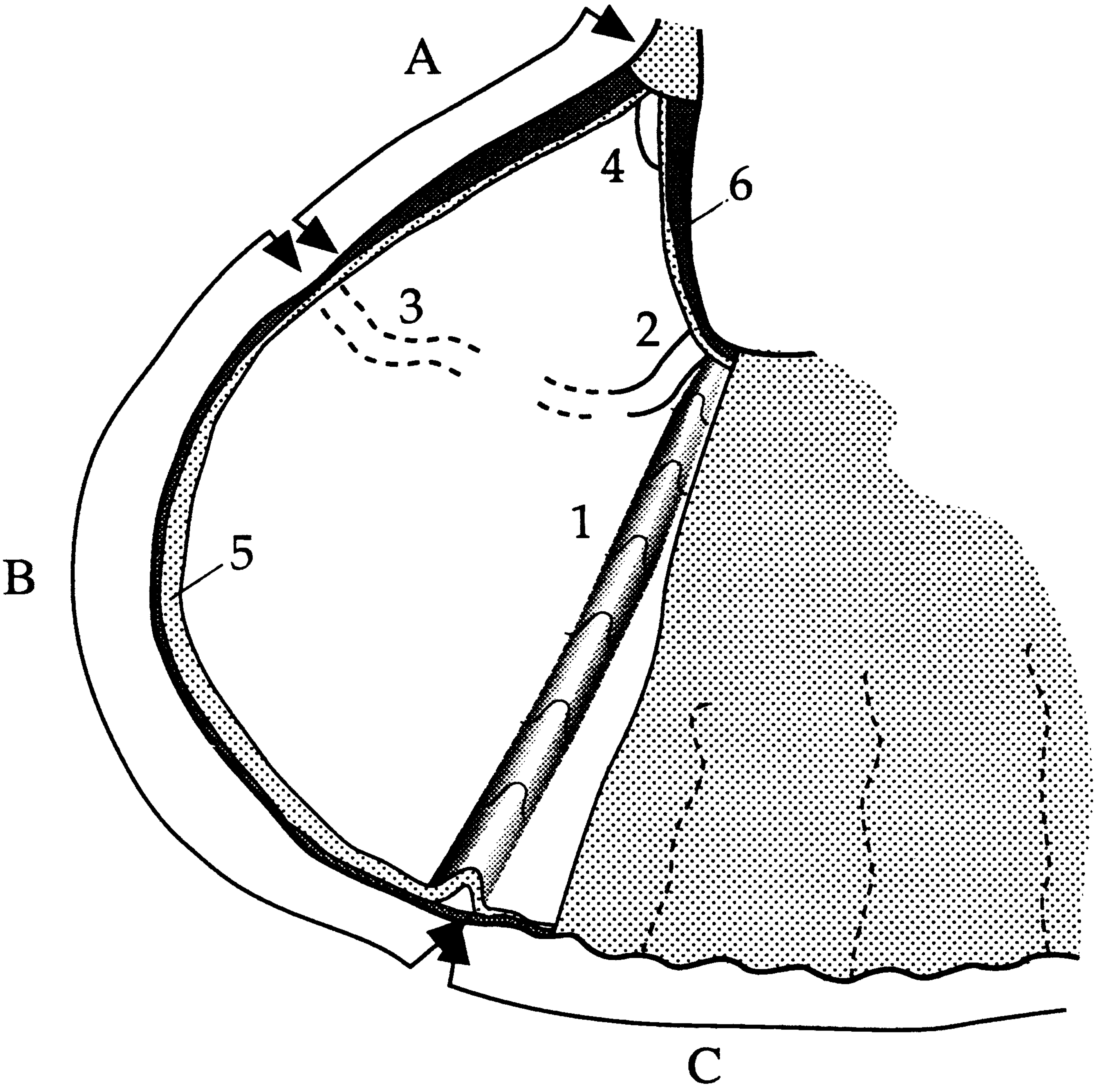

Fig. 2.5 Detail of the pyloric part of the babirusa stomach. The ventral wall has been removed from the pars pylorica and the gastric unit to demonstrate the internal surface differentiations of the dorsal wall.

A: pars pylorica
B: Gastric unit = the wedge-shaped entity representing the distal part of the corpus ventriculi
C: Remainder of the corpus ventriculi (unopened)

1. Mucosal fold separating the gastric unit with gastric glands from the remainder of the corpus with cardiac glands
2. Plica angularis
3. Shallow mucosal folds at the transition of the gastric unit into the pars pylorica
4. Torus pyloricus
5. Tunica mucosa
6. Tunica muscularis

of the corpus region was formed by a fold composed of tunica mucosa and tela submucosa (Fig. 2.5). The fold was very prominent on the dorsal wall of the stomach but became less clear as it ran from the greater to the lesser curvature on the dorsal wall. That side of the fold bordering on the remainder of the corpus had a thin tunica mucosa which thickened as it reached the top of the fold and ran over onto the side of the fold bordering the gastric unit.

The tunica mucosa of the gastric unit thinned out as it reached the border with the pars pylorica, whereas the tunica muscularis thickened. Both tendencies continued in the first part of the pars pylorica. Some shallow mucosal folds could be seen at the transition of the gastric unit into the pars pylorica. The pars pylorica was lined with glandulae pyloricae or pyloric glands. No clear demarcation line between pyloric and gastric glands could be found. Both macroscopic and histological observations indicated that both gland types gradually ran into each other (see histological section). The pyloric glands bordered on the stratified squamous epithelium region of the lesser curvature.

Table 2.3 shows the surface areas covered by each of the different gland types in the babirusa stomachs investigated during the present study. Most striking was the enormous size of the cardiac gland area, covering more than 70% of the total stomach area, and the very small area (8%-12%) covered by the gastric glands. The results for the 1-year-old animal were not different from those of the full-grown animals.

Histology

As indicated above, one non-glandular and three types of glandular areas (cardiac, gastric and pyloric gland areas) could be distinguished in the babirusa stomach. The non-glandular area of the stomach was covered by non-keratinised stratified squamous epithelium. From the luminal surface to the outside of the stomach the following zones could be identified in the stomach wall (names according to Banks (1986) and IVAN (Schaller, 1992)). The most luminal zone of the stomach wall was the tunica mucosa which itself comprised the lamina epithelialis mucosae, the lamina propria mucosae and the lamina muscularis mucosae. The lamina epithelialis mucosa consisted of a simple columnar epithelium which continued into the gastric pits. The bases of the gastric pits were continuous with the exits of the stomach glands. The gastric pits and the glands were embedded in the lamina propria mucosae which sent connective tissue strands alongside individual glands. A thin lamina muscularis mucosae, containing smooth muscle, was present in all regions except the pyloric gland region where it formed a relatively thick layer. At its base, the tunica mucosa bordered the tunica submucosa which contained predominantly connective tissue, blood vessels and adipose cells.

The next major layer in the stomach wall was the main muscle coat of the stomach or tunica muscularis. The tunica muscularis was composed of two layers, usually a thicker inner layer and a thinner outer layer. Considering the relatively complicated arrangement of the different muscle layers in the fundus and the corpus of the babirusa stomach, a clear inner circular and outer longitudinal layer could not always be observed in these stomach parts, the layers sometimes showing different orientations. However, clearly arranged inner circular and outer longitudinal muscle layers were present in the very thick tunica muscularis of the pars pylorica. The final, outer layer of the stomach was formed by the tunica serosa which was composed of a thin layer of connective tissue and a final lining of mesothelium.

In what follows, the lamina epithelialis mucosae and the lamina propria mucosae of the different glandular areas are discussed in more detail.

Cardiac gland area: Fig. 2.6 and Fig. 2.7

The stomach surface was lined by a simple columnar epithelium which became more cuboidal as it moved into the gastric pits or foveolae gastricae. The gastric pits could be quite long and regularly occupied 1/3 to 1/2 of the depth of the combined gastric pit and glands. The density and degree of coiling and branching of the glands seemed to be somewhat variable among individuals, but in general the glands were tubular, branched and coiled at their bases. At regular intervals, several glands ended in a single depression of the surface of the lamina propria

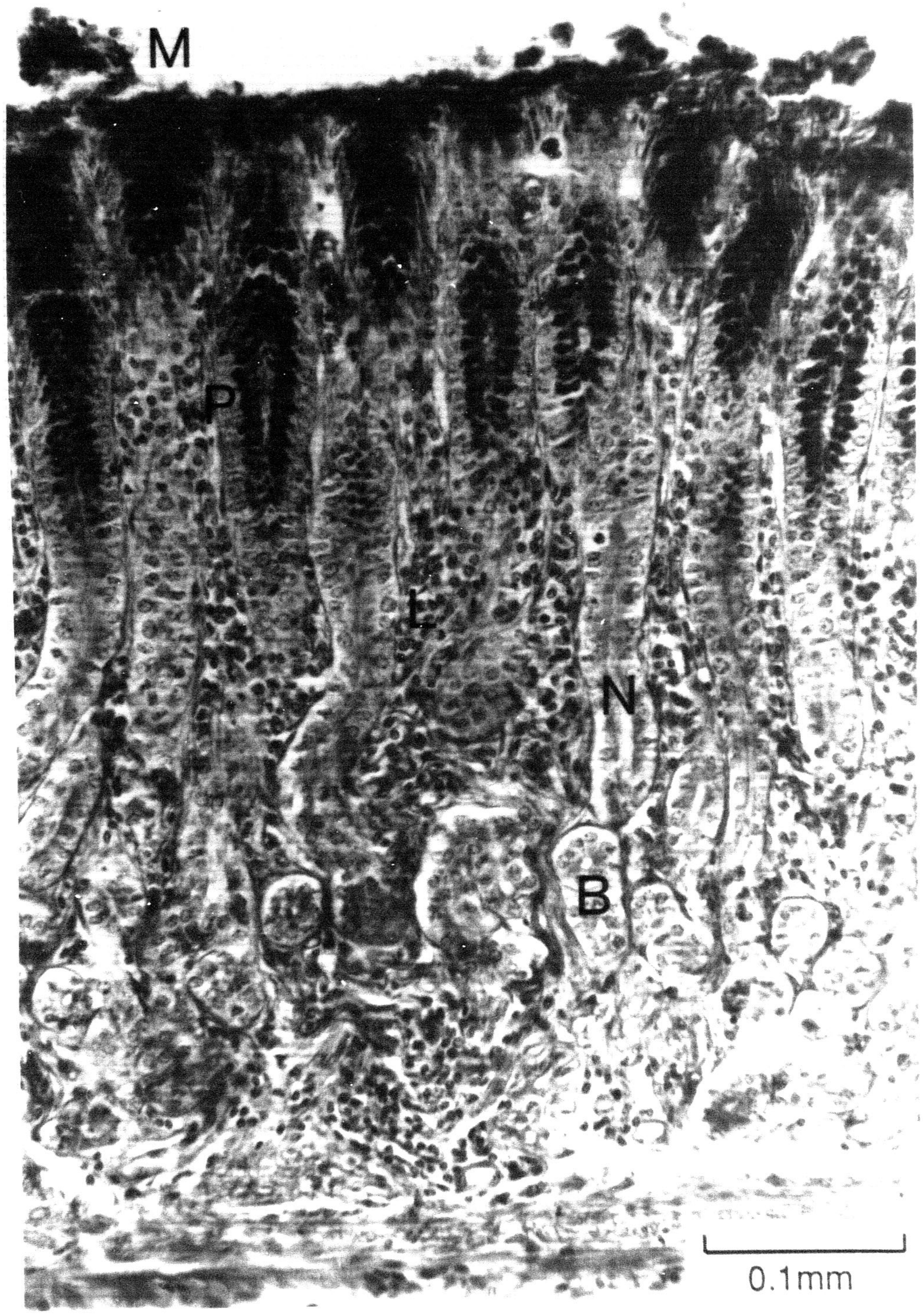

Fig. 2.6 Tunica mucosa of the cardiac gland region of the babirusa stomach. (AB/PAS)

M: Fragments of adherent mucus gel
P: Gastric pit epithelial cells which stained purple with AB/PAS and appear black on the photograph.
N: Cells in the neck region of the cardiac glands which stained red with AB/PAS and appear grey on the photograph.
B: Cells in the basal region of the cardiac glands which stained red with AB/PAS and appear grey on the photograph.
L: Connective tissue of the lamina propria mucosae containing numerous lymphocytes

mucosae, the sulci gastrici or gastric grooves, which separated areae gastricae or gastric fields from one another. At the surface, the nuclei of the epithelial cells were oval in shape and positioned at up to one third of the cell-length from the basal membrane. As the epithelium continued down into the gastric pits the nuclei became rounder and displaced towards the basal membrane. The luminal side of the surface cells was sometimes covered with a dark stained layer of material. When stained with H&E/PAS, the epithelial cells towards the bottom of the gastric pits showed a small, PAS positive area in their cell apex. As the epithelium moved up to the top of the gastric pits, this stained area became larger, more intensely stained, and filled the apical region of the cells up to the luminal border but left the area around the nucleus unstained. The stained apical area reached its maximum size in the cells at the top of the gastric pits and in the surface epithelial cells, but a clear unstained zone always remained between the nucleus and the stained apical area.

The apical region which stained red with PAS, as well as the darkly stained layer of material covering the luminal surface of the stomach, were stained bright blue with AB, the stained area becoming larger from the deeper areas of the gastric pits towards the surface. With AB/PAS, the layer of material covering the luminal surface of the stomach and the apical region of the surface and gastric pit epithelial cells were coloured intensely dark purple-blue (Fig. 2.6). Travelling from the surface to the bottom of the gastric pit, the coloured area in the apex of the cells became smaller, less blue and more purple, violet and eventually PAS-red in colour. In those gastric pits with a wide lumen, an intensely PAS-red coloured substance could sometimes be observed in the centre of the lumen, contrasting sharply with the dark purple colour of the apex of the epithelial cells lining the lumen. HID/AB caused the layer of material covering the luminal surface of the stomach and the apical region of the surface- and gastric pit epithelial cells to be stained grey-purple with a somewhat AB-blue haze (Fig. 2.7). Travelling from the surface to the bottom of the gastric pit, the grey-purple coloured area in the apex of the cells became smaller. The small stained area in the apex of the cells nearer the bottom of the gastric pits tended to be predominantly blue in colour.

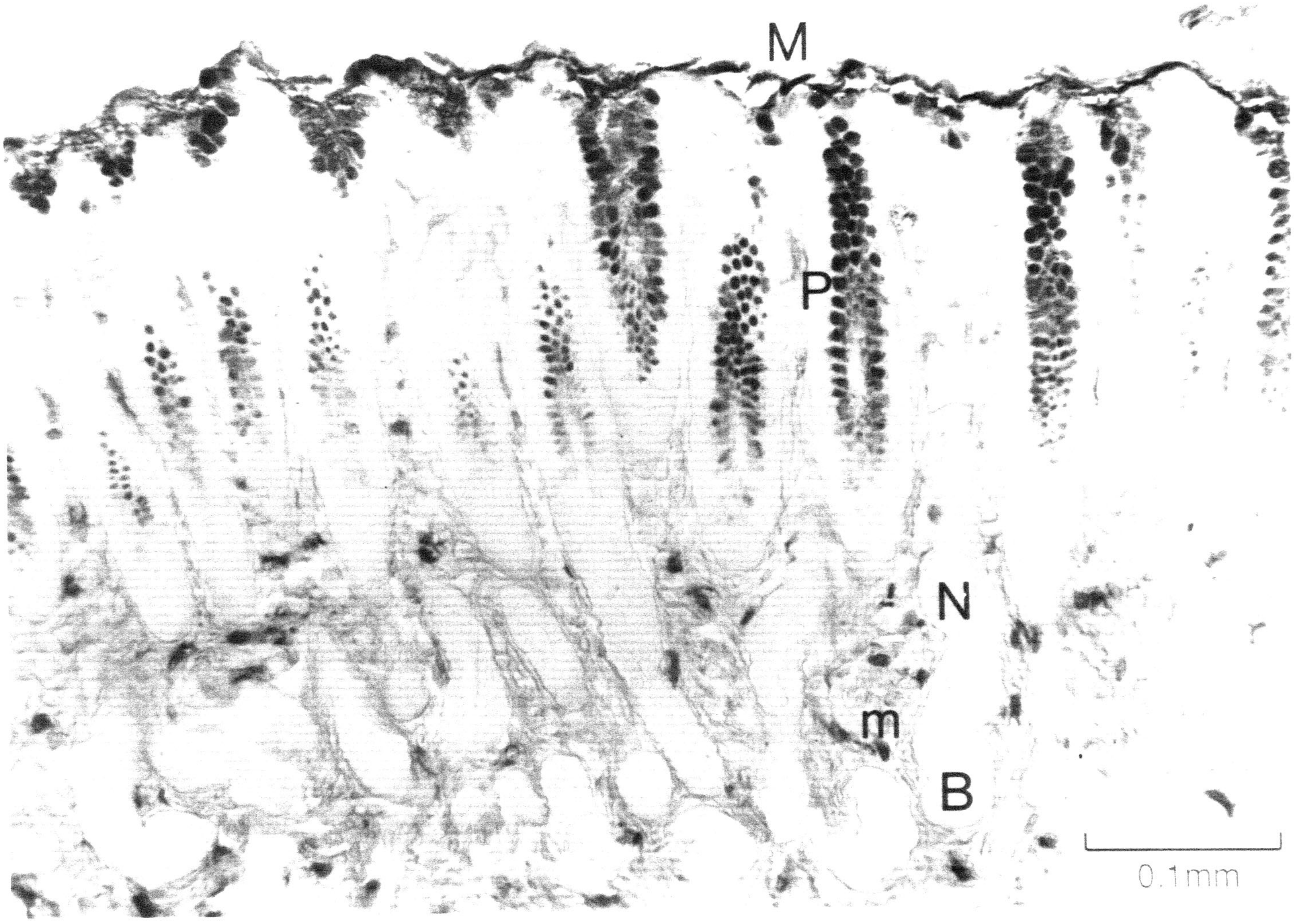

Fig. 2.7 Tunica mucosa of the cardiac gland region of the babirusa stomach. (HID/AB)

M: Fragments of adherent mucus gel
P: Gastric pit epithelial cells. Those closest to the stomach surface stained grey-purple with HID/AB (black on the photograph) whereas those deeper in the pits tended to be predominantly blue in colour (grey on the photograph).
N: Cells in the neck region of the cardiac glands which remained unstained with HID/AB.
B: Cells in the basal region of the cardiac glands which remained unstained with HID/AB.
m: Mastcell stained grey-purple with HID/AB (black on the photograph).

The cells of the neck and base of the glands, were cuboidal or somewhat columnar or pyramidal in shape with a large rounded nucleus positioned at their base. The cells remained completely unstained by AB but showed a PAS positive reaction in their apex, although the staining was much weaker than that in the surface and gastric pit epithelial cells. With AB/PAS only the latter PAS positive reaction was present in these cells (Fig. 2.5). No staining occurred in these cells with HID/AB (Fig. 2.6).

The remainder of the lamina propria mucosae, surrounding the cardiac glands, contained a great many lymphocytes. Both Alcian blue, Alcian blue/PAS and HID/AB stains indicated the presence of mast cells (coloured bright blue in the two former cases and purple-grey-black in the latter) which were especially numerous in the inner region of the lamina propria mucosae surrounding the bases of the cardiac glands. Smaller numbers were also present alongside the gastric pits and in the lamina muscularis mucosae and the tunica submucosa.

Gastric glands: Fig. 2.8

The lamina propria in this region was thicker than that of the cardiac and pyloric gland region. The gastric pits however were shorter than in the two latter regions extending only about 1/5 of the combined depth of the gastric pits and glands. The glands themselves were densely packed, were long straight tubular glands which were rarely branched and only showed coiling at their base. Gastric grooves and gastric fields were formed in the same way as in the cardiac gland region. The luminal stomach surface was covered in a single layer of tall columnar epithelium with nuclei positioned in the base of the cell. Travelling from the top of the gastric pits to their base, the epithelial cells became less tall. When stained with H&E/PAS, the surface and gastric pit epithelial cells reacted strongly PAS positive in their supranuclear region, leaving only a thin band of clear unstained material between the nucleus and the stained top of the cell. This PAS positive staining remained prominent throughout the gastric pit, from its surface to its base (Fig. 2.8).

In the neck region of the glands the parietal cells were most numerous but their numbers gradually decreased towards the base of the gland. At

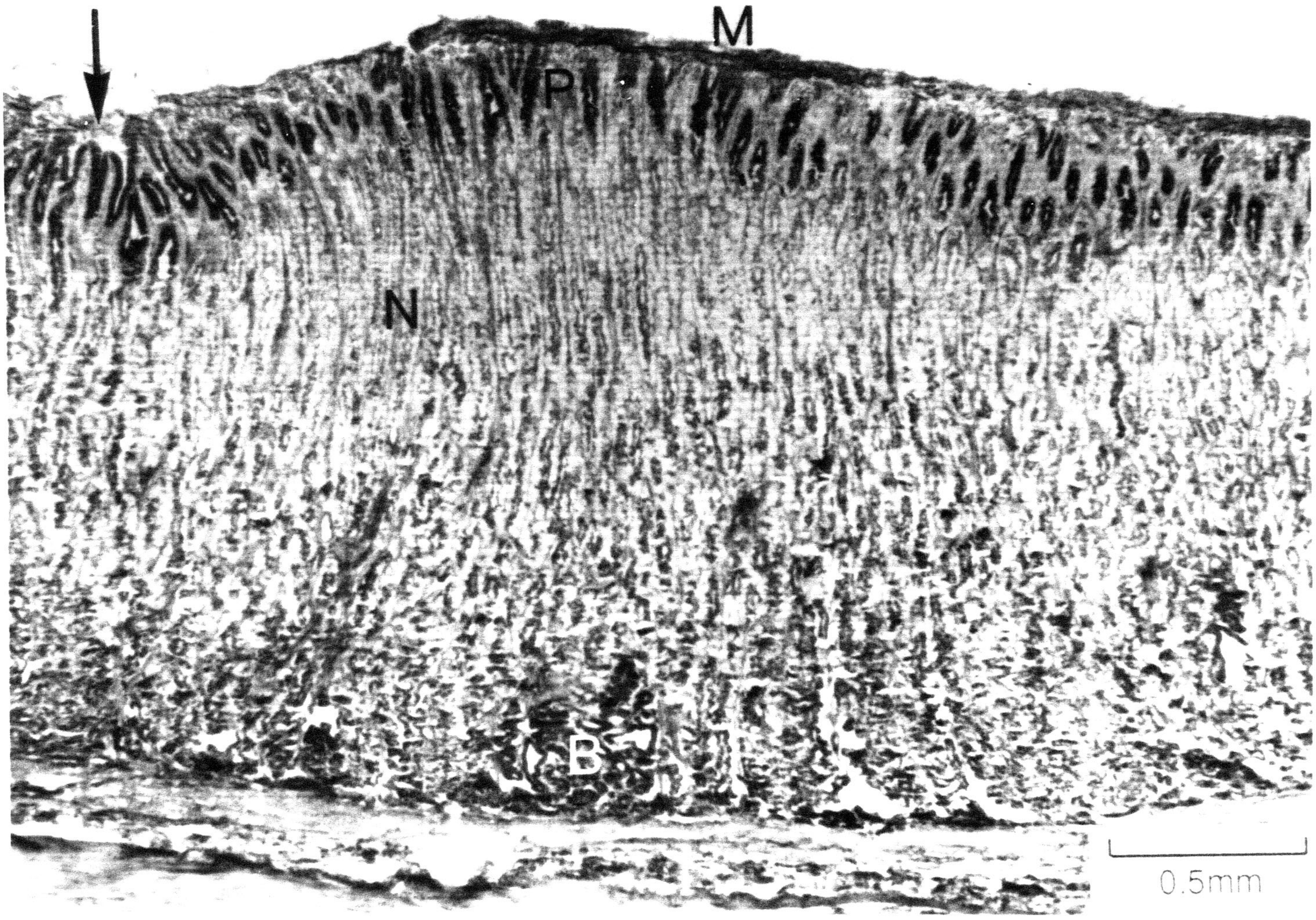

Fig. 2.8 Tunica mucosa of the gastric gland region of the babirusa stomach. (AB/PAS)

M: Fragments of adherent mucus gel.

P: Gastric pit epithelial cells which stained purple with AB/PAS and appear black on the photograph.

N: Mucous neck cells which stained light red with AB/PAS and appear grey on the photograph.

B: Mucous cells in the base of the glands which stained bright red with AB/PAS and appear black on the photograph. They sometimes occupied the entire base of the glands.

Arrow: Gastric groove.

the same time, the number of chief cells (zymogen cells) increased so that in the base of the glands the chief cells were most numerous. When stained with H&E/PAS, cells with a PAS positive supranuclear cytoplasm were present at several places along the entire length of the gland, from neck to base, surrounded with unstained chief and parietal cells. In some places these cells occupied almost the entire base of the gland (Fig. 2.8). When stained with AB only a few cells of the surface and gastric pit epithelium stained positively. None of the other cell types, except for the mast cells in the connective tissue reacted AB positive. With AB/PAS, the dark purple-blue colour could only be detected in a few cells of the surface and gastric pit epithelium. For the remainder, the reaction was as with PAS, except for the blue staining of the mast cells in the connective tissue. HID/AB caused a few cells of the surface and gastric pit epithelium to be stained blue and an even smaller number of cells in the same region to be stained purple-grey. The only other positive staining reaction with HID/AB was obtained in the mast cells which stained dark purple-grey.

Because of the much thicker stacking of the gastric glands compared to both the cardiac or pyloric glands, the amount of connective tissue of the lamina propria mucosae running up between the individual glands was much less. Somewhat thicker strands of connective tissue could be observed clumping several individual glands together but the lobules were not as pronounced as in the pyloric glands. The lymphocytes were much fewer in number the mast cells showed the same distribution as in the cardiac gland area.

Pyloric glands: Fig. 2.9

The lamina propria mucosae was thicker in the pyloric region than in the cardiac gland region but thinner than in the gastric gland region. The gastric pits in the pylorus were much longer than those of the cardiac glands or gastric glands. The pyloric glands themselves were short, tubular, branched and coiled at their base. At regular distances, several glands ended in a single depression on the surface of the lamina propria mucosae, the gastric grooves. Within the gastric fields, the pyloric glands were organised in distinct lobules; groups of pyloric glands separated

Fig. 2.9 Tunica mucosa of the pyloric gland region of the babirusa stomach. (AB/PAS)

M: Fragments of adherent mucus gel with necrotic epithelial cells.
P: Gastric pit epithelial cells which stained purple with AB/PAS and appear black on the photograph.
B: Basal region of the glands showing cells which stained purple with AB/PAS (*) and those which stained red with AB/PAS (+)
Lo: Lobule of pyloric glands surrounded by connective tissue.
Arrow: Gastric groove

from other groups by thicker strands of connective tissue running up from the base of the lamina propria mucosae. The shape of the surface and gastric pit epithelial cells, as well as the shape and orientation of the nucleus in the cells, was similar to those in the cardiac glands. As in the cardiac glands, the surface and gastric pit epithelial cells of the pylorus showed a PAS positive area in their apex. In contrast to the cardiac glands however, the stained area did not become smaller as the bottom of the gastric pit was reached, but stayed prominent throughout. All the pyloric gland cells reacted intensely PAS positive, often leaving no obvious unstained region around the nucleus but filling the entire top of the cell right up to the nucleus. When stained with AB, all surface- and gastric pit epithelial cells showed a positive reaction in those regions of their cells which were PAS positive. In the glands, AB cells occurred interspersed with cells coloured only faintly blue or completely unstained. When stained with AB/PAS, all the surface and gastric pit epithelial cells and some gland cells stained intensely purple-blue. Others only stained PAS positive after AB/PAS treatment (Fig. 2.9). With HID/AB all the surface- and gastric pit epithelial cells and some of the gland cells stained grey-purple. Most of the remaining gland cells stained AB-blue only and a few cells remained unstained.

Lymphocytes were present in the connective tissue of the lamina propria mucosae surrounding the pyloric glands but in smaller numbers than in the cardiac gland area. AB, AB/PAS and HID/AB stains indicated the presence of mast cells (coloured bright blue in the two former cases and purple-grey-black in the latter) which were mostly located in the basal region of the lamina propria mucosae, the lamina muscularis mucosae and the tunica submucosa.

The transition from the stratified squamous epithelium to the glandular epithelium was always abrupt whereas the transition from one glandular type to the other was always a gradual one. The transition of the cardiac glands into the gastric glands took place at the mucosal fold bordering the gastric unit in that region. The tunica mucosa became thicker and more and more parietal and chief cells appeared as the fold was traversed from the cardiac to the gastric side. The place of transition from gastric to pyloric glands was not as clearly visible macroscopically. Microscopically the transition was marked by an increase in the thickness of the tunica muscularis, a reduction in the thickness of the tunica mucosa, an increase in the gastric pit depth and a reduction in the number of parietal and chief cells until the glands were composed of pyloric gland cells only.

4. Discussion

In gross anatomical terms, the babirusa stomach differs from that of *Sus scrofa* mainly by its large fundus and diverticulum, the presence of a gastric unit at the distal end of the corpus and the enormous area covered by cardiac glands as opposed to gastric and pyloric glands.

The large fundus and diverticulum were remarked upon by Davis (1940) and Langer (1973a, 1988). However, the constriction on the greater curvature between these two stomach parts, which was said by Davis (1940) and Langer (1973a, 1978) to be externally visible, was not easy to identify on all stomachs. Depending on the degree of filling of the stomach, quite a number of folds and constrictions could be seen in this area. It was not always clear from the exterior which of these folds corresponded to the border between the two gastric regions. Inspection of the muscle layers and an internal investigation of the transverse fold forming the spiral at the entrance of the fundus (Langer, 1988) were needed to clarify the situation.

The percentages of stomach mucosal surface covered by the fundus and diverticulum found in the present study corresponded well with those reported by Langer (1973a) for an animal said to be an adult (fundus: 37%, diverticulum: 5.7%) and a ten-week old animal (fundus: 37.6%, diverticulum 5.0%). However, the absolute numbers of 299.1cm^2 for the fundus and 46.3cm^2 for the diverticulum which he reported for the adult stomach were very much smaller than those found in the present study (around 1000cm^2 for the fundus and 200cm^2 for the diverticulum in the adult animals). Shrinkage due to fixation could not account for such a large difference. Likewise, methodological dissimilarities between the studies in the way the mucosal surface areas were determined (external estimates (Langer, 1973a) versus mucosal surface area measurement (present study)) could not explain the scale of the differences found.

Investigations in the Berlin museum pointed out that one of the babirusa specimens carried a label indicating that its stomach and intestines had been removed for study by Langer. This particular specimen had a crown rump length of 46cm. The date of birth on the label was 16.11.01. The only other date provided by the label was 19.01.12. According to the time difference between the two dates on the label, just over ten years, the animal in question seemed to be an adult. However, it was not clear that the second date was necessarily the date of death of the animal (Macdonald, pers. comm.). Several adult animals of similar age were measured in Antwerp Zoo and were found to have body lengths of between 115 and 141cm. It is unlikely, therefore that the animal in Berlin museum could be as old as the subtraction of the two dates on the label suggested. It is likely that the animal was much younger, which would explain the smallness of the size of its stomach.

The relative sizes of the different stomach parts in the young animal were very similar to those in the adult animals except for the proportionately larger size of the diverticulum. It is not yet known whether this reflects changes in the relative proportions of the stomach parts from birth to adult size. The larger diverticulum might be of importance immunologically considering the large amount of solitary lymph nodules present in the diverticulum of pigs (Barthol, 1914; Roy, 1973).

A recent review of the available information on the stomach anatomy of wild pigs other than *Sus scrofa* indicated that they were very similar in their anatomy to that of the domestic pig (Macdonald, 1991). No comparable surface area measurements for fundus and diverticulum could be found but descriptions and drawings of the stomachs of the other wild pigs suggest that babirusa is the only member of the Suidae showing such an enlargement in fundus and diverticulum (Owen, 1851; Stewart, 1860; Flower, 1872; Garson, 1883; Langer, 1973a, 1988; Macdonald, 1991).

The confinement of the gastric glands to an easily recognisable unit at the end of the corpus was not described as such by either Vrolik (1849), Davis (1940) or Langer (1973a, 1988) which created doubt about the gross

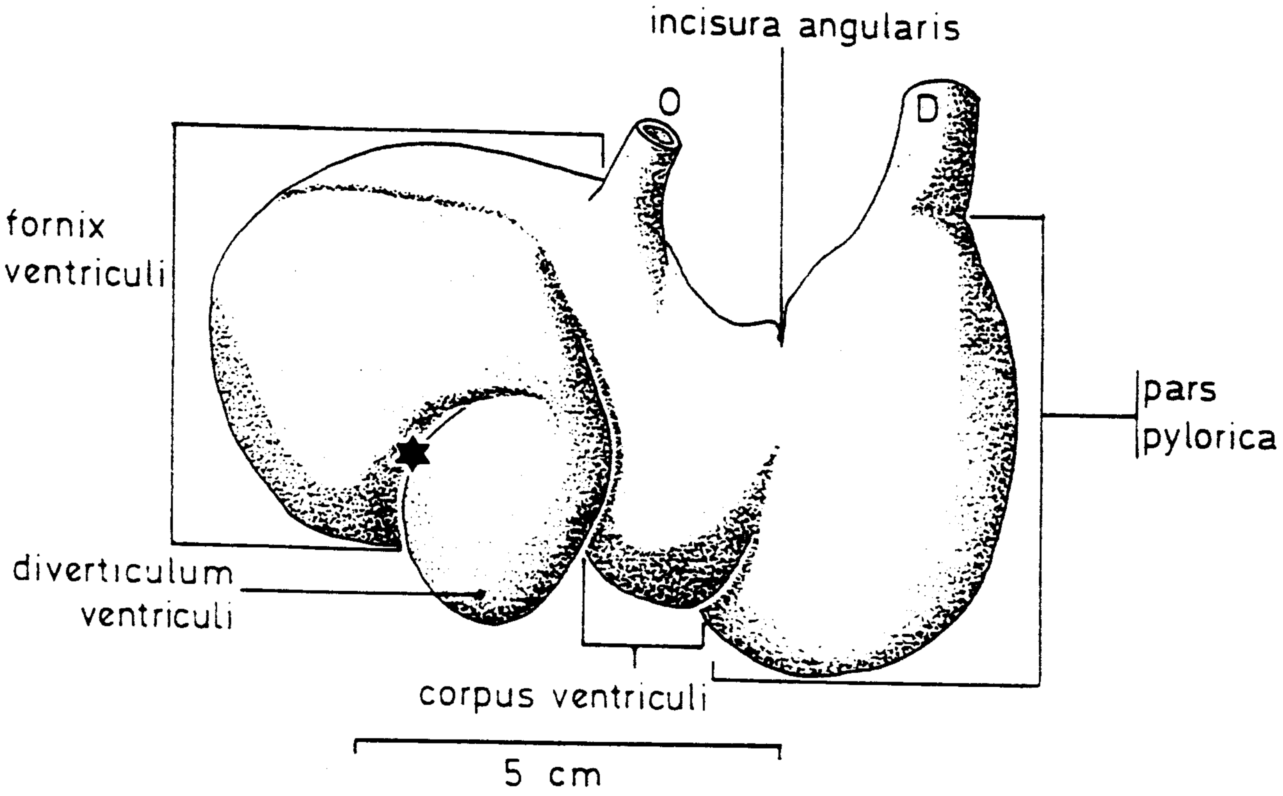

Fig. 2.10 Delineation of the different external gross anatomical regions in the babirusa stomach according to Langer (1988).

O: Oesophagus
D:Duodenum
*: Diverticulo-gastric groove

anatomical position of this gastric unit; was it part of the corpus or a portion of the pars pyloricus? Vrolik (1849), Davis (1940) and Langer (1973a) recognised an external constriction on the greater curvature which marked the distal end of the corpus on the greater curvature. Langer (1973a) indicated that this constriction was formed by the most distal fibrae obliquae internae. However, the figures illustrating the external stomach parts (Langer, 1988) and the layout of the muscle layers (Langer, 1973a, 1978) did not correspond to one another (Fig. 2.10 and Fig. 2.2a). In the first, the pars pyloricus was indicated in such a way that it included a large part of the fibrae obliquae internae of the corpus. Investigations of the muscle layers in the present study indicated that the gastric unit was fully included in the course of the internal oblique fibres of the corpus and was therefore part of that structure. The sometimes-apparent external constrictions demarcating the gastric unit did not correspond to internal muscular folds and were probably caused by the differences in thickness and composition of the stomach wall between the gastric unit, the remainder of the corpus and the pars pylorica.

Vrolik (1849) and Davis (1940) described the mucosal lining in the first part of the pars pylorica as having a reticulated appearance, whereas this was not recognised by Langer (1973a, 1988). It is possible that Vrolik and Davis referred to the surface structure of the gastric unit, which in the present study showed a thick tunica mucosae with well developed gastric fields and grooves. With a bit of imagination, these might possibly be described as having a honeycomb appearance. Davis (1940) also saw other resemblances between the babirusa stomach and that of a ruminant. By considering the reticulated part of the pars pylorica to be the equivalent of the reticulum, he conceived the idea that the end part of the pars pylorica formed the abomasum. The diverticulum, fundus and corpus were thus seen to be the equivalent to the various blindsacs of the rumen. The results of the present study indicated, however, that:

1) all the internal connections between the various stomach parts were very wide and that they could therefore not be regarded as separate chambers

2) the mucosal surface of the gastric unit of the babirusa was not comparable to the keratinised epithelium covered honeycomb folds of the reticulum in the ruminant and

3) apart from the small area of squamous epithelium around the opening of the oesophagus into the stomach, the entire internal lining of the stomach was of a glandular nature.

All of these factors are in agreement with Langer's opinion that the comparison of the babirusa stomach to a typical ruminant stomach was not justified (Langer, 1988). The typical ruminant stomach is multilocular with narrow connections between the different chambers; it has a reticulum with true primary folds formed by the lamina propria mucosae and the lamina muscularis mucosae in a honeycomb arrangement. Only the last chamber of the ruminant stomach, the abomasum, is of a glandular nature; the omasum, reticulum and rumen are covered by keratinised squamous epithelium (Cordier, 1894; Banks, 1986; Langer, 1988).

The distribution of the stratified squamous epithelium and the different gland types over the internal stomach surface as described in the current study corresponded largely with the drawings published by Langer (1973a, 1988). However, a combination of the diagrams Fig. 2.4 and Fig. 2.10 suggests that in the babirusa the gastric glands are completely incorporated within the pars pylorica. The results of the present study indicated that this was not the case; the gastric glands were confined to the gastric unit and were therefore part of the corpus ventriculi. Because of the less than optimal condition of the stomachs studied by Langer (1973a, 1978), he was unable to establish accurately the borders of the pyloric, gastric and cardiac glands at the height of the incisura angularis on the lesser curvature. Research material available to the present study enabled me to indicate that the gastric glands did not reach as far as the lesser curvature, but were separated from it by a narrow strip of cardiac glands. The pyloric glands did border on the stratified squamous epithelium of the lesser curvature.

Although the fundus and diverticulum of the babirusa were of a large size, it may be more important for an understanding of the function of the stomach to consider not just the area covered by the fundus, but the total area of the stomach covered with cardiac glands, which included most of the area of the corpus. For adult animals, the total area covered by fundus and diverticulum in unopened stomachs amounted to about 1000cm^2 (or about 34% of the total surface area) whereas that covered by the entire cardiac gland area comprised over 2000cm^2 (or about 77%). The area of stomach reported by Langer (1988) to be covered by cardiac glands amounted to 52cm^2 another indication that the absolute numbers were too small to represent the stomach of an adult animal.

This large area in the babirusa stomach covered by cardiac glands (about 77%) as opposed to gastric glands (about 12%) and pyloric glands (about 7%) is in sharp contrast with the situation in *Sus scrofa* where the cardiac glands occupy around 33% of the total glandular stomach area, the gastric glands 33% or somewhat more and the pyloric glands 33% or somewhat less (Greenwood, 1882; Haane, 1905; Barthol, 1914; Nickel et al., 1973; Langer, 1988). The area covered by stratified squamous epithelium in the babirusa was small (about 5%), and was similar to that in the domestic pig (6%) (Langer, 1988).

The general structure of the stratified squamous epithelium and the different gland types in the babirusa stomach as shown by light microscopy was very similar to that in *Sus scrofa* (Heidenhain, 1870; Greenwood, 1882; Brade, 1883; Ellenberger and Hofmeister, 1885; Oppel, 1896; Haane, 1905; Bensley, 1910; Barthol, 1914; Trautmann, 1926; Sloss, 1954; Schulz, 1962; Bal and Ghoshal, 1972; Georgieva and Gerov, 1975; Schwab, 1986). The available evidence indicated that the special nature of the babirusa stomach seemed to lie more with the different proportions of the glandular areas rather than with their individual structure.

The different staining methods for mucosubstances indicated the presence of mucus in the surface and gastric pit epithelium of the entire glandular stomach area, the cardiac glands, the pyloric glands and a number of cells throughout the length of the gastric glands of the babirusa stomach. The cardiac glands of the pig were first recognised and described by Greenwood (1882) who also reported the presence of mucous substance in the cells of these cardiac glands. There followed a discussion about the mucous character of these glands (Ellenberger and Hofmeister, 1885; Edelmann, 1889; Bensley, 1902; Haane,1905, Bensley, 1910; Barthol, 1914, Trautmann, 1926; Bensley, 1928) but more modern histochemical techniques, such as those employed in the present study, have confirmed the production of mucosubstances by the cardiac glands of the pig (Schulz, 1962) and several other mammals (Spicer, 1965; Sheahan and Jervis, 1976; Katsuyama and Spicer, 1978; Dougbag and Berg, 1980). The mucous character of the surface and gastric pit epithelial cells as well as the pyloric glands was established early (Greenwood, 1882; Brade, 1883; Ellenberger and Hofmeister, 1885; Bensley, 1902, 1910, 1928; Haane, 1905; Barthol, 1914, Trautmann, 1926) and has likewise been confirmed in recent times for the pig (Bal and Ghosnal, 1972; Georgieva and Gerov, 1975) and other mammals (Spicer, 1965; Sheahan and Jervis, 1976; Katsuyama and Spicer, 1978; Dougbag and Berg, 1981a, b; Suganuma et al., 1981; Asari, 1985; Ota et al., 1991). It was Bensley (1896, 1898) who first recognised two types of "chief cells" in the gastric glands the "neck chief cells" and "body chief cells", the first differing from the latter by their mucous nature. The production of mucosubstances by the mucous neck cells was also demonstrated by more modern techniques and it was found that mucous neck cells of gastric glands commonly stain PAS positive only (Spicer, 1965; Georgieva and Gerov, 1975; Sheahan and Jervis, 1976; Katsuyama and Spicer, 1978; Dougbag and Berg, 1981a; Suganuma et al., 1981; Asari, 1985; Ota et al., 1991).

In the babirusa, PAS positive cells were not confined to the neck of the gland but were present over the entire length of the gland from neck to base. Greenwood (1882), Bensley (1902, 1928) and Ito (1987) mention the possibility of the presence of mucous neck cells throughout the entire length of the gastric gland of the pig to the extent that some glands are only composed of mucous neck cells and parietal cells to the exclusion of chief cells. The PAS positive cells observed in the babirusa gastric glands are therefore likely to represent mucous neck cells as is the case in the domestic pig.

Studies on a variety of mammals indicated that there are large differences in the occurrence and distribution of neutral mucins, sialomucins and sulphomucins within the same gland type among different, and even closely related species (Spicer, 1965; Sheahan and Jervis, 1976; Suganuma, 1981; Asari et al., 1985). The scarcity of studies employing these histochemical techniques for the detection of neutralmucins, sialmucins and sulphomucins in the pig stomach was therefore surprising. Bal and Ghoshal (1972) and Georgieva and Gerov (1975) tested for neutral mucosubstances with the PAS technique in the pyloric and gastric glands respectively. The distribution of the neutral mucosubstances in these areas was the same as that observed in the babirusa stomach. The only other available study tested the cardiac glands of the pig for neutral mucosubstances with PAS and for acid mucosubstances with various techniques which differed from those used in the present study (Schulz, 1962). The results of this study were similar to the results for the babirusa in that only the epithelial cells contained a mixture of the mucosubstances whereas the cardiac gland cells themselves only produced neutral mucosubstances. No other information is available on the distribution of the three types of mucosubstances in each of the different gland types of the pig stomach. The babirusa therefore represents the first member of the Suidae in which a study of this kind has been carried out.

The special histological feature of the babirusa stomach was established to be the large area of cardiac glands. The histochemical methods used in this study indicated that the surface and gastric pit epithelial cells, as well as all the gland cells, produce mucus. The babirusa therefore has a very large stomach surface area where specifically different types of mucosubstances are produced. This naturally leads to questions about the function or functions of this large amount of mucus with respect to the digestive mechanisms of the babirusa.

The mucus present in the stomach can be said to occur in two forms; a water-insoluble mucus gel adhering to the surface of the mucosal lining, and a water soluble mucus which mixes with the gastric juice and the contents of the gastric lumen (Allen, 1989; Allen and Carroll, 1985). Most of the studies on the structure, function and composition of mucus in the stomach have so far concentrated on the mucus-gel adhering to the stomach surface, especially in the gastric gland region of the stomach (Allen and Garner, 1980, Allen, et al., 1982; Rees and Turnberg, 1982; Allen et al., 1986; Allen et al., 1987; Allen, 1989; Crampton, 1988). The function most frequently ascribed to the adherent mucus gel is that of protection against the endogenous secretions of acid and pepsin (Allen and Garner, 1980; Allen et al., 1982; Rees and Turnberg, 1982; Allen et al., 1986; Allen et al., 1987; Crampton, 1988). The mucus gel provides a stable, unstirred layer which prevents the HCO_3^- secreted by the epithelial cells from dispersing quickly into the lumen where a large amount of acid is present. Thus, the H^+ ions are being neutralised as they diffuse into the mucous gel. A pH gradient is established across the mucus layer so that the epithelial cells always have an almost pH-neutral environment. At the same time, the mucus gel provides a diffusion barrier against the high molecular weight pepsin molecules so that the secretion of mucus by the epithelial cells stays in balance with the mucolysis by pepsin on the outer border of the gel. This protective role of the mucus gel is likely to be of special importance in those regions of the babirusa stomach which are in direct contact with acid and pepsin activity i.e. the gastric and pyloric gland area and that area of the corpus which borders on the gastric unit.

Studies on other tissues and species (e.g. the small intestine of the mouse (*Mus musculus*) (Rozee et al., 1982) have indicated that an adherent mucus gel often forms the equivalent of a biofilm with an autochthonous bacterial population on the luminal surface of the organ (Allen, 1989; Costerton et al., 1987). The presence of micro-organisms in the stomach of the pig is well known (Smith and Jones, 1963; Fuller et al., 1978; Kidder and Manners, 1978; Stewart and Chesson, 1993). Nevertheless, the only study concerned with the detection of micro-organism on the surface of the pig stomach concentrated solely on the squamous epithelial region (Fuller et al., 1978). The study of this particular region was probably encouraged by the detection of microbial populations attached to the glycocalyx of the squamous epithelium of the rumen (McCowan et al., 1978).

Micro-organisms inhabiting the mucus gel of the stomach surface have been ascribed several functions including the provision of an ecological barrier against external bacterial pathogens and the digestion of dead epithelial cells (Costerton et al., 1987). The most frequently discussed function, however, is the digestion of plant components which can not be digested by the enzymes produced by the host itself. The physiology of bacterial fermentation has been most extensively studied in the ruminant (e.g. Moir 1965, 1968; McDonald et al., 1981). Bacterial fermentation involves the breakdown of plant structural polysaccharides by means of bacterial enzymes which cannot be produced by the host itself. The fermentation products are mostly volatile fatty acids, bacterial protein, vitamins and gases. Volatile fatty acids are absorbed into the bloodstream through the gastrointestinal lining and form an important energy source for the host animal. The gastrointestinal bacteria are not able to absorb most amino acids and are dependant on ammonia as their nitrogen source. For this purpose, urea created during the degradation of protein is not excreted in the urine but is largely recycled. Urea is transported in the blood to the rumen and flows into the rumen along a gradient where it gets converted to ammonia which can be utilised by the bacteria.

Organisms at the surface of the stomach are likely to assist in the digestion of ingested material since the peristaltic movements of the stomach provide a ready supply of fresh food (Costerton et al., 1987; McCowan, 1978). Micro-organisms attached to the rumen epithelium are also known to consume the oxygen that would otherwise diffuse into the rumen from the tissues, thereby providing the necessary environment for the obligate anaerobic bacteria in the lumen of the stomach (Costerton et al., 1987). They have also been shown to produce urease, the enzyme that converts urea into ammonia, which cannot be produced by the stomach's epithelial cells (Costerton et al., 1987).

Most of the mucus gel lining the stomach tends to disappear with routine fixation methods such as those used in the present study (Rozee et al., 1982; Ota and Katsuyama, 1992). However, a number of stomach samples from animal 0048, which were rapidly preserved in Bouin's fixative, did retain fragments of the surface mucus-gel. When coloured with Gram stain, a dense population of Gram positive bacteria could be seen in the mucus-gel adhering to the surface of the cardiac gland area. A considerable number were also present in the gel of the gastric gland area but the numbers seemed to be fewer in the area of pyloric glands. Only a few micro-organisms could be seen on the surface of the stratified squamous epithelium. Further studies are needed to identify the species of the micro-organisms in the different stomach regions and to estimate their number.

Additional preliminary observations on both untreated and sugar-enriched gastric fluids from another babirusa (animal 0012) confirmed the presence of numerous Gram positive bacteria in the lumen of the fundus and proximal corpus. Micro-organisms were also present in the distal part of the corpus and in the pylorus but again seemed to be much fewer in number. No protozoa were observed. Because of the relatively long time span between sampling and processing, and the aerobic conditions employed, the quantification and identification of the micro-organisms was not attempted as it was unlikely to yield data representative of the situation in the living animal. Nevertheless, these preliminary observations confirm the presence of micro-organisms adhering to the mucus-gel and inhabiting the fluid in the lumen of the babirusa stomach.

It is likely that these organisms engaged in microbial fermentation. Microbial fermentation in enlarged stomach areas is generally associated with the ruminants. Babirusa have never been observed to ruminate, but forestomach fermentation is certainly not limited to the group of ruminantia. Six criteria for ruminant-like digestion have been proposed (Moir 1965; Langer, 1975, 1979):

1. Gastric chambers to store the digesta and slow down its rate of passage through the stomach.
2. Micro-organisms to help to digest food.
3. Microbial fermentation products which are absorbed through the stomach wall.
4. The host makes use of the vitamins produced by the microbes.
5. With the help of microbes, non protein nitrogen can be used by the host.
6. In the young animal an effective ventricular sulcus is necessary.

The applicability of these criteria to the situation in the babirusa is discussed below.

Although the babirusa has an enlarged cardiac gland area (>70% of the total stomach surface area), the internal connection between this area and the gastric unit remains very wide. Many animals with a ruminant-like digestion show a system of folds and/or blindsacs in the stomach which help to slow down the passage of digesta and increase time available for fermentation. This is well illustrated by the two closest family relatives of the pigs, the peccaries (Tayassuidae) and the hippos (Hippopotamidae). The stomach of the peccary is characterised by two blindsacs emptying into a central gastric pouch (not to be confused with the gastric unit in the babirusa) via a blindsac junction (Cuvier, 1835; Edelmann, 1889; Pernkopf and Lehner, 1939; Langer, 1973a, 1978, 1979). The blindsacs together with the gastric pouch form the forestomach which then empties into the glandular stomach. The basal region of the gastric pouch and some areas of the blindsacs are covered with cardiac glands whereas the remaining regions in the structures are covered with stratified squamous epithelium. In the hippopotamus, the forestomach is composed of two blindsacs and a connecting chamber and is covered with squamous epithelium of a villous nature. The connecting chamber possesses a very characteristic series of transverse folds, the function of which is believed to be to slow down the rate of passage of food (Thurston et al., 1968; Langer, 1973a, 1975,1976, 1988; Macdonald and Hartman, 1983). In the babirusa, a shallow spiral fold was found at the entrance of the fundus ventriculi, but this did not really compartmentalise the stomach. However, as in the colobine monkeys (subfamily Colobinae), the size of the gastric gland area may be sufficient to permit enough separation of the ingested food in the proximal region of the fundus and corpus from the acid and pepsin produced in the gastric unit (Bauchop and Martucci, 1968; Bauchop, 1978). It may thus allow the food to be present in a mucous and micro-organism rich environment for sufficiently long to allow microbial fermentation to take place (Bauchop, 1968, 1978).

Even if the rate of passage of ingesta in the babirusa was slowed down, it is unlikely to be slow enough to allow as thorough a degradation of tough plant cell wall components of grasses to take place as has been seen in the hippopotamus (*Hippopotamus amphibius*) (Arman and Field, 1973) or in grazing ruminants (Hofmann, 1989). This suggests that the babirusa is more likely to be specialised in the fermentation of cell contents rather than cell wall components. Grasses are known to have greater amounts of cell wall components and lesser amounts of cell solubles compared to fruits or browse (mostly parts of dicotyledonous plants such as tree leaves, flowers and many herbs) (Bodmer, 1990). Non-ruminant fermentation is a prominent feature among frugivores and intermediate frugivore/

browsers (Hofmann, 1989; Bodmer, 1990). Even among frugivore or frugivore/ browser ruminants, the rumen is less extensively developed than that of a grazing ruminant. It has a smaller capacity, has fewer subdivisions and has larger openings between compartments, and thereby permits a faster passage of digesta (Hofmann, 1989). Both frugivore and frugivore/ browser ruminants and non-ruminants have shown the ability to select those plant types and plant parts which are relatively high in cell solubles and low in cell wall components (Kiltie, 1981; Sauer, 1983a, b; Owen-Smith and Cooper, 1983, 1989; Dubost, 1984; Pellew, 1984; Cooper et al., 1988; Hofmann, 1989; Dubost, 1990; Dasilva, 1992). For this reason Hofmann (1989) suggested the replacement of the term "browsers" with the more accurate term "concentrate selectors". The structure of the babirusa stomach suggests that the babirusa may be categorised as a non-ruminant forestomach fermenting frugivore or frugivore/ concentrate selector. Fermentation may be very important for the breakdown of the relatively small amounts of cell wall components, especially mechanical fruit protection mechanisms such as protective peels and coverings, and for the detoxification of chemical plant protection mechanisms such as toxins (Bodmer, 1990).

However, there are certain conditions that must be met in order for micro-organisms to survive and function optimally. One of these is the presence of a relatively stable, near-neutral pH in that part of the stomach where fermentation occurs. On one occasion (animal 0004) the pH in the stomach lumen was measured with a pH meter 90 min. after death (and 3 hours after feeding). The results were as follows: diverticulum pH=6.4, fundus pH=5.6, corpus pH=5.3, gastric unit pH=3.7, pars pylorica pH=4.4, duodenum pH=7.2. The highest acidity occurred in the gastric unit and the pars pyloricus, whereas the pH in the cardiac gland region ranged from 5.3 to 6.4. Animals provided with enlarged stomachs with a small area of squamous epithelium but a very large area of cardiac glands include Colobinae leaf-eating monkeys and the macropod marsupials (Macropodidae) (Moir, 1968; Bauchop, 1978; Langer, 1980, 1988; Chivers and Hladik, 1980). The pH in the cardiac gland areas of these stomachs was in the range of 5 to 7 which fits well with the values obtained in the stomach of the babirusa. For both of these other groups of animals extensive studies have indicated the presence of gastric micro-organisms and microbial fermentation (Moir, 1965, 1968; Bauchop and Martucci, 1968; Bauchop, 1978).

Luminal stomach mucus is also thought to perform a buffering function (Moir, 1968; Vallenas et al., 1971). Microbial fermentation results in the production of volatile fatty acids (VFA) which then diffuse out of the lumen through the wall of the stomach to be utilised by the host. It was suggested that the mucus buffers the acidity resulting from the VFA so that the luminal pH is kept near neutral at all times; this is essential for the survival of the microflora.

Other conditions that need to be met are the anaerobic nature of the stomach lumen and the conversion of urea into ammonia. It is not yet known whether the micro-organisms in the mucus-gel adhering to the stomach surface of the babirusa are able to provide conditions comparable to those created by the micro-organisms adherent to the squamous epithelium of the rumen wall.

No information is as yet available on the presence, amounts and proportions of VFA produced in the babirusa stomach. The production of VFA as a product of fermentation and the absorption of these substances through the wall of the non-ruminating stomach has been measured for the peccaries and hippos (Langer, 1978, 1979; Thurston et al., 1968; Lochmiller, 1989). However, not only can VFA be transported efficiently across non-glandular stratified epithelium but it can also cross cardiac gland epithelium, as has been measured in the domestic pig (Argenzio and Southworth, 1974; Clemens et al., 1975), Colobinae leaf-eating monkeys (Bauchop, 1968, 1978), macropod marsupials (Moir, 1965, 1968) and camels (Camelidae) (Vallenas and Stevens, 1971; Vallenas et al., 1971). There appears, therefore, to be no structural reason why VFA, if produced in the stomach of the babirusa, would not be able to be absorbed through the mucosa of the cardiac gland area into the blood stream.

No information is as yet available to answer the last three criteria for ruminant-like digestion. It is not known whether the babirusa utilise microbial vitamins, whether the ability for non-protein utilisation by stomach micro-organisms stimulates urea recycling and makes the babirusa less dependant on good quality protein in the diet, and whether the sulcus ventriculi, which has a similar shape to that of the other pigs is more functional as a gastric groove in the babirusa than in the other pigs.

In conclusion it can be said that the presence of an enlarged cardiac gland area in the stomach, the presence of micro-organisms in the mucus gel adherent to the stomach surface as well as in the lumen of the stomach and the suitability of the pH environment within the cardiac gland area for the survival and reproduction of micro-organisms strongly suggest that non-ruminant fermentation of food stuffs is likely to take place in the babirusa. Since the stomach anatomy did not show any features that would prolong the retention time of food stuffs, it is likely that the babirusa will be specialised in the fermentation of more digestible food components such as plant solubles. These characteristics fit well with those defined for the class of herbivores called frugivore/ concentrate selectors which, as the name indicates, tend to select more easily digestible food items which are then fermented in the stomach. This hypothesis will be tested in the next two chapters by comparing the digestion of different fibre fractions as well as dry matter and organic matter between babirusa and *Sus scrofa* and by allowing babirusa to forage and select food items in a semi natural enclosure.

5. Conclusions

In addition to the large size of the babirusa stomach, the most important functional difference between it and those of the other pigs was the very large area covered by cardiac glands (more than 70% of the total stomach surface area compared to about 33% in the domestic pig (*Sus scrofa*)). The cardiac glands were shown to produce mucus. Micro-organisms were present in both the mucus gel adhering to the stomach and within the lumen of the stomach: the pH in the stomach lumen was suitable for the survival of micro-organisms. From these results it was hypothesised that the babirusa was a non-ruminant foregut fermenter specialised in the fermentation of plant solubles and more easily digestible fibres. Gastric glands were confined to a small, easily identifiable region occupying the distal end of the corpus ventriculi which was named the "gastric unit".

CHAPTER 3: COMPARATIVE DIGESTION OF DRY MATTER, FIBRE AND ORGANIC MATTER BY BABIRUSA AND *Sus scrofa.*

1. Introduction

The large area of cardiac glands in the stomach of the babirusa (about 70-80% of the total stomach area compared to only about 33% in the domestic pig), together with the presence of micro-organisms in the surface mucus gel and stomach lumen suggested that the babirusa was a foregut fermenter. The structure of the stomach was such that it was unlikely to create a large delay in the passage of digesta and appeared to indicate that it might be more specialised in the fermentation of easily digestible food components rather than fibre. In the improved domestic pig breeds such as the Large White x Landrace it has been shown that most fermentation of cellulose and hemicellulose occurs in the large intestine with little fermentation in the stomach (Keys and DeBarthe, 1974). Recent studies with Chinese Meishan pigs (an unimproved Asian pig breed) demonstrated that when given the same diet, these pigs tended to have a larger gutfill and a heavier large intestine than the European breeds (especially when given fibre) (Fevrier et al., 1988; Kyriazakis et al., 1993). They also digested all nutrients (including fibre and energy) more efficiently than the European breeds and especially so with respect to the more fibrous foods (Fevrier et al., 1988; Kemp et al., 1991). These observations suggest that the Chinese Meishan are more efficient caeco-colic fermenters than the European pig breeds.

The three pig types used in this study therefore represented three potentially different digestive mechanisms. If fermentation in the babirusa stomach is more important than caeco-colic fermentation then we can expect this species to demonstrate a higher digestibility of dry matter and organic matter than the two domestic pig breeds but a lower digestibility of the more difficult to digest fibre fractions. In a similar fashion, if CM are more efficient caeco-colic fermenters than the LW and the babirusa, and if most of the cellulose digestion occurs in the large intestine then we can expect the CM to have higher digestibilies for the more difficult to digest fibre fractions than the other two pigs.

This study was designed to compare the digestibility of different fibre fractions as well as dry matter and organic matter by these three types of pig, based on the understanding that they may differ from one another in the proportion of fermentation occurring in the stomach and caecum and colon.

2. Materials and methods

Animals and housing

Two species of pig were used for this study, *Babyrousa babyrussa,* the babirusa and *Sus scrofa,* the domestic pig. All babirusa used in this study were housed at Antwerp Zoo, Belgium. The age and sex of the animals used can be found in Table 3.1. It was not possible to weigh the animals throughout the experiment. Some of the younger animals had however been weighed shortly before the start of the experiment and these weights are indicated in Table 3.1. The starting weight of the other young animals and adult animals was estimated from previous weighings.

Table 3.1. Identification, sex, age and weight of the babirusa used for the dried grass fibre digestibility study. (studbook numbers according to Plasa (1993)) (??= animal of unknown age when it arrived in Europe from Indonesia)

Animal number	Sex	Age (years)	Weight
0047	Male	?? >8	95-100kg estimated
0049	Male	?? >8	95-100kg estimated
0155	Male	1	31kg
0048	Female	?? >8	66kg
0050	Female	?? >8	56kg estimated
0143	Female	2	48kg estimated
0139	Female	2	48kg
0158	Female	1	32kg estimated

Each babirusa had access to an individual indoor enclosure of approximately 2 by 3m with a concrete floor and straw for bedding, and an individual sand-filled outdoor enclosure of variable size without vegetation. More details about the housing and normal daily management of the babirusa in this institution can be found in Leus et al. (1992). Animals 0047 and 0049 always completely ate their meal immediately after it was offered and the pellets could therefore be offered to them on the concrete floor of their indoor enclosure. All other babirusa were provided with a metal food-bowl in their indoor enclosure. Every enclosure contained an automatic drink nipple to provide free and continuous access to water.

The species *Sus scrofa* was represented by two different breeds of domestic pig, one improved breed (F1 hybrid Large White x Landrace pigs = LW) and one unimproved breed (purebred Chinese Meishan = CM). Eight female LW pigs were obtained from the Edinburgh School of Agriculture pig herd and eight female CM pigs from the Cotswold Pig Development Company Ltd (Lincoln, UK). Pigs of both breeds were of similar age and were fed *ad libitum* on a high quality commercial pig food (Ultra wean meal and Ultra lean meal, Dalgety Agriculture) after weaning. At a live weight of 44.6±2.7kg and 43.6±1.9kg for LW and CM respectively, the pigs were moved into a metabolism unit. The unit contained sixteen pens of approximately 2 by 2m with a perforated floor surface raised 0.5 m above the ground. The floor surface retained the faeces but drained away the urine. Each pen was provided with its own food trough and automatic drink nipple so that animals always had free and continuous access to water. LW and CM were allocated to alternate pens in order to avoid an effect of place.

Foods

According to the experimental treatment, animals were fed a fixed amount of a basal diet in the form of pellets with the addition of a certain amount of dried grass as the fibre component, also in the form of pellets. The basal diet was composed of 4/5 barley and 1/5 soya bean meal with addition of the necessary vitamins and minerals (Table 3.2). Dried grass was chosen as the fibre component. Grasses are characterised by a high proportion of cell wall compared to cell solubles and contain fibres which are difficult to digest (Bodmer, 1990). The inclusion of dried grass as the fibre source was therefore thought to both allow the CM to express their potentially higher capacity in digesting grass fibre and allow the babirusa to express their higher capacity in digesting the dry matter and organic matter fractions in the diet and their lower capacity in the digestion of grass fibre.

Table 3.2. Composition and chemical analyses of basal diet and dried grass (g/kg fresh weight).

	basal diet	dried grass
Ingredients:		
Barley	793	0
Soya bean meal	180	0
Mineral and vitamin mix	20	0
Wafolin	5	0
Chromic oxide (Cr_2O_3)	2	0
Dried grass	0	1000
Components:		
Dry matter (DM)	890.00	900.16
Ash	45.97	85.49
Organic Matter (OM)*	843.99	816.13
Neutral Detergent Fibre (NDF)	134.66	396.70
Acid Detergent Fibre (ADF)	57.14	207.37
Chromic oxide	1.20	0.00

* OM = DM - Ash

Because it was not possible to collect all the faeces of the babirusa during the faeces collection period (animals always had access to the outdoor enclosures and therefore only faeces produced inside but not contaminated with straw, or produced outside but not contaminated with sand could be collected) it was decided to use the chromic oxide (Cr_2O_3) indicator ratio technique for the determination of digestibilities according to Kotb and Luckey (1972). Using this indicator, the total amount of faeces produced could be determined from the equation:

daily dose Cr_2O_3 (g) / concentration of Cr_2O_3 in faeces (g/kg DM) = faeces (kg DM) produced per day.

Design

The study with the babirusa was carried out from mid-July to mid-October 1992 and was followed by the study with the LW and CM from late-October 1992 to late-January 1993. Each study consisted of three 4-week periods. During the first period animals were fed a fixed amount of basal diet aimed to be just above the maintenance requirements of the animals to ensure that the appetite of the animals would always be large enough to consume all the food offered to them. During periods 2 and 3 this basal diet was supplemented with a certain fixed amount of dried grass. Within each period, the diet was fed to the pigs for three weeks without collection of the faeces to ensure that all traces of the previous diet had disappeared from the digestive tract and to allow the pigs to get used to the diet fed and stabilise their intake. During the fourth and final week of each period, daily faecal samples were collected.

Since the babirusa used for the study were of different sex and ages, the amount of basal diet offered needed to be adjusted according to the individual. The amounts of the basal diet offered to and eaten by the individual babirusa can be found in Table 3.3. During period 1, the babirusa ate all or nearly all the food that was offered to them. When the same amount of basal food was offered in the beginning of period 2 together with 200g grass, animals 0155, 0139, 0050, 0048 and 0143 ate less of the basal diet and selected against the grass pellets which were left. For all babirusa, except the adult males 0047 and 0049, the amounts of basal diet fed to the animals had to be reduced during the second period to ensure that all the food offered to them would be eaten. Babirusa 0155, 0048, 0050 and 0143 also selected the basal diet pellets and left the grass pellets. For this reason, the pellets had to be ground and the food fed as a meal so that the animals could not select against the grass pellets. This method of grinding the food was started well before the onset of the faeces collection period. As is clear from Table 3.3 the animals did not always consume all the food offered to them. It was the mean amount of basal diet and dried grass consumed per animal during the faeces collection week that was used for the further calculations of digestibility coefficients.

Table 3.3 Mean intake (mean (g/day) ± stan. dev.) of basal diet and dried grass by the babirusa during the faecal collection periods.

Animal	Period 1		Period 2				Period 3			
	basal offered	basal eaten	basal offered	basal eaten	grass offered	grass eaten	basal offered	basal eaten	grass offered	grass eaten
0047	1200	1200±0	1200	1200± 0	200	200± 0	1200	1200± 0	300	300± 0
0049	1200	1200±0	1200	1200± 0	200	200± 0	1200	1200± 0	300	300± 0
0155	850	850±0	700	681±24	200	166±38	700	636±29	300	232±31
0158	850	850±0	700	700± 0	200	200± 0	700	700± 0	300	300± 0
0139	700	700±0	450	450± 0	200	200± 0	450	425±17	300	258±30
0050	700	697±6	400	305±75	200	101±76	400	302±35	300	163±41
0048	700	694±7	450	426±12	200	176±15	450	281±40	300	97±60
0143	700	700±0	500	496±107	200	133±47	500	388±31	300	120±15

Originally, it was intended to feed all animals 200g grass during period 2 and 400g during period 3. Because of the babirusa's reluctance to eat the dried grass, however, it was decided to offer only 300g to the babirusa in period 3 and 150g and 300g to the LW and CM in periods 2 and 3 respectively. The LW and CM pigs received 1200g of the basal diet for the first 18 days of the first period. Another knock-on effect of the babirusa's reluctance to consume grass was that the amount of basal food fed to them after the first period had to be reduced. As a consequence it was decided to lower the intake of the LW to 950g for the remainder of the study. The animals continued to put on weight which indicated that the ration was still slightly above their requirements for maintenance. During period 2, LW and CM received 950g of basal diet pellets mixed with 150 g of dried grass pellets. During period 3 the same amount of basal diet was fed, mixed with 300g of dried grass pellets. All CM and LW pigs (with the exception of one CM animal) ate all the food offered to them.

Management

The pigs were fed twice per day, once in the morning and once in the evening, equal proportions being fed each time. Every morning the refusals (from the babirusa and the one CM) were collected and weighed. During the fourth and final week of each period, faecal samples were collected twice a day, once in the morning and once in the evening. All the faecal samples from each pig during a certain period were pooled and frozen. At the end of the period, the faeces were thawed, thoroughly mixed and a representative sample was dried at 60°C. This dried sample was then used for chemical analyses. During each faeces collection week, daily samples of the food were also collected and dried at 60°C. Later, equal amounts of each dried, daily food sample representing a certain pig type and experimental period were pooled and mixed. It was this sample that was used for chemical analyses. Chemical analyses of the food showed that the variations in the composition between the foods offered during different periods and to different pig species were very small and the use of pooled food samples was therefore justified. Food refused by the pigs during the faeces collection week were collected daily, weighed and dried at 60°C.

Chemical analyses

All food and faecal samples were dried at 60°C to constant weight, put in a desiccator and weighed for the determination of the dry matter (DM) content. These dried samples were then used for further analyses. Food and faecal samples were analysed for Neutral Detergent Fibre (NDF), Acid Detergent Fibre (ADF) and Ash. Determination of the Ash content was carried out by igniting the samples in a furnace at 500°C overnight after which the residue was put in a desiccator and weighed. The organic matter (OM) of food and faeces was determined by: DM - Ash = OM. The NDF analyses was carried out according to the method of Robertson and Van Soest (1977) including a treatment of the sample with a heat stable α-amylase (ex. *Bacillus subtilis*). ADF analysis was carried out according to the method by Goering and Van Soest (1970), however the analysis was not carried out in sequence with the NDF analyses but directly from the dried sample. The NDF method extracts the soluble substances from the plant cell walls, and starch residues are digested with α-amylase. The NDF residue therefore consists mostly of hemicellulose, cellulose and lignin (Goering and Van Soest, 1970; Robertson and Van Soest, 1977). With the ADF method, hemicellulose is also extracted so that mostly cellulose and lignin alone remain in the residue (Goering and Van Soest, 1970; Van Soest, 1985; Stanogias and Pearce, 1985). Therefore, the hemicellulose content = NDF - ADF. Because the food offered to some babirusa had to be presented as a meal rather than in the form of pellets, it was not possible to immediately weigh the proportion of basal diet and grass in these refusals. However, since the ADF content of the basal diet and the dried grass was very different, the proportion of basal diet and dried grass in the refusals could be calculated from the ADF content of the refusals.

The concentration of Cr_2O_3 in the faeces and food was determined by means of an S.P. 90 atomic absorptiometer. After calculation of the total amount of faeces produced per pig per day from the concentration of Cr_2O_3 detected in the faeces, the daily amount of DM, NDF, ADF and OM excreted per day could be determined. The digestibility coefficients of DM, NDF, ADF and OM in the total diet were then calculated by:

(amount consumed - amount excreted) / amount consumed = digestibility coefficient

The total amount of DM, NDF, ADF and OM excreted in the faeces from grass alone was determined by subtracting the amount of DM, NDF, ADF and OM excreted in the faeces during period 1 from the total amount of DM, NDF, ADF and OM excreted during periods 2 or 3 after adjusting for differences in intake between the periods. The digestibility coefficients were then calculated in the same fashion as above.

Statistical analyses

The results were analysed by analyses of variance with pig type and period as variates. During periods 2 and 3, one babirusa (0143) had access to horse-chestnuts which had fallen into her enclosure from a nearby tree and its results from these periods therefore had to be excluded. Its data were treated as missing values.

3. Results

Digestibility of the total diet (basal diet + dried grass) (Table 3.4)

For both DM and OM there was a significant effect of breed as well as period whereas the interaction between breed and period was non-significant. For all periods, the digestibility of DM for the babirusa was not significantly different from that for the LW. The digestibility of DM for the babirusa was, however, less than that of the CM during periods 1 and 2 ($p<0.01$ and $p<0.05$ for period 1 and 2 respectively) but not during period 3. The digestibility of OM for babirusa was significantly higher than that for LW in period 1 ($p<0.05$) and that for CM in period 3 ($p<0.05$) and just failed to be significantly different from LW in period 3 ($p=0.062$). The same trend could be found between babirusa and CM in period 1 and between babirusa and LW and CM in period 2, but this was not significant.

Table 3.4 Digestibility coefficients of different components of the total diet (=basal diet+dried grass) for LW, CM and babirusa (BA).

Period	Pig type	Component			
		DM	OM	NDF	ADF
1	LW	0.7781	0.8014	0.2938	0.0763
	CM	0.7911	0.8109	0.2906	0.1068
	BA	0.7619	0.8237	0.3357	0.1068
2	LW	0.7834	0.8039	0.4655	0.4040
	CM	0.7987	0.8154	0.4768	0.4148
	BA	0.7705	0.8185	0.5106	0.3865
3	LW	0.7511	0.7712	0.4936	0.4639
	CM	0.7531	0.7713	0.4696	0.4447
	BA	0.7411	0.7976	0.5086	0.4167
s.e.d.		0.0066	0.0051	0.0155	0.0220
Significance:					
pig type		**	***	*	NS
period		***	***	***	***
pig type x period		NS	NS	NS	NS

(* = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$)

The digestibilities of DM and OM for LW and CM were not significantly different from one another in any of the periods. However, there seemed to be a trend for the digestibility of DM for CM to be higher than that for the LW in periods 1 and 2 which caused there to be a significant difference in digestibility between CM and babirusa during these periods.

For both LW and CM, the digestibility of the total diet DM in period 3 was lower than that in period 1 or 2 ($p<0.01$ and $p<0.001$ for LW and CM respectively). There also seems to be a trend in this direction for the babirusa, but because of the large standard deviation of the mean digestibility of DM in period 3 this was not statistically significant. This trend was however significant for the digestibility of OM which was significantly smaller in period 3 than in period 1 for all three pig types ($p<0.05$ for LW and babirusa; $p<0.001$ for CM). For LW and CM, the digestibility of OM in period 3 was also significantly smaller than that in period 2 ($p<0.01$ for LW and $p<0.001$ for CM) whereas this was not the case for babirusa.

The digestibility of NDF by babirusa was significantly larger than that by LW in period 2 (p<0.05) and that by CM in period 3 (p<0.05). There was a trend for the digestion of NDF in the total diet by the babirusa to be larger than that by both the LW and CM in all periods, but apart from the instances indicated above these effects were not statistically significant. The digestibility of ADF from the total diet was not significantly different among the three pig types. For all three pig types, the digestibility of NDF and ADF in period 1 was significantly lower than that in period 2 or 3 (p<0.001).

Digestibility of dried grass only (Table 3.5)

No significant differences for the digestibility of DM and OM from dried grass were present between the pig types in either period 2 or 3. The digestibility of DM and OM in period 3 was significantly less than that in period 2 for LW and CM and a trend in the same direction was found for the babirusa.

Table 3.5 Digestibility coefficients of different components of dried grass for LW, CM and babirusa (BA).

Period	Pig type	Component			
		DM	OM	NDF	ADF
2	LW	0.8169	0.8206	0.8273	0.9620
	CM	0.8456	0.8447	0.8692	0.9392
	BA	0.8297	0.8152	0.7372	0.6605
3	LW	0.6664	0.6717	0.7145	0.8575
	CM	0.6336	0.6407	0.6676	0.7878
	BA	0.7012	0.7333	0.6607	0.6289
s.e.d.		0.0552	0.0484	0.0620	0.0746
Significance:					
pig type		NS	NS	NS	***
period		***	***	***	*
pig type x period		NS	NS	NS	NS

(* = p<0.05, ** = p<0.01, *** = p<0.001)

The three pig types did not differ in the digestibility of NDF from dried grass. The digestibility of ADF by babirusa was, however, significantly less than that by both LW and CM in period 2 ($p<0.01$) and that by LW in period 3 ($p<0.05$). There was a suggestion that the digestibility of ADF by the babirusa in period 3 was also less than that by the CM in the same period but this effect was not significant. The digestibility of NDF and ADF by CM in period 3 was significantly lower than that in period 2. A trend in this direction existed for LW and for the NDF digestibility by babirusa, but this was not significant.

4. Discussion

It was expected that if, in the babirusa stomach, fermentation was more important than caeco-colic fermentation, and if the digesta retention time in the stomach was too short to allow extensive fermentation of the more difficult to digest fibres, that babirusa would show a higher digestibility of dry matter, organic matter and NDF than the two domestic pig breeds and that there would also be a lower digestibility of the more difficult to digest fibre fraction (ADF).

The digestibility of NDF for babirusa was significantly larger than that of LW in period 2 and that of CM in period 3 and there was a strong suggestion that the babirusa digested NDF from the total diet more efficiently than both the LW and CM in all three periods. The digestibility of NDF from the dried grass alone however did not differ between the three pig types. For ADF, the situation was reversed. There were no differences between the three pig types for the efficiency of ADF digestion in the total diet. However, babirusa were less efficient in the digestion of the ADF which originated from dried grass than were the LW and CM.

Non-ruminating foregut fermenters are known to be specialised in the fermentation of the more easily digestible plant components such as plant cell solubles and hemicellulose (Hofmann, 1989; Bodmer, 1990). The main reason for this is the relatively short retention time of digesta which does not allow extensive fermentation of the more difficult to digest food fractions such as cellulose (Moire, 1965; Hofmann, 1989; Bodmer, 1990). The observation that babirusa were more efficient in the digestion of total diet NDF and less efficient in the digestion of dried grass ADF fits well with these characteristics of non-ruminant forestomach fermentation. The main difference between the NDF and ADF residue is the inclusion of hemicellulose in NDF (Goering and Van Soest, 1970; Robertson and Van Soest,1977; Van Soest, 1985; Stanogias and Pearce, 1985). Hemicellulose is usually more digestible than cellulose and lignin (Van Soest, 1985). Also, monocotyledonous plants such as grasses are known to have a greater proportion of cell wall components and less cell solubles, and are therefore more difficult to digest than dicotyledonous plants and fruits (Bodmer, 1990). A less efficient digestion of ADF from dried grass can therefore be expected of a non-ruminant foregut fermenter.

In the peccary, another forestomach fermenter and close relative of the pigs, it was shown that practically no cellulose digestion occurred in the forestomach whereas 30% more volatile fatty acids (VFAs) were present in the forestomach compared to the caecum and colon (Shively et al., 1985; Lochmiller et al., 1989). It was therefore concluded that in the peccary, most of the fermentation occurred in the forestomach. This fermentation represented the fermentation of more easily digestible plant cell compounds such as starch whereas the digestion of cellulose was mainly restricted to the caecum and colon (Lochmiller et al., 1989). In the domestic pig, only a small amount of VFAs are present in the cranial half of the stomach. By far the largest proportion of VFAs are produced in the caecum and the colon (Argenzio and Southworth, 1974; Clemens et al., 1975). Correspondingly, it was found that almost all the cellulose and 80% of the hemicellulose was digested in the large intestine of the domestic pig (Keys and DeBarthe, 1974).

The higher digestibility of total diet NDF and lower digestibility of dried grass ADF in the babirusa suggests that, as in the peccary, most fermentation will occur in the stomach rather than the caecum and colon and that the fermentation in the stomach will be that of the more digestible plant cell solubles (e.g. starch) and hemicellulose. If less fermentation was to occur in the caecum and colon and if cellulose digestion was mainly confined to the caecum and colon, then this would result in a lower digestibility of dried grass ADF, as was indeed observed in the babirusa.

The specialisation of the babirusa in the stomach fermentation of plant cell solubles and hemicellulose may also be reflected in the trend towards a higher digestibility of OM from the total diet by this species compared to the LW and CM in all periods; the differences were significant in a number of instances. The reluctance of the babirusa to eat the dried grass pellets could possibly be explained in part by the animals' smaller capacity to digest ADF from dried grass. It may also be relevant that prior to the study the babirusa were accustomed to eating a fairly succulent diet of fruit and vegetables supplemented with a much smaller quantity of dry commercial pellets. A diet of dry pellets alone was therefore quite strange to them.

Apart from the early work by Mitchell (1916) no studies appear to have concentrated on the intestinal tract of the babirusa. Both the work of Mitchell (1916) and personal observations suggest that the anatomy of the small and large intestines of the babirusa are very similar to those of the domestic pig, with no obvious differences in size or proportion being apparent. More detailed work, however, is necessary to investigate the dimensions of the different parts of the intestinal tract in comparison to those of *Sus scrofa*, and the other pigs, and in particular to examine the retention time of digesta in the stomach and the intestines. The amount and type of VFAs produced along the gastro-intestinal tract of the babirusa remain unknown, and it would be of interest to determine the relative importance of fermentation in the stomach as opposed to that in the large intestine.

The digestibility of DM from the total diet for the babirusa was not different from that of the LW but was smaller than that of the CM during periods 1 and 2. The reason for this is likely to be the trend towards higher digestibility of total diet DM by the CM compared to the LW. Although there seemed in some instances to be a trend for the digestive capacity of the CM to be better than that of the LW, no significant differences were found between the digestibility of DM, NDF, ADF and OM from the total diet as well as that from dried grass by LW and CM. This is in contrast to previous studies investigating the digestion of nutrients, energy and nitrogen by LW and CM pigs (Fevrier et al., 1988; Kemp et al., 1991). In these experiments, CM digested all nutrients and energy more efficiently than LW and this was especially so with respect to foods with a more fibrous content (Fevrier et al., 1988; Kemp et al., 1991). In a number of studies CM were found to have a larger gut fill (Fevrier et al., 1988; Kyriazakis et al., 1993) and longer digesta retention time (Fevrier et al., 1988) than the LW. The weight of the colon of CM was also found to be heavier than that of LW, especially when the animals were fed a high fibre diet (Fevrier et al., 1988). The latter observations suggest that the CM are superior to the LW in their ability to digest fibre in the caecum and colon.

The reason why no significant differences in the ability to digest DM, NDF, ADF and OM were found between CM and LW pigs in the present study may be due to one or a combination of two factors. Firstly, in the studies by Fevrier et al. (1988) and Kemp et al. (1991) digestibilities were determined by total faeces collection, whereas in the present study only samples of faecal material were taken and the digestibilities determined according to the Cr_2O_3 indicator ratio technique. There are a number of problems associated with the latter technique such as obtaining representative samples of faeces and difficulties with the determination of the chromium concentration (Kotb and Luckey, 1972; Saha and Gilbreath, 1993). The housing and management of the babirusa, however, did not allow the complete collection of the faeces. In order to keep the method of digestibility determination the same among all three pig types it was decided to use the Cr_2O_3 indicator ratio technique throughout the study. This technique may not have been sensitive enough to show up the differences in digestive capacities between LW and CM in a statistically significant way. Another difference between the studies by Fevrier et al. (1988) and Kemp et al. (1991) and the present study lies in the nature of the fibre used. Fevrier et al. (1988) used wheat bran and Kemp et al. (1991) employed oat husk meal with a small amount of straw meal, whereas the fibre source in the present study was dried grass. It is well known that fibres from different sources have different digestibilities (Morgan et al., 1984; Low, 1985; Stanogias and Pearce, 1985; Dierick et al., 1989; Morgan, 1989) and it is possible that the differences in digestive capacity between LW and CM are smaller when grass fibre is fed than when the diet contains a cereal fibre.

A reduction in the digestibility of DM and OM and of NDF and ADF in diets with a higher fibre content, which reached statistical significance in several instances during the present experiment, is a well known phenomenon (Morgan et al., 1984; Low, 1985; Stanogias and Pearce, 1985; Sandoval et al., 1987; Dierick et al., 1989; Morgan, 1989; Fevrier et al., 1988; Kemp et al., 1991). The potential reduction of digestion of all nutrient types by the inclusion of fibre in the diet is thought to work through a variety of mechanisms. These include decreased digesta retention time and therefore reduction in the amount of time that food is subjected to digestion and fermentation, gel-formation, water holding properties, and the prevention of access of digestive enzymes to food residues (Morgan et al., 1984; Low, 1985; Stanogias and Pearce, 1985; Sandoval et al., 1987; Dierick et al., 1989; Morgan, 1989). The significantly lower digestibility of NDF and ADF in the total diet during period 1 was probably due to the low fibre content of the meal and the fibre being of cereal origin (Morgan et al., 1984). The overall high digestibility of the grass ADF for the LW and CM pigs may be explained by the fact that the grass was fed in the form of pellets composed of finely ground material.

The present study indicated that the babirusa is not able to digest grass fibre better than the domestic pigs. On the contrary the digestibility of ADF was less in the babirusa. However, babirusa did digest NDF and OM from the total diet better than the domestic pigs. This strongly suggests that in the babirusa, fermentation in the stomach is more important than in the large intestine and that fermentation in the stomach largely concerns the more digestible food components. Even among the most efficient foregut fermenters, the ruminants, there are a number of species which have specialised in the fermentation of more easily digestible foods such as fruits, flowers and dicotyledonous leaves and herbs (Dubost, 1984; Hofmann, 1989; Bodmer, 1990). The evolutionary advantages to the babirusa of foregut fermentation of cell solubles and more easily digestible fibre may include the capability of the microflora in the stomach to transform lower-quality protein into high-quality microbial protein; this can then be digested by the host's own enzyme system. The advantages may also include the ability of the micro-organisms to utilise non-protein nitrogen such as urea for protein construction. The synthesis of vitamins by micro-organisms, the fermentation of mechanical defence structures of fruit such as peels and seed-coats and the potential detoxification of chemical defence compounds in the food would appear to be further advantages (Moir, 1965, 1968; Hofmann, 1989; Bodmer, 1990).

Non-ruminant foregut fermenters and ruminating frugivore/concentrate selectors are known to be able to select food items and plant parts which are more easily digestible (Kiltie, 1981; Sauer, 1983; Owen-Smith and Cooper, 1983, 1989; Dubost, 1984; Pellew, 1984; Cooper et al., 1988; Hofmann, 1989; Bodmer, 1990; Dasilva, 1992). The foraging and selection of food items by babirusa in a semi-natural enclosure was investigated and the results form the subject of the next chapter.

5. Conclusions

Babirusa were not able to digest grass fibre better than domestic pigs. On the contrary, the digestibility of the Acid Detergent Fibre (= cellulose + lignin) component of grass was less in the babirusa than in the domestic pigs. However, babirusa were able to digest Neutral Detergent Fibre (= hemicellulose + cellulose + lignin) and Organic Matter from the total diet better than the domestic pigs. This strongly suggested that in the babirusa, the fermentation in the stomach is more important than that in the large intestine, and that fermentation in the stomach largely concerns the more digestible food components (hemicellulose and plant cell solubles).

CHAPTER 4: FORAGING AND OTHER BEHAVIOUR OF BABIRUSA IN A SEMI-NATURAL ENVIRONMENT

1. Introduction

Studies of behaviour and diet in the wild, or in semi-natural conditions, have been carried out on a number of wild pig and peccary species (common warthog *Phacochoerus africanus* : Geigy, 1955; Frädrich, 1965; Field, 1970; Monfort, 1974; Cumming, 1975; Mason, 1982; Rodgers, 1984, bushpig *Potamochoerus larvatus*: Skinner et al., 1976; Breytenbach and Skinner, 1982; Jones, 1984; Seydack, 1990, Forest hog *Hylochoerus meinertzhageni*: d'Huart, 1978, the wild boar *Sus scrofa*: Briedermann, 1976, 1990; Genov, 1981, Howe et al., 1981; Baber and Coblenz, 1987; Dardaillon, 1987, Gerard et al., 1991, the collared peccary *Tayassu tajacu*: Sowls, 1984; Robinson and Eisenberg, 1985; Corn and Warren, 1986, the white lipped peccary *Tayassu pecari* (Kiltie, 1981) and the domestic pig *Sus scrofa* (e.g. Stolba and Wood-Gush, 1989). No comparable studies have been carried out on the babirusa. General behavioural studies of babirusa in the wild are limited to one study of the behaviour of five animals on the Togian island of Pangempan (Selmier, 1983) and the recently made video recordings of wild babirusa on the northern mainland of Sulawesi (Patry and Capiod, 1989; Patry, 1990). Information with respect to the foraging behaviour and the plants and plant parts selected by babirusa in the wild is therefore scarce. Several behavioural studies have been carried out on animals in captivity (Geoffroy-St-Hillaire and Cuvier, 1842; Bowles, 1986; Macdonald et al, 1989; Leus et al, 1992, Macdonald et al, 1993) but these studies concentrated mainly on social and reproductive behaviour. In none of these studies did the animals have access to a large area with natural "wild" vegetation. The possibilities for the study of foraging behaviour under those circumstances were therefore limited.

From the characteristics of the stomach anatomy and the results of the comparative digestibility study it was hypothesised that the babirusa are non-ruminant foregut fermenters specialising in the fermentation of the more easily digestible cell solubles rather then cell walls. If this is the case then we would expect foraging babirusa to select, and show a preference for, the more easily digestible plant parts. Thus, this section of the thesis reports the results of the first detailed observations of babirusa foraging. Observations of the behaviour of the animals in the semi-wild condition of a French zoo allowed hypotheses to be made with regard to the diet and behaviour of babirusa in their habitat in Indonesia.

2. Materials and Methods

The study was carried out from the 12th to the 19th May 1993 at l'Espace Zoologique, the zoo at St Martin la plaine, France. Two animals were used in the study; an adult male, Piet (studbook number 0094), born at Antwerp Zoo on 23.02.88 and moved to St Martin on 22.11.91 and an adult female, Rosalie (studbook number 0139), born at Antwerp Zoo on 11.06.90 and moved to St Martin on 05.11.92 (Plasa, 1993). The animals had been kept together since the arrival of Rosalie at St Martin. In both zoos the animals were handled daily by their keepers and were accustomed to, and were at ease with the close proximity of people.

Enclosure

The enclosure used was an old abandoned cherry orchard of approximately 1250m^2 situated on an east sloping hill within the zoo. The orchard had been abandoned for several years and had been left to grow wild. A map of the enclosure, drawn to scale, illustrates the layout of the vegetation (Fig. 4.1). The enclosure was divided into 21 zones. Zone 1 represented an area of bare compact soil without vegetation. The temporary night shed, labelled zone 2, was constructed from wooden plank walls and a corrugated roof. The inside was bedded with straw. Zone 18 was a large compost heap of loose soil and old animal bedding material (e.g.. straw).

In order to determine the nature of the plant material that was available to the animals the vegetation in the different zones was characterised. Zones 5, 6, 8, 11, 12, 13, 17, 19, 20 and 21 had a dense vegetation composed of only one or two species of shrubs, the nature of which is indicated on the map. In order to describe the more heterogeneous vegetation in zones 3, 4, 7, 9, 10, 14, 15 and 16, the area covered by each species was

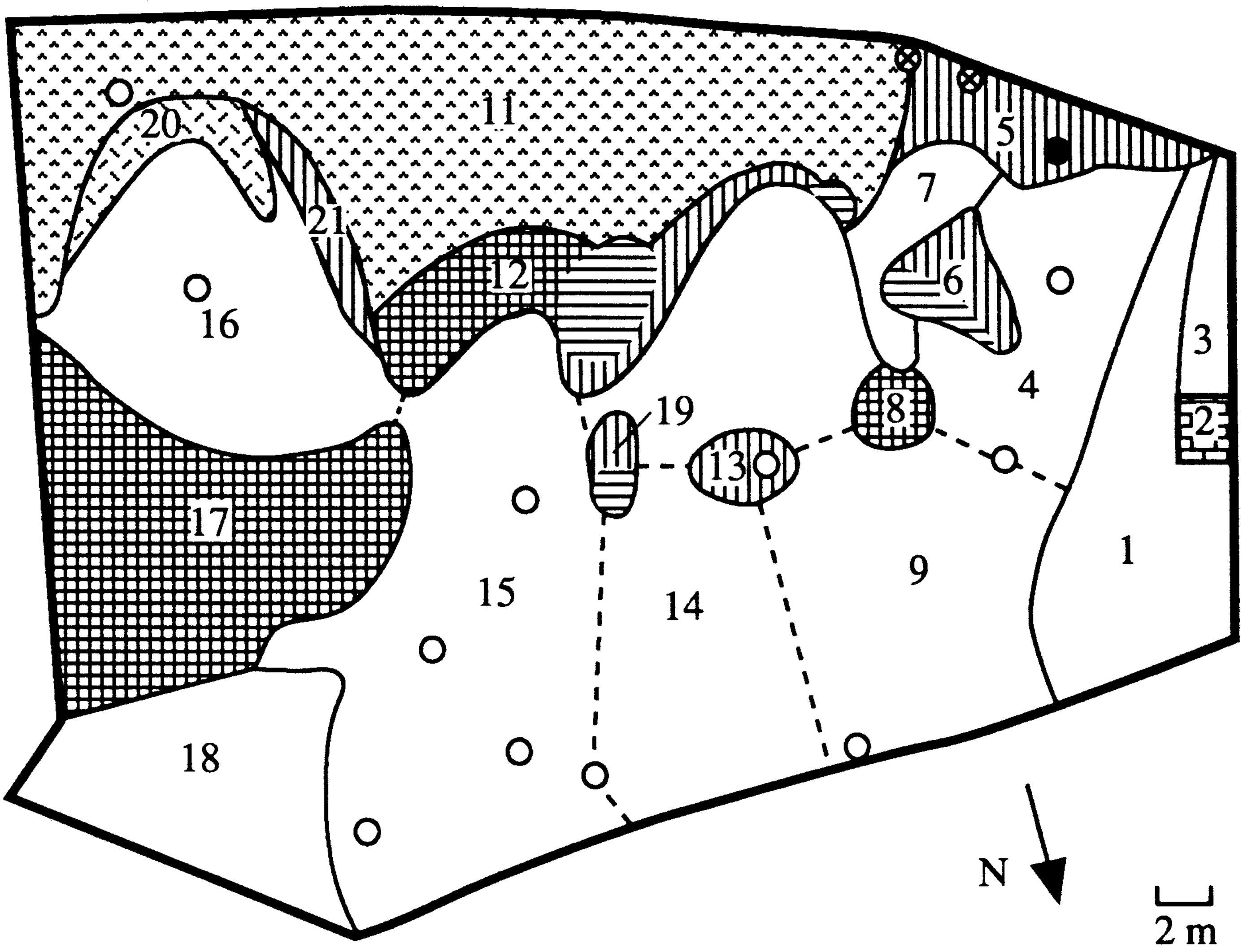

Fig 4.1 Map of the enclosure with semi-natural vegetation. The shading refers to zones with a uniform vegetation. Each zone in the enclosure was allocated a number (1-21).

▥ Brambles (*Rubus* sp.)
▤ Broom (*Cytisus scoparius* (L.) Link)
▦ Mixture of Brambles and Broom
⬚ Blackthorn (*Prunus spinosa* L.)
▧ Common Nettle (*Urtica dioica* L.)
▣ Night Shed
○ Cherry tree (*Prunus* sp.)
⊗ Midland Hawthorn (*Crataegus laevigata* (Poiret) DC.)
● Pear tree (*Pyrus* sp.)

estimated. This method consisted of throwing a $0.5m^2$ quadrat over the shoulder into the vegetation of each zone. All the plants within the quadrat were identified and the percentage of the $0.5m^2$ area covered by each species of plant recorded. The percentage of bare ground within the quadrat was also recorded. This procedure was repeated several times, the number of repetitions depending on the size of the zone and the degree of uniformity of the vegetation within the zone. Apart from the plant species recorded within the quadrats, a list was drawn up of all the species found within the enclosure that were not covered by a quadrat. The species of plants found within the enclosure were summarised into 6 categories: grasses, trees, shrubs, herbs, fungi and bare ground. For each zone, the mean percentage area covered by each of the plant categories was calculated from the percentage of area covered by each of the categories in each of the quadrats thrown within that zone.

Diet

The nature of the vegetation within the enclosure was such that it was felt that it could not provide an adequate diet for the babirusa. The animals, therefore continued to receive their normal diet, all be it in smaller quantities. During the study the animals received 2kg fruit and vegetables and 150g pellets and grains representing a daily intake of 380g dry matter, 45g crude protein, 22g fat, 70g non-starch polysaccharides and 5MJ digestible energy.

To disturb the normal routine of the animals as little as possible the animals were fed together in the shed and the diet was offered in two equal portions, one at about 8.00h and one at about 18.00h. Water was offered in a large trough which was put inside the shed during the night and outside against the wall of the shed during the day. The animals therefore always had free access to water.

Procedure

The animals were moved from their normal quarters to the shed in the experimental enclosure during the afternoon before the first day of observation. They were offered their evening meal and spent the remainder of the day and night in their shed. On the first day of observation, the animals received their morning meal in the shed. Half an hour later they were released into the experimental enclosure for the first time. Observation started after 30 minutes had elapsed, when the animals seemed at ease within their enclosure.

During the first day, observations were carried out from outside the enclosure until 16.00h in order to let the animals get used to their new living situation. The animals stayed mainly in the north side of the enclosure during that time and could easily be observed from the fence with the aid of binoculars. After 16.00h on the first day and for the remaining time of the study, observations were carried out from within the enclosure. The animals seemed very at ease with the observer in close proximity and could be followed as closely as 3 metres by the observer without signs of anxiety. Most of the time it was possible to determine with the aid of binoculars precisely what it was the animals were doing and what they were eating.

Observations were carried out during five consecutive days (14-18 May). The timing of the study was governed by building plans in the zoo. This meant that it could only be carried out during the same period as the diet selection study (see Chapter 5) which was taking place in different zoos. The number of days that could be spent observing the animals in France was therefore limited. Detailed observation sessions were carried out for a total of 6 hours each day. Male and female were observed alternately for half an hour, the starting animal being switched from day to day. Every minute it was recorded what the animal was doing (see behaviour categories below), in which of the zones in the enclosure this behaviour was carried out and how close it was to the other animal (in contact, less than 1m away, between 1 and 5m away, between 5 and 10m away, between 10 and 20m away or more than 20 m away). When the animal was eating, the plant species and plant part being eaten was recorded. Each half-hour session yielded 31 recordings, starting at time 0 and ending at time 30. During the first 3 days 3 hours of detailed observations were carried out in the morning (between 8.30 and 13.30) and 3 hours in the afternoon (between 13.30 and 18.30). During these days it became evident that the animals tended to sleep most of the time during the afternoons. In order to attempt to coincide the detailed observations with the active periods of the animals, the animals were observed for 4 hours during the morning and for 2 hours during the afternoon during the last two days. Long periods of sleep outside the detailed observation periods were monitored by 15-minute spot checks. If the animals were still lying in the same place after 15 minutes, they were recorded as having slept during those 15 minutes. The information from the 15-minute spot checks was only used to indicate when during the day the animals slept. All other results relate to the data gathered during the 6 hours of detailed observation per day. As a consequence of the small amount of activity during the afternoon, the data for morning and afternoon were pooled for analysis and will be discussed together.

When in the text it is said that the animals performed a certain behaviour for x min out of a total of y minutes, it is meant that out of a total of y one-minute time-scan observations the animal was recorded to be performing that behaviour on x occasions. Since the observations were not continuous, it can not be implied that the animal spent x continuous minutes performing a certain behaviour

Behaviour categories

The behaviour exhibited by the animals was classified in the following categories:

Standing (S): The animal is standing still onto all four legs.

Walking (W): The animal is moving around at walking pace.

Trot (T): The animal is moving around faster than a walking pace.

Run (R): The animal is galloping.

Sniff ground (SG): The animal is standing still on all four legs or is walking around with its nose either on the ground surface or not more than 5cm above it. The animal could often be heard sniffing.

Sniff vegetation (SV): The animal is standing still on all four legs or is walking around while moving its nose through the vegetation. The nose is held more than 5cm above the ground surface and the animal can often be heard sniffing.

Sniff object (**SO**): The animal is standing still on all four legs and is sniffing an object in the enclosure (e.g.. tree, fence, stone, shed etc.) but the object is not manipulated or prodded with the nose.

Manipulating object (**MO**): The animal is manipulating an object in the enclosure with its snout and/or feet without taking it into its mouth.

Manipulating straw (**MS**): The animal is manipulating and rummaging through the straw provided for bedding with its snout, feet and/or body.

Sniff observer (**SOb**): The animal is sniffing the observer.

Sniff faeces (**Sf**): The animal is standing still on all four legs and is sniffing its own or the other animal's faeces.

Sniff urine (**Su**): The animal is standing still on all four legs and is sniffing its own or the other animal's urine.

Sniff bones (**Sb**): The animal is standing still on all four legs and is sniffing old animal bones that were unearthed in the enclosure without the bones being manipulated or taken into the mouth.

Sniff pig (**SP**): The animal is standing still on all four legs and is sniffing the body (but not the ano-genital region) of the other pig without manipulating or prodding with the nose.

Orientate (**O**): The animal is standing still on all four legs, or is walking around, while the head is moved in the direction of a sound, a smell or a visual cue.

One leg up (**OLU**): The animal takes approximately three paces, halts briefly while lifting one of the front legs a short distance of the ground, and moves its head in the direction of a sound, a smell or a visual cue. This sequence of walking three paces and lifting the front leg while orientating is usually repeated several times.

Probe (**P**): The animal puts its snout deep in the soil (until just in front of its eyes) and moves its snout vertically up and down through the soil, displacing the soil with the bridge of its nose. The animal may be standing still or can be walking slowly while performing this behaviour.

Ploughing (**Pl**): The animal puts its snout in the soil to such a depth that the soil is just in front of its eyes, whereupon it kneels and slides forward onto its chest. The head and front part of the body are pushed forward through the sand and alternately canted left and right. This sometimes results in the body being tilted to such an extent that the animal rolls onto its side and back.

Sniff ano-genital region (**SAG**): The male animal is sniffing, licking and/or nuzzling the ano-genital region of the female.

Walk + Sniff ano-genital region (**W+SAG**): The male animal is walking behind the female and is following her around while keeping his nose close to, or in contact with, her ano-genital region.

Run + Sniff ano-genital region (**R+SAG**): The male animal is running behind the female and is following her around while keeping his nose pointed in the direction of her ano-genital region.

Nose-nose contact (**NN**): Both animals are standing still on all four legs while their noses are in contact with one another.

Nuzzling (**N**): The animal is nuzzling (pushing with the nose and/or licking) the body of the other animal (but not the ano-genital region).

L<-N: The animal is lying down as a consequence of being nuzzled by the other animal. Nuzzling may continue while the animal is lying down.

N->L: The animal is nuzzling the other animal and the latter lies down as a consequence. The animal may continue nuzzling the other animal while it is lying down.

Rub pig (**RbP**): One animal is rubbing its body against the body of the other animal.

Rub object (**RbO**): The animal is rubbing its body against an object in the enclosure (e.g.. tree, fence, shed etc.).

Rub observer (**RbOb**): The animal is rubbing its body against the legs of the observer.

Scratching (**Scr**): The animal is scratching its own body with one of its hind legs.

Stretching (**Str**): The animal is stretching its body by stretching its front legs forwards or its hind legs backwards.

Drinking (**Dr**): The animal is drinking from the trough provided.

Biting (**E**): The animal takes an item into the mouth and may bite or chew it but the item is not ingested.

Eating (**E**): The animal takes an item into its mouth and the item is ingested.

Smacking (Sm): The animal has just eaten something and even though the item is completely ingested the animal keeps on making smacking noises for a little while longer in an almost exaggerated way.
Lying alone (LA): The animal is lying down while the other animal is active.
Lying together (LT): Both animals are lying down
Defecate (D): The animal is defecating
Urinate (U): The animal is urinating
?: The animal was out of sight

3. Results

Vegetation

The botanical composition of the zones with a uniform vegetation is indicated on the map of the enclosure (Fig. 4.1). The vegetation in each of these zones was very dense and did not allow for any herbal undergrowth. The results of the botanical investigation of the zones with a more heterogeneous vegetation is indicated in Table 4.1. Trees are indicated on the map of the enclosure and are therefore not included in the table. Seedlings of trees were occasionally found inside a quadrat but took up an area of less than 1% and were therefore only recorded as 'present'. The latter also applies to the fungi which were present in zones 14 and 15. Zones 3, 15 and 16 were largely composed of grass and only contained a limited amount of shrubs and herbs. In zone 3 the grass was mainly tall and flowering whereas the grass in zone 16 was dense, reasonable short (15-20cm) and in most instances not in bloom. Zone 15 was also covered by short grass though it was less dense than in zone 16; patches of bare soil could be seen. The other zones contained grass interspersed with varying proportions of shrubs and herbs. Zone 4 and 10 were characterised by tall, flowering grass interspersed with a variety of tall herbs. In zones 7, 9 and 14, the grass was growing between a thin covering of low bramble shrubs (*Rubus*). The predominant herbal fraction in zone 7 was wood sage (*Teucrium scorodonia* L.) and in zone 9 and 14 lady's bedstraw (*Galium verum* L.). The large standard deviations in some instances reflects the rather patchy nature of the vegetation in those zones. A complete list of the plants found in the zones with

Table 4.1 Percentage of the ground surface covered by grass, shrubs, herbs and bare soil in each of the zones in the enclosure with a heterogeneous vegetation. (data = mean±stand. dev.)

Zone	Vegetation (%)			
	Grass	Shrubs	Herbs	Bare Soil
Zone 3 (n=2)	83.±6.0	2± 1.0	12± 8.0	3±3.0
Zone 4 (n=6)	57±27.3	7±14.7	35±28.0	1±3.0
Zone 7 (n=4)	69±26.7	18±14.6	4±14.0	0
Zone 9 (n=7)	59±21.1	14±16.9	27±26.9	0
Zone 10 (n=7)	37±29.1	6± 5.2	41±25.3	15±17.9
Zone 14 (n=7)	60±24.0	25±16.6	9± 5.8	6±13.7
Zone 15 (n=11)	69±28.5	4± 7.4	8± 8.1	18±23.1
Zone 16 (n=7)	87± 7.2	2± 2.6	10± 7.3	2± 4.2

heterogeneous vegetation, including those which did not happen to be included in the quadrats is given in Table 4.2. This list combined with Table 4.1 indicates that the babirusa had access to a wide variety of plant material in the categories of grasses, herbs, woody plants and even fruits (unripe cherries).

Behaviour

General

The complete list of different behaviours recorded over the 5 days are those indicated in the materials and methods section. Table 4.3 gives an overview of the distribution of the recordings over the different behaviours. Some of the behaviours were summarised to make the table

Table 4.2: Inventory of plants found in the zones of the enclosure with heterogenous botanical compostion.

Scientific name	English name	Family	Zones							
			3	4	7	9	10	14	15	16
Grasses:										
Graminae	Unidentified	Poaceae*	+	+	+	+	+	+	+	+
Anthoxanthum odoratum L.	Sweet vernal Grass	Poaceae	+	+	-	+	-	+	+	+
Bromus hordeaceus L.	Soft-brome	Poaceae	+	+	+	+	+	+	+	+
Helictotrichon pubescens (Hudson) Pilger	Downy Oatgrass	Poaceae	+	+	-	+	+	+	+	+
Holcus lanatus L.	Yorkshire-fog	Poaceae	-	-	+	-	-	-	+	-
Poa annua L.	Annual Meadow-grass	Poaceae	+	+	+	+	+	+	+	+
Poa pratensis L.	Smooth Meadow-grass	Poaceae	+	+	+	+	+	+	+	+
Trees:										
Crataegus laevigata (Poiret) DC.	Midland Hawthorn	Rosaceae	-	-	-	-	-	-	-	-
Prunus	Cherry	Rosaceae	-	+	-	+	-	+	+	+
Pyrus L.	Pear	Rosaceae	-	-	-	-	-	-	-	-
Shrubs:										
Prunus spinosa L.	Blackthorn	Rosaceae	-	-	-	-	-	-	-	+
Rosa L.	Rose	Rosaceae	-	-	-	+	-	+	+	-
Rubus L.	Brambles	Rosaceae	+	+	+	+	+	+	+	+
Cytisus scoparius (L.) Link	Broom	Fabaceae	+	+	+	-	+	+	+	+

Table 4.2 continued

Scientific name	English name	Family	Zones							
			3	4	7	9	10	14	15	16
Herbs:										
Achillea millefolium L.	Yarrow	Asteraceae**	-	+	+	-	+	+	-	-
Cirsium arvense (L.) Scop.	Creeping Thistle	Asteraceae	+	-	+	+	-	-	-	-
Cirsium vulgare (Savi) Ten.	Spear Thistle	Asteraceae	-	+	-	-	-	-	-	-
Hieracium lachenalii Gmel.	Hawkweed	Asteraceae	-	+	+	-	-	-	-	-
Helianthus annuus L.	Sunflower	Asteraceae	+	-	-	+	-	-	-	-
Inula L.	Fleabanes	Asteraceae	-	-	-	+	-	-	-	-
Sonchus arvensis L.	Perennial Sow-thistle	Asteraceae	+	-	+	-	-	-	-	-
Taraxacum Wigg.	Dandelions	Asteraceae	+	+	+	+	+	+	+	+
Daucus carota L.	Wild Carrot	Apiaceae	-	+	+	+	-	+	-	+
Echium vulgare L.	Viper's-bugloss	Boraginaceae	-	+	-	-	-	-	-	-
Myosotis L.	Forget-me-nots	Boraginaceae	+	+	+	+	+	+	+	+
Arabidopsis thaliana (L.) Heynh.	Thale Cress	Brassicaceae	+	-	-	-	+	+	+	+
Barbarea vulgaris R.Br.	Winter-cress	Brassicaceae	+	-	+	+	-	+	+	+
Diplotaxis tenuifolia (L.) DC.	Perennial Wall-rocket	Brassicaceae	+	+	+	+	+	+	+	+
Cerastium arvense L.	Field Mouse-ear	Caryophyllaceae	-	+	-	-	+	+	+	+
Silene vulgaris Garcke	Bladder Campion	Caryophyllaceae	-	-	-	-	+	+	-	-
Bryonia dioica Jacq.	White Bryony	Cucurbitaceae	-	+	-	-	-	-	+	-
Trifolium repens L.	White Clover	Fabaceae	+	+	+	+	+	+	+	+
Vicia hirsuta (L.) Gray	Hairy Tare	Fabaceae	+	-	-	+	-	-	-	-
Vicia sativa L.	Common Vetch	Fabaceae	+	-	-	+	-	+	+	-
Fumaria officinalis L.	Common Fumitory	Fumariaceae	-	+	-	+	-	+	+	-
Geranium molle L.	Dove's-foot Crane's-bill	Geraniaceae	-	-	-	-	-	+	+	-
Geranium robertianum L.	Herb-Robert	Geraniaceae	-	-	-	-	-	+	+	-

Table 4.2: continued

Scientific name	English name	Family	Zones							
			3	4	7	9	10	14	15	16
Lamium purpureum L.	Red Dead-nettle	Lamiaceae	-	-	-	-	-	-	+	+
Teucrium scorodonia L.	Wood Sage	Lamiaceae	-	-	+	-	-	-	-	-
Orobanche caryophyllacea Smith	Bedstraw Broomrape	Orobanchaceae	-	-	-	+	-	+	-	-
Papaver rhoeas L.	Common Poppy	Papaveraceae	+	-	-	-	-	-	-	-
Rumex acetosa L.	French Sorrel	Polygonaceae	+	+	+	+	+	+	+	+
Rumex acetosella L.	Sheep's Sorrel	Polygonaceae	+	+	+	+	+	+	+	+
Clematis vitalba L.	Traveller's-joy	Ranunculaceae	-	-	-	-	-	+	-	-
Ranunculus acris L.	Meadow Buttercup	Ranunculaceae	-	+	+	+	+	+	-	-
Sanguisorba minor Scop.	Salad Burnet	Rosaceae	+	+	+	+	+	+	-	-
Sanguisorba officinalis L.	Great Burnet	Rosaceae	-	-	-	+	-	-	-	-
Galium verum L.	Lady's Bedstraw	Rubiaceae	+	+	+	+	+	+	+	+
Galium aparine L.	Cleavers	Rubiaceae	-	+	+	+	+	+	+	+
Galium mollugo L.	Hedge Bedstraw	Rubiaceae	+	+	-	+	+	-	-	-
Verbascum nigrum L.	Dark Mullein	Scrophulariacea	-	-	-	-	-	-	+	+
Veronica arvensis L.	Wall Speedwell	Scrophulariaceae	-	+	-	-	+	+	+	+
Urtica dioica L.	Common Nettle	Urticaceae	-	-	+	-	-	-	-	+
Valerianella locusta (L.) Laterr.	Common Cornsalad	Valerianaceae	-	+	+	+	+	+	+	+
Viola arvensis Murray	Field Pansy	Violaceae	-	-	-	-	-	+	+	-
Unidentified 1***	Unidentified 1	?	-	+	+	+	+	+	+	+
?	Mushrooms	?	-	-	-	-	-	+	+	-

+ = Present in this zone / - = Not present in this zone/ * = Gramineae / ** = Compositae /
*** = An unidentified non-flowering plant with up to 20 cm long, roughly haired, shallowly serrate leaves, wider at the top than at the base with an obtuse tip. The leaves were organised in a rosette and had a white latex in their veins.

more compact (see table legend). The behaviours could broadly be categorised in two groups: lying and active behaviour.

Table 4.3. Number of recordings, percentage of total number of recordings and percentage of the total number of recordings of active behaviour for each category of behaviour expressed by two babirusa in a semi-natural environment.

Behaviour Categories	No. recordings	%Total Recordings	%Active Behaviour
S (Standing)	22	1	2
W (Walking)	94	5	9
R (Running)	3	<1	<1
T (Trotting)	13	<1	1
SG (Sniff ground)	210	11	21
SV (Sniff vegetation)	56	3	6
P (Probing)	51	3	5
Pl (Ploughing)	12	<1	1
SO (Sniff object)	25	1	3
Ob (Contact observer)	21	1	2
Soc. beh.	66	4	7
RbO+Str+Scr	26	1	3
B (Biting)	21	1	2
E (Eating)	201	11	20
Dr (Drinking)	15	<1	2
Sm (Smacking)	4	<1	<1
D (Defecating)	13	<1	1
U (Urinating)	13	<1	1
O (Orientating)	73	4	7
OLU (One leg up)	39	2	4
MS (Manipulate straw)	19	1	2
MO (Manipulate obj.)	13	<1	1
?	1	<1	<1
total	999		100
LA (Lying alone)	78	4	
LT (Lying together)	783	42	
Total	1860	100	

Social behaviour = SP+SAG+(W+SAG)+(R+SAG)+NN+N+L<-N+N->L+RbP

Ob = SOb (Sniff observer)+RbOb (Rub observer)

RbO+Str+Scr = Rub object + Stretching + Scratching

The animals were usually asleep while lying down. By far the largest time was spent lying or sleeping. **LA** and **LT** together representing 46% of the recordings. Of the total observation time of 19 hours (or 1140 min.) in the morning and 19 hours in the afternoon (this includes the 15 min. spot checks), the animals were both lying or sleeping at the same time for 384 min. in the morning and 846 min. in the afternoon. One animal lay or slept while the other was active for 23 min. in the morning and 55 min. in the afternoon. Since the animals usually tended to lie down simultaneously, male and female spent a similar proportion of their time in this way, with the afternoon being the preferred time for lying and sleeping. Considering the small proportion of activity taking place during the afternoon, results of the detailed observations in the morning and afternoon periods are pooled and discussed together during the remainder of this chapter.

Out of the 783 instances where the animals were recorded to be lying together (**LT**), their bodies were in contact on 460 occasions, the animals usually lying side by side. In all of the remaining **LT** occasions (323) they were lying less than one metre apart. Table 4.4 illustrates the distance between the animals during the times when one or both animals were awake. Since each recording refers to the position of both animals, no distinction between male and female can be made and the data for the two animals will be discussed together. Apart from when they were sleeping, the animals were seldom recorded to be in contact with one another. For 52% of the recordings the animals were between one and five metres apart and in 92% of the recordings, the animals were less than 10 metres apart.

The other behaviours occupying a large proportion of the time were **E** (11%) and **SG** (11%). All other remaining behaviours each occupied only a small proportion of the recordings. A more detailed discussion of a number of behaviour groups will follow below.

Table 4.5 indicates in which zones the two broad groups of behaviour, sleeping and active behaviour, were mostly carried out. A consequence of the animals being so close to one another most of the time is that when one animal was recorded in a certain area, the chances were high that the

Table 4.4 Number of times the two babirusa were recorded to be in contact or a certain distance away from one another during the observation period.

Date	Distance					
	C	<1 m	>1 m <5 m	> 5 m <10 m	>10 m <20 m	>20m
14/05/93	9	66	155	44	11	4
15/05/93	12	44	79	21	23	7
16/05/93	12	57	137	35	14	1
17/05/93	8	24	66	7	4	0
18/05/93	5	38	124	46	16	6
TOTAL	46	231	561	153	68	18
%	4	21	52	14	6	2

other animal was also present in that area at the same moment in time. The data for male and female were therefore amalgamated. Lying only occurred in zones 1, 2, 10 and 15 with the largest preference for the shed (zone 2) the door of which stayed open all day. The three zones where most of the active behaviour was performed were zones 1, 15 and 18; together they accounted for 65% of the recordings. Other popular zones were 2, 4, 9, 10, 14 and 16. It is noteworthy that none of the popular zones had a dense shrub vegetation. Most of the least popular zones (3, 5-8, 11-13, 17, 19 and 20) were almost completely covered by shrubs. The few recordings that were made in the shrub-covered regions refer to instances when the animal was present at the edge of the zone but had not gone between the shrubs. The small opening in the dense shrub vegetation connecting zone 15 with zone 16 was partly concealed by overhanging branches. Zone 16 was not visited by either animal until day 4. Some of the zones which were visited only a few times, or not at all, were of a much smaller size than the more popular zones. This suggests that by the laws of chance, it was less likely for the babirusa to be recorded in those zones. It is important to note, however, that these smaller zones were also not visited outside the recorded time periods and that the larger shrubby zones were also largely ignored during these periods of time. This suggests that the babirusa had a preference for the more open vegetation, rather than the dense shrubby vegetation.

Table 4.5 Total number of recordings made in each zone of the enclosure with a division of the total number of recordings of active behaviour, the percentage of the total number of recordings of active behaviour and the number of recordings of lying made in each zone of the enclosure.

Zone	Behaviour Category				
	Active	%Active	LA	LT	Total
1 (bare soil)	168	17	0	31	199
2 (shed)	88	9	47	611	746
zones with heterogenous vegetation:					
3	2	<1	0	0	2
4	39	4	0	0	39
7	1	<1	0	0	1
9	84	8	0	0	84
10	39	4	7	49	95
14	30	3	0	0	30
15	224	22	24	92	340
16	56	6	0	0	56
zones with dense uniform vegetation:					
5	3	<1	0	0	3
6	2	<1	0	0	2
8	1	<1	0	0	1
11	0	0	0	0	0
12	1	<1	0	0	1
13	3	<1	0	0	3
17	0	0	0	0	0
18(comp. heap)	256	26	0	0	256
19	0	0	0	0	0
20	0	0	0	0	0
21	0	0	0	0	0
?	2	<1	0	0	2
Total	999	100	78	783	1860

In the following paragraphs a number of behaviour groups will be discussed in more detail.

Orientation

At some instances, the pigs would interrupt the behaviour they were engaged in and would switch into **O** or **OLU** behaviour. These behaviours seemed to be stimulated by a sound, a visual cue or both. For example, the animals would react in this way when the chimpanzees (*Pan troglodytes*) in the neighbouring enclosure started to scream, or when a person walked past the pen, or when the Barbary sheep (*Ammotragus lervia*) in the enclosure opposite congregated at the fence. The distribution of the recordings of this behaviour over the five days is indicated in Table 4.6.

It was remarkable, even for this small data set, that:

1) **ULO** behaviour was almost exclusively performed by the female and
2) for both male and female, but especially the female, the amount of **O** and **ULO** seemed to decreased quite dramatically after day one.

These observations strongly suggest that both **O** and **ULO** behaviours were an expression of heightened vigilance and unease in the animal. This is not surprising since the animals had only just been introduced into these strange surroundings. What is remarkable is the rapidity with which the animals became accustomed to their new situation.

The extend to which this vigilance was caused by the presence of the observer was investigated as is indicated in Table 4.7. Those instances in which it seemed that the animal was orientating towards the observer were recorded as **OOb**. The behaviour **SOb** refers to sniffing the observer and **RbOb** to rubbing against the legs of the observer. Only the female showed a very high score for **OOb** during the first day. Both animals engaged in direct contact with the observer only during the second day and they both seemed at ease during these contacts. The data suggest that on the first day, the behaviour of both animals was affected by the new situation but this effect disappeared thereafter. Only the female seemed to be especially concerned with the presence of the observer during the first day. This effect also disappeared from the second day onwards.

Table 4.6 Number of recordings of O and ULO behaviour demonstrated by the male and female babirusa during the observation period.

Male	O	ULO	Sub Total	Female	O	ULO	Sub Total	TOTAL
14/05/93	19	2	21	14/05/93	23	22	45	66
15/05/93	4	0	4	15/05/93	6	7	13	17
16/05/93	8	0	8	16/05/93	7	3	10	18
17/05/93	0	0	0	17/05/93	0	3	3	3
18/05/93	2	0	2	18/05/93	4	2	6	8
TOTAL	33	2	35		40	37	76	112

Foraging and eating

Those behaviours mostly associated with the searching for food were believed to be **SG, SV, P** and **MS**. These behaviours were regularly interrupted in order to consume an item that was encountered during the behaviour. It is likely that foraging was not the only function of these behaviours, e.g. straw could also have been manipulated in order to make a nest, but there was no opportunity to separate out these different functions during the present study. Other behaviours that may be related to foraging to some extent were **SO, MO** and **B**. The recordings under **SO** mainly included the sniffing of non-edible objects such as the shed, large stones, trees, the fence, urine and faeces. Only one recording related to the sniffing of one of the old bones that was dug up by the animals. The manipulation of objects without them being taken into the mouth (**MO**) included the manipulation of the shed door (1x), stones (2x), a branch (1x), the rosette of an unidentified plant (1x), the dug-up bone (1x) and grass sods (7x) mostly related to the unearthing of the bones beneath it (6x). The manipulation of objects which included taking them into the mouth (**B**) was recorded for tree bark (1x), a branch of broom (1x), a broom flower (1), a *Prunus* branch (1x), a bramble branch (1x), a bramble leaf (1x), an unidentified item found in compost heap (1x), a peanut pod found on the compost heap (1x), a piece of construction wood (1x), a little clump of earth (1x) and a number of cherry branches (10x). All of these items except for the cherry branches were taken into the mouth very briefly and were then spat out. The cherry branches were often more than 7mm in diameter and were usually held in the mouth somewhat longer. In some instances the branches were chewed or were bitten to pieces before they were dropped onto the ground again and ignored. They were never consumed, but it is possible that fragments of bark and juice were ingested. Although ploughing behaviour (**Pl**) caused the soil to be turned over, it was not considered to be related to foraging behaviour. It was never interrupted for the eating of items that had been uncovered and the animal often walked away from the ploughed site without inspecting whether any edible things had become available. Previous studies (Leus et al., 1994) have indicated that ploughing behaviour has a scent marking function rather than a foraging function.

Table 4.7 Number of recordings made of behaviour related to the observer demonstrated by the male and female babirusa during the observation period.

Male	SOb	OOb	RbOb	Sub Total	Female	SOb	OOb	RbOb	Sub Total	TOTAL
14/05/93	0	4	0	4	14/05/93	0	20	0	20	24
15/05/93	1	0	4	5	15/05/93	1	3	4	8	13
16/05/93	1	3	4	8	16/05/93	0	1	2	3	11
17/05/93	0	0	0	0	17/05/93	2	0	0	2	2
18/05/93	1	1	1	3	18/05/93	1	3	1	5	8
TOTAL	3	8	9	20		4	27	7	38	58

The recordings for **SG, SV, P** and **MS** for the two animals are illustrated in Table 4.8. Most recordings were made of the animal sniffing the soil. The nose would move just above the soil and hover above items found on the ground, some of which were eaten. Sniffing the vegetation and probing the soil seemed to be of equal importance but were performed less frequently than **SG**. Not much time was spent manipulating the straw in the shed which might be explained by the fact that the food offered to the animals in the shed was not deliberately concealed in the straw. Considering the large amount of time spent on behaviours **SG, SV** and **P** remarkably few recordings were obtained of items being manipulated and prepared before eating. The only exceptions were the manipulation of the grass sod to uncover old bones, the manipulation of the old bones themselves to get them out of the earth, and the manipulation of the cherry branches. Another behaviour that was occasionally observed but did not occur during the observation recordings was the holding down of long bramble branches with one of the forefeet, while the leaves were eaten. Compared to the total amount of recordings for **E** (=201), the occasions where an item was taken into the mouth and not eaten (**B**=21) were very few. This suggests that the first and most important selection of the food items is carried out by smell rather than by taste. No differences could be found between the results for the male and the female.

Table 4.8. Number of recordings made of the different types of foraging behaviour demonstrated by the male and female babirusa in a semi-natural environment.

Animal	SG	SV	P	MS	TOTAL
Male	89	35	24	6	154
Female	121	21	27	13	182
TOTAL	210	56	51	19	336

Those items eaten by the animals are listed in Table 4.9. The patchy distribution of the small amount of data did not allow valid statistical examination of the differences in behaviour between the male and the female or between the different items eaten. The importance of the results therefore lies more with the quality of what was eaten rather than with its quantity. Nevertheless, the data do suggest that the three most important food items consumed were bramble leaves, unripe cherry fruits and the feed that was offered to them by the zoo staff. A short discussion of each food item follows below:

Cherry (*Prunus*) leaves:
The cherry leaves eaten were either plucked from branches and shoots at about the head height of the animal, or were eaten off the ground. The leaves appeared to be fully grown.

Cherry (*Prunus*) twigs:
Short twigs with a diameter of about 7mm or less that had fallen from the cherry trees onto the ground were chewed and eaten completely.

Cherry (*Prunus*) fruits:
Unripe green cherries which had fallen onto the ground were eaten. Cherries were especially consumed during sessions of ground sniffing (SG) behaviour. Small fruits were eaten in their entirety, whereas the stone of the larger specimen was either sometimes spat out or at other times consumed also. The records referring to the eating of cherries represented 16% of the total number of E recorded.

Bramble (*Rubus*) leaves:
The leaves of the bramble bushes were ingested in one of several different ways; by biting off and eating the entire tip of a branch; by picking larger leaves off the branches one by one; by taking the branch in the mouth at some distance from the top and ripping off the leaves as the mouth was quickly pulled towards the top of the branch. The branches of the brambles tended to be thin and stringy rather than thick and woody. The thorns on the branches were therefore small and did not seem to present a problem to the animals. When branches were too long they were sometimes held to the ground with one of the forefeet while the leaves were being picked. There is a suggestion that the bramble leaves were slightly more favoured by the female than by the male. In total, the

Table 4.9 Number of recordings made of the eating of different plants and plant parts by babirusa in a semi-natural environment.

Food item	Male	Female	Total
Bramble leaf (*Rubus* sp.)	16	45	61
Cherry leaf (*Prunus* sp.)	3	4	7
Rose leaf (*Rosa* sp.)	0	4	4
French Sorrel leaf(*Rumex acetosa* L.)	0	1	1
Unidentified 1 leaf	0	1	1
Grass leaves	5	1	6
Downy Oatgrass leaf (*Helictotrichon pubescens* (Hudson) Pilger)	9	0	9
Soft-brome ears(*Bromus hordeaceus* L.)	2	0	2
Cherry fruit (*Prunus* sp.)	18	14	32
Cherry twig (*Prunus* sp.)	2	3	5
Herb rhizome	1	0	1
Old bones	5	1	6
?	8	3	11
Offered food	28	27	55
TOTAL	97	104	201

recordings referring to the eating of bramble leaves represented 30% of the total number of E recorded.

Rose (*Rosa*) leaves:
The leaves of the wild rose bushes were eaten in the same fashion as those of the bramble bushes. Again the thorns did not seem to be a hindrance to the animals.

Downy oatgrass (*Helictotrichon pubescens* (Hudson) Pilger) leaves:
This grass was present in its mature, tall form and was flowering. Its leaves were delicately picked off one by one, by taking the leaf in the mouth and pulling it off the stem by a gentle upward and outward toss of the head. No other part of the grass was eaten. Only the male was observed to eat this grass. The 9 recordings in Table 4.9 represent 9 minutes of practically non-stop picking and eating of the leaves. It was also eaten on one other occasions by the male when he was not under timed observation.

Soft-brome (*Bromus hordeaceus* L.) ears:
This grass was also present in its mature form, with its head of ears organised in a way which was similar to that of oats. The little ears were delicately picked off the head of the grass one by one in the same fashion as the leaves from the stems of the downy oatgrass. No other part of the grass was eaten. Again, only the male was observed to eat this grass and it was also eaten by him on other occasions when he was not under timed observation.

Grass leaves:
On a few occasions leaves of grass were eaten when it was not possible to identify the grass species. The female was only observed to eat grass leaves once whereas the male would eat grass more regularly (also outside the recording periods).

French sorrel (*Rumex acetosa* L.) leaves:
Only on one occasion did the female bite off a piece of a large leaf of this plant and eat it. Neither of the animals was seen to eat any part of this plant on any other occasion.

Herb roots:
On one occasion, the male was seen to eat a little tuft of fine roots such, as those from a herb, which he had found on the compost heap. This behaviour was not demonstrated on any other occasion by either animal.

Leaves of unidentified plant 1:
Only on one occasion did the female bite a piece of a leaf from this plant and eat it. Neither the female nor the male was seen to eat any part of this plant on any other occasion within or outwith the periods of observations.

Old bones:
On two occasions, once in zone 1 and once in zone 15, the animals unearthed old animal bones. During the first incident, a small part of a single, reasonably large bone (about 6 by 12cm) lay exposed but unrecognised as such (by the observers) on the surface of the earth. The bone was discovered by the male babirusa while he was engaging in **SG** behaviour. The bone was dug out of the ground by lifting the exposed piece of bone with the help of both snout and fore feet. Once clear of the earth, the bone was sucked and moved around in the mouth by both male and female babirusa. It was not clear whether the bone was also chewed, or whether parts of it were ingested. It was recorded as having been eaten. The second set of bones was discovered almost simultaneously by both animals while they were engaged in **SG** behaviour. The bones were completely covered by a grass sod which appeared to have grown over them. The base of the grass sod was manipulated and levered up by means of the snout and forefeet. The roots of the grass did not appear to anchor the grass firmly in the ground. The uncovered bones were a set of vertebrae of a size comparable to those of a cat. Individual vertebrae were taken into the mouth by both male and female after which they were extensively sucked and chewed. The bones were largely spat out again but fragments were heard being ground up, and were ingested. Since both of these occasions were of short duration and isolated instances in time, they did not occupy a large proportion of the recordings. The distribution of the recordings between male and female relates directly to which animal was being observed at that moment in time when the bones were discovered: largely the male.

Feed:
Most of the food offered to the animals in the morning by the zoo staff was eaten prior to the release of the animals into the enclosure. Since the door to the shed stayed open at all times, it was possible for the animals to return to the shed whenever they wished and to search for any remaining food. The recordings referring to the eating of offered food represented 27% of the total number of E recorded.

Another item that was eaten by the female outwith the observation periods was the flower heads of the salad burnet (*Sanguisorba minor* Scop.). The female was observed on several occasions delicately biting off the flower heads of this plant one by one. On one occasion, several minutes were spent picking and eating these flower heads non-stop. The male was never observed to eat any part of this plant.

The regions of the enclosure used by the animals for foraging behaviour (=SG+SV+P+MS) and eating (E) are illustrated in Table 4.10. The bare soil in zone 1 was sniffed by both animals but did not offer very much to eat apart from the occasional cherry. For both animals, the score for eating in zone 2 was larger than that for foraging which might again be explained by the fact that the food was relatively easily obtained. Probing (P=51 in total) was only performed in the loose soil of area 18. Both animals also engaged in a large amount of "surface foraging" (SG+SV) in area 18. It was often not possible to identify what the animals were eating in this zone, but of the identifiable items, cherries were mainly consumed. Cherries were often eaten by both animals in area 15 thereby contributing significantly to high score for E in this region (17 of 40 recordings). The short grass in zone 15 may have made the cherries easier to find, thereby explaining the concentration of foraging behaviour in this region. Cherries were also eaten in zone 16 which also had reasonably short grass. The other major item eaten in zone 15 were bramble leaves from the edges of zones 12 and 19. The high score obtained by the female for E in zone 9 is almost completely explained by the consumption of the bramble leaves in this region (23 of 28 recordings). These same results also contribute to the apparently greater preference of the female for bramble leaves (see Table 4.9).

Social behaviour

Those activities which can be described as social behaviour between the two pigs were **SP, RbP, NN, N, N -> L, L <- N**, and **SAG, W+SAG** and **R+SAG** (combined under social behaviour in Table 4.3). The nature of these behaviours were described and discussed in detail by Leus et al. (1992). They were often seen in the context of reproductive behaviour. The **SAG** behaviour was however the only behaviour that could be described as having an identifiable function. It appeared that sniffing the ano-genital region of the female was the male's way of detecting oestrus in the female. In the present experiment **SAG** behaviour was only performed by the male; the records of **SAG** during the periods that the female was being observed refer to the female having her ano-genital region inspected by the male. The results for **SAG** behaviour are represented in Table 4.11.

Table 4.11 Number of times the male babirusa was recorded sniffing the ano-genital region of the female while both were standing (SAG), walking (W+SAG) or running (R+SAG).

Date	SAG	W+SAG	R+SAG	TOTAL
14/05/93	2	1	0	3
15/05/93	5	1	0	6
16/05/93	5	4	3	12
17/05/93	3	2	2	17
18/05/93	4	4	6	14
TOTAL	19	12	11	42

It appears that there was a gradual increase in total **SAG** behaviour as time progressed. More importantly, however, was the change in the manner and intensity with which the behaviour was performed by the male, and the way in which the female reacted to this. During days one and two, the male inspected the vulva of the female on isolated occasions and only rarely walked behind her for a short distance with his nose close to her vulva. The female was fairly indifferent to this behaviour. From days three to five, however, the male began to follow the female babirusa much more persistently and over longer distances. The female was no longer indifferent to this attention, but would try to run away from the male. This behaviour reached its climax on day 5, when large distances

Table 4.10. Number of recordings of foraging behaviour (F) and eating (E) made in each zone of the enclosure.

Animal	Behaviour	Zone																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Male	F	10	6	0	5	0	0	0	0	11	9	0	0	1	6	39	10	0	57
	E	0	28	0	2	3	0	0	0	1	19	0	0	2	2	23	2	0	15
Female	F	25	13	0	11	0	0	0	0	10	0	0	0	0	1	20	18	0	84
	E	4	23	0	6	0	2	0	1	28	0	0	0	0	5	17	11	0	7
TOTAL	F	35	19	0	16	0	0	0	0	21	9	0	0	1	7	59	28	0	141
	E	4	51	0	8	3	2	0	1	29	19	0	0	2	7	40	13	0	22

F = SG+SV+P+MS
Zones 19-21 were never visited.

were covered in the enclosure by the male running after the female with his nose pointing in the direction of her vulva. During the afternoon of day 5 the male also became less indifferent to the presence of the observer. Several indicators of aggression such as forward pointing of the ears, a characteristic body posture with a slightly raised head, and slight growling noise (see Leus et al., 1992 and Macdonald et al., 1993) were demonstrated by the male.

None of the visual signs of oestrus which are characteristic to the human eye (Leus et al, 1992) could yet be detected on the female's vulva. However, the behaviour of both animals suggested that oestrus was imminent. No mating was observed during the five days of the study period. However, 123 days after the last day of the study, on 18/09/93 a female piglet was born. Since the normal gestation length of the babirusa is about 158 days (Reinhard and Frädrich, 1983; Vercammen, 1991) this means that the female was approximately one month pregnant at the time of the study. The courtship behaviour of the male demonstrated during the present study could not be explained in the light of this event.

The other social behaviours observed such as **NN, N, L<-N, N->L, RbP** and nose in the air behaviour have been observed in previous studies in relation to either reproductive (Leus et al., 1992) or agonistic behaviour (Macdonald et al., 1993).

4. Discussion

This study reports the first observations of babirusa behaviour in a semi-natural environment. Despite the short observation time, it provided a series of important indications with regard to the behaviour and diet of babirusa in the wild.

The use of space by the animals was not random. There appeared to be a positive avoidance of those areas with a rather dense shrub vegetation. The avoidance of these areas was not solely due to the inadequacy of the vegetation as a source of food, since one of the most frequently consumed items, bramble leaves, formed an important part of the vegetation in these areas (see Fig. 4.1). Despite the novelty of the enclosure and the situation and despite the apparent vigilance of the animals during the first day, they did not choose to remain out of sight in the shrubby areas but chose to remain in those areas with a more open vegetation. The thorny nature of the bramble and blackthorn shrubs may have played a role in this decision, although the thick, rough skin of the babirusa might be expected to provide a certain degree of protection against thorns. Observation of wild babirusa in the north of Sulawesi indicated that the animals were extremely vigilant when they came out of the forest into the open area of a natural salt lick, disappearing back into the forest at the least sound or smell (Patry and Capois, 1989; Patry, 1990, Patry pers. comm.). One possible explanation for the difference in behaviour of the zoo animals may have been their unfamiliarity with the semi-natural conditions of the new enclosure. Both animals had spent the first parts of their lives in enclosures with little or no vegetation. The fact that the entrance to zone 16, which was partly concealed by overhanging branches, was not explored until the fourth day of the study, but thereafter received relatively frequent visits, would seem to be consistent with this explanation. For captive animals unfamiliar with dense vegetation, fear of predation may have been associated with the shrubs rather than with the open spaces as is the case in the wild.

The animals spent a large proportion of their time lying or sleeping, possibly because the main part of their diet was offered to them and they were therefore not under pressure to move about looking for food. Observations both in the wild (Patry and Capois, 1989; Patry, 1990) and in captivity (Leus et al., 1992; Leus pers. observ.) indicate that the babirusa are not nocturnal animals and appear to sleep throughout most of the night. However, sleeping during the late morning and afternoon was also observed in other captive situations (Leus et al., 1992) and in the wild, where the animals usually slept through the hottest periods of the day around midday (Selmier, 1983). The weather during the study period was very variable ranging from sunny and warm to chilly and wet. The animals were not observed to sleep outside when it rained; most of the sleeping took place in the shed. This means that when given the choice, the babirusa chose to sleep in the shed under a cover of the straw provided rather than to build a nest out of natural substances in the outdoors. In those instances when the animals did sleep outdoors, no nest was built.

Domestic pigs in a semi-natural environment will construct nests out of branches and tufts of grass if offered no alternative (Stolba and Woodgush, 1989). The building of nests out of branches, leaves, grass and other natural material both for sleeping and for parturition is a common feature of all wild pigs with the exception of the warthogs which live in excavated burrows (Frädrich, 1965, 1967; Radke, 1991). Sleeping nests constructed by wild babirusa have been described by Deninger (1910) and Selmier (1978) and are said to be similar to those of the Eurasian wild pig (*Sus scrofa*). Female babirusa in captivity will incorporate branches into their parturition nest of straw if these are made available (Leus et al., 1992). The lack of nest building activity in the present study could be the result of a reluctance to visit zones with shrubby vegetation, in order to collect nest building material. Alternatively, it could indicate that the straw in the shed provided a perfectly satisfactory replacement material with which to fulfil the babirusa's motivation for nest building in captivity.

The foraging behaviour of the babirusa consisted out of a mixture of **SG**, **SV**, **P** and **MS** behaviour with most recordings being obtained for **SG**. Walking around with the nose close to the ground was a prominent feature of the behaviour of wild babirusa (Selmier, 1983) and has previously been associated with those in captivity; babirusa search in this way for leftover food items and items of food which may have fallen into their enclosure (Leus et al., 1992). The results of the present study also indicate that very few items were taken into the mouth and then discarded. This suggested that the animals were making a selection of food items by smell rather than by taste. A selection of food items based primarily on olfactory signals is considered a typical aspect of concentrate selectors whereas grass eaters have been found to possess more taste buds which are used to test grass palatability by taste (Hofmann, 1989).

Probing only occurred in the loose soil of zone 18. Apart from digging up the bones and the grass sod, no rooting in compact soil was observed. Rooting in the ground with the snout is a predominant feature in the foraging behaviour of most pigs and peccaries (Frädrich, 1967). Domestic pigs in a semi-natural environment were observed to use their snout to turn over clumps of grass and sedge sods, and to dig up tree roots in search of both the roots themselves and any worms which may be found between them (Stolba and Wood-Gush, 1989). Similar behaviour has been observed in the Eurasian wild pig *Sus scrofa* (Briedermann, 1976; Howe et al., 1981; Baber and Coblenz, 1987), the bearded pig *Sus barbatus* (Pfeffer and Caldecott, 1986) and the pigmy hog *Sus salvanius* (Oliver, 1980, 1991). Warthogs (*Phacochoerus africanus*) are very good diggers and can excavate, often with the aid of their tusks, in very compact soil which has baked hard in the sun. Warthogs dig both for the unearthing of roots and tubers and to create burrows (Geigy, 1955; Frädrich, 1965; Field, 1970; Monfort, 1974; Cumming, 1975; Mason, 1982; Rodgers, 1984). Roots and tubers are also very important items in the diet of the bushpig (*Potamochoerus larvatus*), but it has been noted that there is a preference for rooting shortly after rainfall, when the soil is softer (Cumming, 1975; Jones, 1984). Like the babirusa, bushpigs make use of the bridge of their nose rather than the rhinarium for digging. Rooting is also said to be less common in the forest hog (*Hylochoerus meinertzhageni*) (Frädrich, 1967; d'Huart, 1978, 1991).

From the present study it was apparent that the babirusa will root in loose soil and will overturn grass sods when these are not anchored too firmly in the soil. It was obvious, however, that the babirusa inflicted much less damage on the enclosure than wild boar or domestic pigs would have done in a similar time span. After one week of occupation, the only region with upturned soil was zone 18. This lack of extensive digging behaviour by captive babirusa has been noted several times before (Bowles, 1986; Leus et al., 1992). In Lore Kalamanta National Park in Sulawesi, the hunters and guides easily distinguished the tracks of *Sus celebensis* from those of babirusa because of the shape of their furrows. Babirusa make shallow, straight lined furrows, whereas *Sus celebensis* dig deeper and can thrust their snouts in lines that radiate from one spot (Selmier, 1978). It has been suggested that the inability to turn over more compact soil is due to the lack of the well developed rostral bone supporting the rhinarium which is present in other pigs (Stehlin, 1900; Macdonald, 1993).

The turning over of the grass sods only took place after the discovery of bones beneath them following SG behaviour. The roots of the grass sods were not inspected for invertebrates. Observations in the wild, however, have indicated that babirusa will break open rotting wood in search of worms and other invertebrates (Selmier, 1978). Animals in captivity and in the wild have been observed to put their snouts deep into wed mud and to come up with a mouthful of this material; the mud is then allowed to trickle out of the sides of the mouth (Leus et al., 1992; Patry, pers. comm.). It was suggested that invertebrates might be collected in this way (Leus et al., 1992). The present study did not shed light on the extent to which babirusa will eat roots, tubers and invertebrates that might be turned up during rooting behaviour. Only once was the male observed to eat a tuft of herbal roots from zone 18. The soil in this zone was rather dry and did not seem to contain many invertebrates of any kind.
Apart from the food that was offered to them, the items most eaten by the babirusa were bramble leaves and the unripe fruits of the cherry trees. Other items consumed more than once included cherry leaves, cherry twigs and rose leaves. They demonstrated a careful selection of plant parts when eating grass and herbs, selecting the leaves of downy oatgrass (*Helictotrichon pubescens* (Hudson) Pilger), the ears of soft-brome (*Bromus hordeaceus* L.) and the flowers of salad burnet (*Sanguisorba minor* Scop.). These results suggest that the babirusa in the wild will make a careful selection of the plants and plant parts which are available and that they may to show a preference for fruits and dicotyledonous plant parts rather than grasses. The ease and eagerness with which the animals detected and uncovered the old bones suggest that babirusa also include a certain proportion of animal matter in their diet.

All pigs and peccaries have a diet which is composed of a mixture of leaves, flowers, fruits, stems and roots of dicotyledonous and monocotyledonous plants together with a certain amount of animal matter in the form of invertebrates, small vertebrates and carrion (Frädrich, 1967). The difference between the diets of different pig species seems to lie more with the differences in the proportions of each of the diet's constituent parts than with the kind of constituents themselves.

Warthogs predominantly feed on grasses, taking only a small proportion of dicotyledonous plant parts and animal matter (Geigy, 1955; Frädrich, 1965; Field, 1970; Monfort, 1974; Cumming, 1975; Mason, 1982; Rodgers, 1984). During the wet season, the aerial parts of the grasses are preferred. During the dry season more rhizomes are eaten because of the decline in digestibility of the aerial parts of the grasses during that season (Field, 1970; Cumming, 1975; Mason, 1982; Rodgers, 1984). When grazing on short grasses, or digging, warthogs take on a characteristic posture of kneeling on the carpal joints of their front legs (Frädrich, 1965; Field, 1970; Monfort, 1974; Cumming, 1975; Mason, 1982). Babirusa have never been observed to graze on short grasses, either in the present study or in the past (Bowles, 1986; Leus et al., 1992). Warthogs also feed on the leaves of taller grasses which they pick in the same fashion as the babirusa (Cumming, 1975). The cropping of seed heads of tall grasses by warthogs is done by taking the stem into the mouth and moving the mouth towards the top of the grass. When the flower head is reached this is pulled off by a short upward toss of the head (Cumming, 1975). The male babirusa was observed to pick the seed ears directly off the soft-brome grass (*Bromus hordeaceus* L.).

Fruit and aerial herbaceous material together with roots, tubers and rhizomes form the most important items in the diet of the bushpig (Skinner et al., 1976; Breytenbach and Skinner, 1982; Jones, 1984; Seydack, 1990). Bushpigs showed a high degree of selectivity in the plant species and plant parts eaten and this selection was partly season-dependant (Breytenbach and Skinner, 1982). The subterranean fraction of the diet becomes more important during drier seasons (or in drier areas). Rooting also tends to be especially prominent after showers of rain (Breytenbach and Skinner, 1982; Jones, 1984; Seydack, 1990). With the exception of fruits, it seems leaves and other aerial parts of trees and shrubs were seldom part of the diet of bushpigs (Skinner et al., 1976; Breytenbach and Skinner, 1982; Jones, 1984; Seydack, 1990).

The composition of the diet of the Eurasian wild pig is very dependent on the ease of access which the animals have to agricultural sites, and to forest trees with a potentially high production of autumn fruits such as acorns and beach nuts (Briedermann, 1976, 1990; Genov, 1981; Dardaillon, 1987, Gerard et al., 1991). During a good fruiting year, acorns and beach nuts comprise more than 50% of the diet from October to August (Briedermann, 1976, 1990). Even during the remaining months of the year they form important food items. When agricultural products such as potatoes and grains are accessible, they often form a major part of the diet during the late spring and summer months (Briedermann, 1976, 1990; Gerard et al., 1991). During bad fruiting years, agricultural products together with subterranean plant parts and herbal material become more important. When no agricultural products are available, fruit and seeds remain the preferred items and are consumed whenever these are available (Baber and Coblentz, 1987). Roots are included more during the dry seasons, and herbaceous material and grasses during the wet season. When no fruits or agricultural products are available, herbaceous material and roots make up the bulk of the diet (Howe et al., 1981; Dardaillon, 1987). Generally, very few tree and shrub leaves are eaten (Briedermann, 1976, 1990; Howe et al., 1981; Baber and Coblentz, 1987). Although animal products are always present, the proportion remains small (Briedermann, 1976, 1990; Genov, 1981; Howe et al., 1981; Baber and Coblentz, 1987).

Fruit also appears to be the preferred food of the bearded pigs, their body condition largely depending on its availability (Caldecott and Pfeffer, 1986). Some populations of this species will travel long distances in search of fruits (Caldecott, 1993). Sedentary populations bridge the non-fruiting season with roots and shoots as well as agricultural products found in local gardens (Caldecott and Pfeffer, 1986).

Peccaries occur in a wide range of habitats from tropical through to arid environments. In tropical rain forests they are predominantly frugivorous (Kiltie, 1981) whereas the diet of peccaries in the arid region is characterised by a high inclusion of the both pads, flowers and fruits of cactuses, especially the prickly pear cactus *Opuntia* (Corn and Warren, 1986; Taber, 1991; March, 1991; Schmidt, 1991). The nutritional value of the cactus is thought to be low and its importance probably lies with the provision of water in these arid regions (Sowls, 1984). Collared peccaries (*Tayassu tajacu*) and White lipped peccaries (*Tayassu pecari*) are known to root and ingest subterranean plant parts whereas the Chacoan peccary

(*Catagonus wagneri*) does not seem to root very often (Taber, 1991). All three species supplement fruit and/or cacti with herbaceous matter, a limited amount of shrub and tree leaves, flowers, grass and animal matter (Kiltie, 1982; Corn and Warren, 1986; Taber, 1990; March, 1991; Schmidt, 1991).

The scarce information on the diet of babirusa in the wild, as well as their behaviour in zoo enclosure and in the semi-natural conditions of the present study indicate that babirusa cannot be considered grazers like the warthogs. Grass may be included in the diet but is not likely to represent the main constituent. The warthog excluded, all other pigs and peccaries seemed to have a marked preference for fruits. The ingestion of unripe cherry fruits in the present study, the inclusion of fruit in the diet of wild animals (Selmier, 1983) and the preference for fruit expressed by animals in captivity (see Chapter 5) make it likely that fruit forms an important part of the diet of babirusa in the wild.

Leaves of shrubs and trees formed a very small proportion of the diet of all the other pig species. This is in contrast to a number of observations for the babirusa. In the present study bramble leaves were one of the most eaten items, and leaves of wild roses and the cherry trees were also readily consumed. Babirusa in captivity readily consume leaves of the wide range of shrub and tree species that are offered to them (Chapter 5) and go to considerable lengths to forage leaves of trees in, or next to, their own enclosure; animals in several zoos were regularly seen to stand on their hind legs while leaning against a wall or fence to reach the leaves of overhanging trees (Leus and Macdonald pers. comm.). Female babirusa in Surabaya Zoo were also observed to stand upright on their hind legs without any support for prolonged periods of time while eating the leaves of the few trees in their enclosure (Macdonald et al., 1993). Early reports of the diet of babirusa in the wild included tree leaves (Valentijn, 1726). At the present moment, however, it is only possible to conclude that the leaves of shrubs and trees are likely to form a part of the diet of babirusa. The extend of their importance in the diet will require more extensive and prolonged studies in the wild or in semi-natural conditions where the animals are dependant on growing vegetation for a larger proportion of their total diet.

Contrary to the other pig and peccary species, the babirusa in the present study did not consume any of the wide range of herbs available apart from the flowers of the salad burnet (Sanguisorba minor Scop.) which were consumed by the female. However, one of the favourite food items of the babirusa in Lore Kalamanta, Sulawesi is said to be *Elatostema* (Urticaceae) a non-stinging herb of the nettle family. Furthermore, babirusa in Surabaya and Jakarta Zoo are fed relatively large quantities of "kangkong" (*Ipomoea aquatica* Forsk. (Conv.)), a water plant, which is readily eaten by them. Although herbs are likely to be in short supply in the lowland rain forest, babirusa do seem to include a certain proportion of herbs in their diet. The importance of this fraction in the diet, once again can only be assessed by further studies.

Babirusa in captivity have been observed to catch and eat small vertebrates such as mice, rabbits, ducks and pigeons (Leus et al., 1992). The trapping of small vertebrates as well as the inclusion of carrion and invertebrates in the diet is known of all wild pig species. The interest of the babirusa in the old bones found in the enclosure is therefore unremarkable among the Suidae.

The diets of ungulates have so far been considered to represent a continuous series between the browser and grazer extremes (McNaughton and Georgiadis, 1986; Hoffmann, 1989). Browsers are less capable of digesting plant cell wall constituents than grazers and therefore carefully select more easily digestible plant parts with a large amount of easily accessible plant cell contents. Because of these characteristics, Hoffmann (1989) suggested the more accurate term "concentrate selectors" as a replacement for "browsers". Bodmer (1990) argued that this continuum of ungulate diets should be extended with the inclusion of frugivores: Frugivores maintain a diet of fruits throughout the year, intermediate frugivores or frugivore/concentrate selectors feed on fruits when these are available and supplement their diet with browse, concentrate selectors maintain a diet of parts of mostly woody dicotyledonous plants throughout the year, intermediate concentrate selectors/grazers switch between concentrate selection and grazing whereas pure grazers subsist on a diet of almost exclusively grasses all year round (McNaughton and Georgiadis, 1986; Hoffmann, 1989; Bodmer, 1990). It is noteworthy that many frugivores and frugivore-concentrate selectors are non-ruminant foregut fermenters, whereas the concentrate selectors through to the grazers are mostly ruminants (Bodmer, 1990). This difference in digestive strategies reflects the nature of the vegetation consumed by each group. Grasses contain more cell wall constituents and less cell solubles whereas fruits herbs and woody plants contain more cell contents and less cell wall constituents. Foregut fermentation is important even in frugivores in order to digest the cell wall constituents and the various structural fruit protection mechanisms. The efficiency of this digestive mechanism becomes more and more important as more browse, and especially grasses are incorporated into the diet.

5. Conclusions

When given access to a semi-natural enclosure most of the foraging by the babirusa was carried out by walking around with the nose close to or on the ground surface while sniffing. Rooting only took place in that part of the enclosure with very loose sand and was never observed in regions with a more compact soil. The two most important food items consumed by the babirusa (in addition to the food that was offered to them by the zoo staff) were bramble leaves and cherry fruits. The animals demonstrated their ability to carefully select certain plant parts when eating herbs and grasses. These results suggested that the babirusa belongs to the category of "non-ruminant foregut fermenting frugivore/ concentrate selectors", animals which have the ability to carefully select those plants and plant parts which are more easily digestible. The latter include fruits and dicotyledonous plant parts rather than monocotyledonous plants such as grasses. The lack of extensive rooting suggested that roots are less important to the diet of the babirusa than they are to those of other pigs. Leaves formed only a minor proportion of the diet of other wild pigs but results of the present study suggested they might be more important to the babirusa.

CHAPTER 5: ANALYSES OF DIETS FED TO BABIRUSA IN CAPTIVITY

1. Introduction

Information on the composition of the diet of babirusa in the wild is limited to a few general statements, indicating that they eat leaves, roots and fruits as well as invertebrates, meat and fish (Valentijn, 1726; Whitten, et al, 1987; Macdonald, 1991). Despite this lack of information on their food habits in the wild, babirusa have been successfully kept in captivity for at least 200 years. The first babirusa kept in Europe were housed in la Menagerie du Roi, Paris, and were fed on a mixture of grass, herbs, roots, fruits and grains as well as occasional animal matter (Geoffroy-St-Hillaire and Cuvier, 1842). In more recent times babirusa in zoos around the world are still fed a mixture of roughly the same items. When visiting zoos housing babirusa it was noticed that the relative proportions of these items fed to the babirusa seemed very different from zoo to zoo and that the animals showed preferences and dislikes for certain products.

In this chapter an analysis will be presented of the nature of ingredients in and the nutritional composition of the diets fed to babirusa in zoos world-wide. The nature of the ingredients offered and the preferences and dislikes of the animals for some of these food items will be discussed in the light of the hypothesis of non-ruminant forestomach fermenting presented in chapter 2 and the results of the digestion and foraging study in chapters 3 and 4 respectively. The nutritional composition of the diets will be assessed according to the protein and energy requirements of the babirusa as estimated from prediction equations developed for modern pig breeds. The feasibility of application to the babirusa of a food selection technique designed to measure the protein requirements of pigs will also be investigated.

2. Materials and methods

Collection of data

Between March 1991 and May 1993 all zoos world-wide housing babirusa (16 zoos in Europe, 7 in the United States and 2 in Indonesia) were sent a questionnaire. A copy of the questionnaire can be found at the end of the materials and methods section. It requested information on the constituents of the diet, the way in which the food was offered, the daily amounts fed and the preferences and dislikes of the animals. It was requested that the amounts given would be for adult males and females. Additional information was gathered during personal visits to some of the European zoos. Data of a sufficiently detailed nature that allowed analysis of the diet's nutritional contents was received from a total of 19 zoos (13 from Europe and 6 from the United States) containing a total of 79 babirusa (38 males and 41 females). Each zoo was allocated a code number and will be referred to by means of this number throughout this section of the thesis. One zoo had two slightly different diets for the two groups of babirusa in different locations of the zoo and was allocated two code numbers.

Analyses

Items fed to the animals were divided into four categories: 1) fruit and vegetables (**F&V**); 2) pellets, grains, bread, nuts and oils (**P&G**); 3) meat, fish and eggs (**Meat**); 4) forage (including grass, hay, alfalfa, hydroponic barley, branches, leaves etc.). The amount of dry matter (DM), crude protein(CP), fat, Englyst fibre (EF) and digestible energy (DE) for individual items within these categories was calculated from the data published by Holland et al. (1991), ADAS (1986), Jones (1979) and Schemmel et al. (1969). The nutrient content of commercial pellets was calculated either from the labels sent by the zoos, or in the absence of labels estimated from available information for similar pellets. Englyst fibre represents the fibre fraction often referred to as non-starch polysaccharides (NSP) which are the polysaccharides left over after the starch has been digested away (Englyst, 1989). Digestible energy equals the total energy potential contained in the feedstuff, minus the undigested energy contained in the faeces of a certain animal species. Metabolisable energy (=DE - energy retained in urine - energy retained in excreted gasses) is a better measurement of the true amount of utilisable energy in the feed stuff but has the disadvantage that it is not only dependant on the feed item but also on the metabolic state of an individual pig at the moment in time when the feed item is ingested. The DE is therefore considered to be the best pig-independent descriptor of a feedstuff (Whittemore, 1993). The best estimate for DE values for foods fed to the babirusa were either derived from values measured in the domestic pig (ADAS, 1986) or it was calculated from the formula:

$$\text{DE(MJ/kgDM)} = \frac{\text{CP(g/kgDM)} \times 18 + \text{Ether extract(g/kgDM)} \times 31.5 + \text{carbohydrate(g/kgDM)} \times 16.3 - \text{EF(g/kgDM)} \times 14.9}{0.96}$$

which was adapted from the equation published by the EAAP Working Group Provisional Equation (Batterham,1990). The equation is based on the observation that crude protein (CP), lipid (Ether extract), carbohydrates in general and fibre all contribute different proportions to the overall DE value of the diet (Morgan et al., 1984; Whittemore, 1993).

When certain items were not given daily, but more than three times per week, the total amount per week was divided by 7 to establish a daily rate. If this daily rate was equal to, or more than 50g, the item was included in the overall calculations.

Information on the nature and amounts of forage ingested was often too vague to allow even rough analyses of its nutritional composition. Because of this, the basal diet without the forage included will be discussed first and compared between the zoos and between male and female animals. Afterwards, an overview and brief discussion of the different kinds of forage fed by all the zoos will be given and the effect of forage on the daily intake of protein and other nutrients will be discussed for a few zoos which fed a fixed amount of forage daily and all year round. Data on vitamin and mineral supplements were often too vague and will not form part of the present study.

INTERNATIONAL BABIRUSA DIET RESEARCH QUESTIONNAIRE

* Please attach additional sheets or copies if necessary

** If the answer to a certain question is not known or the information not available do not leave blanks but please put "not known" in the space provided.

*** In case of multiple choice, it is possible that more than one of the given options is applicable to your situation.

I. ADMINISTRATIVE INFORMATION

1. A. Name of the Institution:

B. Name and title of person reporting:

2. List of all babirusas kept at this moment:

Sex	Name and/or Number	(Estimated) Date of Birth	Mother (name and/ or number)	Father (name and/ or number	Arriving Date

II. DIET

1. Basic diet of an adult animal (> 3 years old).

A. FRUIT AND VEGETABLES:

ITEM	AMOUNT (weight)		FORM (raw, cooked, with or without peel, whole, pieces...)	FREQUENCY (daily, once a week, seasonal,...)
	male	female		

B. COMMERCIAL PELLETS AND GRAINS:

ITEM	AMOUNT (weight)		FORM (wet, dry, powder, pellets...)	FREQUENCY (daily, once a week, seasonal,...)
	male	female		

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C. GRASS, LEAVES AND BRANCHES:

ITEM	AMOUNT (weight)		FREQUENCY (daily, once a week, seasonal...)	PARTS EATEN (entirely, only bark...
	male	female		

D. OTHERS (meat...)

ITEM	AMOUNT (weight)		FORM	FREQUENCY (daily, once a week, seasonal...
	male	female		

2. Vitamin and/or mineral supplements:

ITEM	AMOUNT (adults)		FREQUENCY	ADMINISTRATION (in water, on food, injected...
	male	female		

3. Do the animals have access to a salt lick: yes / no

4. A. How much water do the animals drink each day?

B. Is the water supplied by:

- ○ automatic drinknipple
- ○ watering-trough
- ○ natural watercourse (..........)
- ○ others (..........)

III. FEEDING METHODS

1. Are the animals fed:

○ singly

○ all together

○ in different groups

age/sex composition of the groups:

____

____

____

____

____

2. At what time(s) are the animals fed each day. What is fed at each meal? Is there any fixed order in which food items are offered?

3. How is the food offered to the animals? (e.g. on the floor or in a manger, as separate items or mixed, in separate locations in the pen, branches suspended over pen...)

IV. FEEDING BEHAVIOUR

1. In your opinion, do the animals show:

   A. A clear preference for certain food items. If so, how is this shown? (e.g. an item that is always eaten first or part of an item e.g. banana but not the skin.)

   B. A clear dislike for certain food items? If so, how is this shown? (e.g. an item that is never eaten completely etc.)

2. Are there items which are eaten by the animals when they are offered in one form but not when they are offered in another form? (e.g. a certain fruit item that is eaten with the peel, but not when the peel is removed in advance; or items that are accepted as a whole, but not when they are cut to pieces etc.)

3. A. What bedding is used?

B. What nesting material is provided?

* for males:

* for females:

C. From what age is nesting material provided?

4. Which of the following items: branches, trunks, leaves, grass, earth, wet mud, faecal material, bedding material, nesting material: is used by the animals for:

- playing: ______
- eating: ______
- nest building: ______

V. VETERINARY ASPECTS

1. By experience: which items cause distress or sickness of the animal after being eaten:
(in case there was suspicion but not certainty that the item caused the distress, underline the item)

ITEM	AMOUNT GIVEN TO ANIMAL	AGE OF ANIMAL	SEX OF ANIMAL	SYMPTOMS

2. By experience: which items are absolutely indispensible in the diet, i.e. they cause sickness or distress when they are not included in the diet.
(if you suspect that the symptoms shown by the animal at that time are caused by the absence of the item in the diet, but you are not sure, underline the item)

ITEM	SYMPTOMS	MINIMUM AMOUNT OF ITEM REQUIRED TO AVOID DISTRESS

3. Does the eating of certain items (maybe in certain amounts) have clear consequenses on the composition and consistency of the faeces? (without causing distress or sickness)

ITEM	AMOUNT GIVEN	EFFECT ON FAECES

4. If possible, give a weight list of your animals:

Name and/or number	Sex	(Estimated) Date of Birth	Date of weighing	Weight

==

VI. COMMENTS AND ADDITIONAL INFORMATION OR OBSERVATIONS?

==

COPY OF RESULTS DESIRED: YES / NO

3. Results

Basal diets without forage

A complete list of the **F&V**, **P&G** and **Meat** items fed to the babirusa is illustrated in Table 5.1. Babirusa were fed a wide variety of fruit and vegetables. The most frequently included items were apples, bananas, lettuce and oranges, probably because these are most available. The diet of the babirusa in most zoos was built up around a relatively fixed set of core items which were easily available all year round. These core items were then supplemented with smaller amounts of seasonal fruits and vegetables. Potatoes were usually fed boiled but were sometimes also offered raw. The opposite is true for carrots which were usually fed raw but sometimes also boiled. Most zoos fed bananas without the peels to avoid ingestion of pesticides, but a few institutions fed bananas with peels. Grains were fed in a number of different ways from ground to sprouting. Most zoos included a commercial pellet for herbivores or cattle, the brand of which varied from zoo to zoo. These pellets were included in the table under the name "herbivore pellets". Apart from these, commercial pellets for horses or pigs were also fed. Dog chow came in the form of pellets and biscuits and was included with the pellets and grains group for the analyses.

The total amounts of food fed each day to male and female animals is illustrated in Fig. 5.1. The amount of food was plotted in ascending order according to the amounts fed to the males to illustrate the wide range of amounts fed (males: 1400g - 4770g; females: 1400g - 4450g). Zoo 20 only housed female animals and zoo 11 only housed male animals, explaining the zero values for males and females in these institutions respectively. In 9 cases, male and female animals were fed the same amount of food, whereas in the other 9 cases the females were fed a smaller amount of food. The female ration expressed as a percentage of that of the male was not consistent, ranging from 63% (zoo 4) to 98% (zoo 6) (Table 5.2). The range of amounts fed to the males appears more continuous than that for the females, 12 out of 20 zoos feeding their females between 2 and 3kg of foods.

Table 5.1 List of Fruit and vegetables (F&V), Pellets and grains (P&G) and Meat items fed to babirusa in captivity.

Item	Form	No zoos
F&V		
Acorns	raw	2
Apple	with peel	19
Aubergine	raw with peel	2
Avocado	raw without stone	1
Banana	with and without peel	18
Broccoli	raw	3
Cabbage	raw	4
Carrots	raw and boiled	15
Cauliflower	raw	3
Celery	raw	8
Cherries	with stones	2
Chicory	raw	2
China cabbage	raw	2
Coconut	raw	1
Corn-salad	raw	1
Cucumber	raw with peel	5
Endive	raw	3
Fennel	raw	3
Fodder beet	raw	3
French beans	raw	1
Grapefruit	without peel	1
Grapes	with peel and stone	4
Green cabbage	raw	1
Horse-chestnuts	raw	1
Kale	raw	1
Kiwi	with peel	4
Kohlrabi	raw	2
Lamb's lettuce	raw	1
Leek	raw	6
Lettuce	raw	15
Mandarins	without peel	1
Medlar	raw	1
Melon	with peel	2
Nectarins	without stone	1
Onion	raw	3
Oranges	without peel	11
Parsley	raw	1
Peach	with peel and stone	4
Pears	with peel	5
Pineapple	with peel	6
Plums	with peel and stone	7

Table 5.1 continued

Potatoes	raw and boiled	8
Pumpkin	raw with peel and seeds	2
Radish	raw	1
Red beets	raw	2
Red cabbage	raw	1
Salsify	raw	1
Savoy	raw	1
Soya sprouts	raw	1
Spinach	raw	3
String beans	raw	1
Sweet chestnut	raw	5
Turnips	raw	1
Water melon	raw with peel	1
White cabbage	raw	2
Yams	raw and cooked	5
Zucchini	with seeds and peel	1
<u>P&G:</u>		
Barley	dry	1
Biscuits	dry	1
Bran	dry	4
Bread	brown and white	7
Corn on the cob	fresh	1
Corn	fresh and dry	5
Corn oil	fluid	1
Dog chow	pellets/biscuits	5
Germinated corn	fresh	1
Germinated wheat	fresh	3
Herbivore pellets	pellets dry	12
Horse pellet	pellets dry	1
Maize meel	dry	2
Nutritional yeast	dry	1
Peanuts	dry	4
Pig pellet	pellets dry	5
Rice	cooked	2
Rolled corn	dry	1
Rolled oats	dry	8
Soya meel	dry	1
Sunflower seeds	dry	2
Textured grain	dry	1
Toast	brown and white	1
Vegetable oil	fluid	1
Walnuts	with shell	1
Wheat	dry	1
Wheat	ground	1

Table 5.1 continued

<u>Meat:</u>		
Beef Meat	raw and boiled	3
Chicks (one day old)	whole	6
Crickets	whole	1
Egg	raw and boiled, with shell	5
Fish	raw	2
Grasshoppers	whole	1
Mice	whole, skinned	1
Rats	whole, skinned	1
Skimmed milk powder	dry	1

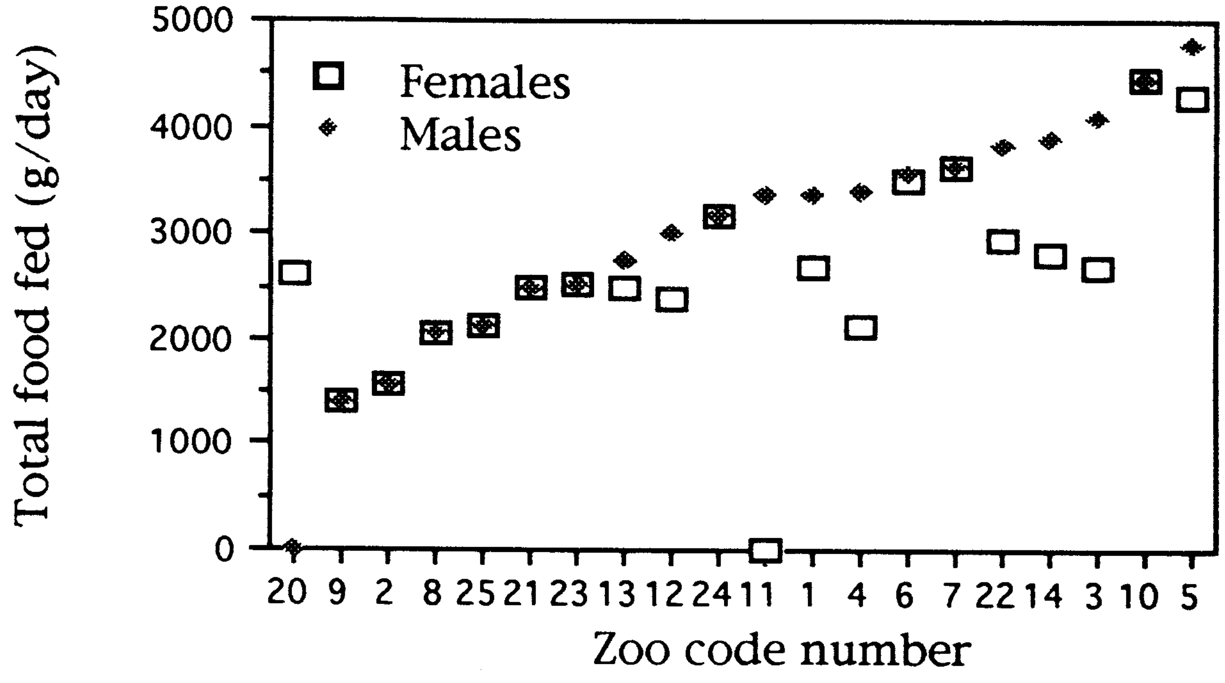

Fig. 5.1. Total amount of food fed to male and female babirusa in captivity.

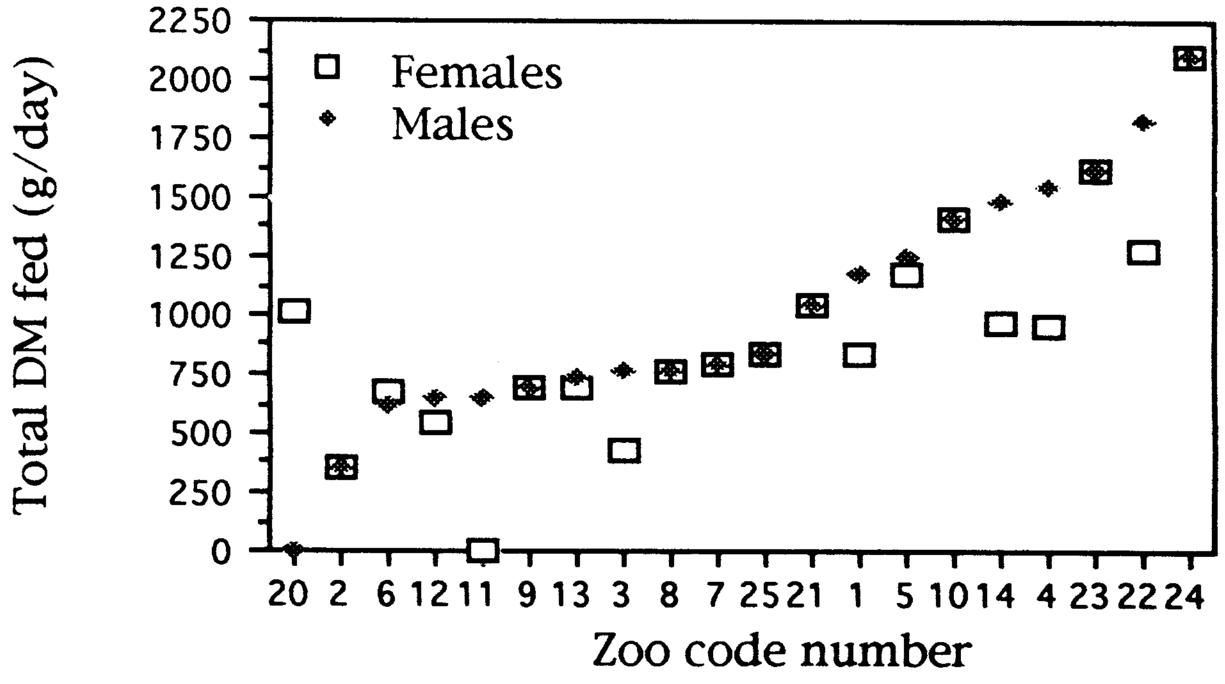

Fig. 5.2. Total amount of dry matter (DM) fed to male and female babirusa in captivity.

The amount of dry matter (DM) that is offered each day to males and females is illustrated in Fig. 5.2. The data were again plotted in an ascending fashion according to the amounts fed to the males. As for the total amount of food fed, there is a large range in the amount of DM received by the animals, ranging for both males and females between 355g and 2108g. Note however that the sequence of the zoo code numbers on the x-axis is different from that in Fig. 5.1. This demonstrates that the zoos feeding the highest amounts of food are not necessarily those which also feed the highest amounts of DM. This is well demonstrated by zoos 24, 23, 11, 6, 5 and 3. The change in the sequence of the zoo code numbers on the x-axis of the figures does not allow for an easy overview of the variation between the different zoos for the main diet criteria. For this reason, the amounts of the different food categories and the amounts of DM, CP, fat, EF and DE fed daily to male and female babirusa in the different zoos were summarised in Table 5.1b and 5.1c. For eight zoos, the DM rations for females were proportionally lower than those for males. The percentage of the male DM ration fed to the female did not always correspond with the percentage of the male fresh food ration fed to the female (Table 5.2). Zoo 6 seemed to be feeding its female slightly less food in wet weight (98%) whereas in fact she is receiving slightly more DM (8.8%) than the male. In the opposite direction, females in zoo 1 received 79% of the male fresh weight ration but only 69% of the male DM ration.

The discrepancy between the total amount of food fed and the amount of DM fed appears to be explained by differences in the proportions of the various food categories (fruit and vegetable (**F&V**); pellets, grains, bread, nuts and oils (**P&G**); and meat, fish and eggs (**Meat**)) within the diet. Figures 5.3a, b and 5.4a, b and Table 5.1b indicate that both for males and females, those zoos which feed their animals a large amount of **F&V** are generally also those zoos in which the animals receive relatively little DM. Vice versa, those zoos which feed their animals a lot of **P&G** are generally also those zoos in which the animals receive a relatively large amount of DM.

The differences in the proportions of the different food categories fed to the animals in different zoos also explains the inconsistency in the sequence of the zoo code numbers on the x-axes of Fig. 5.5-5.7. These

Table 5.1b Total amount of food (fresh weight), dry matter (DM), Fruit and Vegetables (F&V), Pellets and Grains (P&G) and Meat fed to male (M) and female (F) babirusa in captivity.

Zoo Code No.	Total Amount food fed (g/day)		Total DM fed (g/day)		Total F&V fed (g/day)		Total P&G fed (g/day)		Total Meat fed (g/day)	
	M	F	M	F	M	F	M	F	M	F
1	**3375**	2675	**1175**	831	**2400**	2000	**975**	675	**0**	0
2	**1570**	1570	**356**	356	**1200**	1200	**320**	320	**50**	50
3	**4100**	2685	**762**	431	**3665**	2400	**350**	200	**85**	85
4	**3390**	2140	**1539**	949	**1540**	1040	**1300**	800	**550**	300
5	**4770**	4270	**1250**	1173	**3770**	3270	**940**	940	**60**	60
6	**3550**	3490	**617**	671	**3360**	3300	**190**	190	**0**	0
7	**3617**	3617	**789**	789	**2862**	2862	**655**	655	**100**	100
8	**2070**	2070	**765**	765	**1370**	1370	**580**	580	**120**	120
9	**1400**	1400	**695**	695	**700**	700	**700**	700	**0**	0
10	**4450**	4450	**1409**	1409	**3300**	3300	**1150**	1150	**0**	0
11	**3355**	/	**648**	/	**3055**	/	**300**	/	**0**	/
12	**3000**	2400	**641**	548	**2680**	2080	**200**	200	**120**	120
13	**2735**	2485	**734**	685	**2200**	1950	**415**	415	**120**	120
14	**3900**	2800	**1491**	967	**2000**	1600	**1220**	820	**680**	380
20	/	2630	/	1011	/	1740	/	890	/	0
21	**2500**	2500	**1044**	1044	**1500**	1500	**1000**	1000	**0**	0
22	**3825**	2925	**1828**	1276	**2000**	1700	**1825**	1225	**0**	0
23	**2520**	2520	**1619**	1619	**920**	920	**1600**	1600	**0**	0
24	**3160**	3160	**2108**	2108	**900**	900	**2260**	2260	**0**	0
25	**2140**	2140	**834**	834	**1440**	1440	700	700	**0**	0

Table 5.1c Total amount of crude protein (CP), fat, Englyst fibre (EF) and digestible energy (DE) contained in, and the protein:energy ratio of, the diet fed daily to male (M) and female (F) babirusa in captivity.

Zoo Code No.	Total Amount CP fed (g/day)		Total Amount fat fed (g/day)		Total Amount EF fed (g/day)		Total Amount DE fed (MJ/day)		Protein:Energy ratio (CP(g)/DE(MJ))	
	M	F	M	F	M	F	M	F	M	F
1	**181**	123	**48**	33	**313**	216	**15**	11	**12**	11
2	**43**	43	**43**	43	**20**	20	**6**	6	**7**	7
3	**108**	69	**34**	26	**162**	100	**10**	5	**11**	13
4	**218**	137	**142**	82	**160**	115	**21**	13	**10**	10
5	**144**	146	**137**	135	**247**	237	**18**	17	**8**	9
6	**53**	54	**23**	23	**92**	88	**8**	9	**7**	6
7	**55**	55	**23**	23	**61**	61	**8**	8	**7**	7
8	**80**	80	**63**	63	**84**	84	**12**	12	**7**	7
9	**123**	123	**30**	30	**219**	219	**9**	9	**14**	14
10	**158**	158	**46**	46	**227**	227	**20**	20	**8**	8
11	**82**	/	**42**	/	**124**	/	**8**	/	**10**	/
12	**60**	56	**11**	11	**88**	75	**9**	8	**7**	7
13	**76**	71	**19**	19	**94**	91	**10**	10	**7**	7
14	**346**	205	**151**	88	**335**	209	**22**	14	**16**	14
20	**/**	160	**/**	49	**/**	158	**/**	15	**/**	10
21	**190**	190	**91**	91	**245**	245	**14**	14	**14**	14
22	**399**	262	**129**	89	**472**	337	**24**	16	**17**	16
23	**236**	236	**51**	51	**325**	325	**19**	19	**12**	12
24	**364**	364	**81**	81	**517**	517	**29**	29	**13**	13
25	**167**	167	**50**	50	**186**	186	**12**	12	**14**	14

Table 5.2 Percentages of the male's rations fed to the female babirusa in captivity

Zoo code number	% Total food	% F&V	%P&G	% Meat	% DM	% CP	% Fat	% EF	% DE
1	79.26	83.33	69.23	/	70.71	67.58	68.64	69.05	71.36
3	65.49	65.48	57.14	100.00	56.56	63.73	74.39	61.75	53.67
4	63.13	67.53	61.54	54.55	61.64	63.05	57.81	71.99	61.69
5	89.52	86.74	100.00	100.00	93.89	101.36	99.19	96.15	94.07
6	98.31	98.21	100.00	/	108.81	102.07	97.86	96.51	115.46
12	80.00	77.61	100.00	100.00	85.49	92.90	95.96	85.51	86.41
13	90.86	88.64	100.00	100.00	93.29	94.06	98.67	96.81	92.88
14	71.79	80.00	67.21	55.88	64.80	59.35	58.53	62.55	62.37
22	76.47	85.00	67.12	/	69.81	65.80	69.17	71.46	68.52

/ = No meat was fed in these zoos.

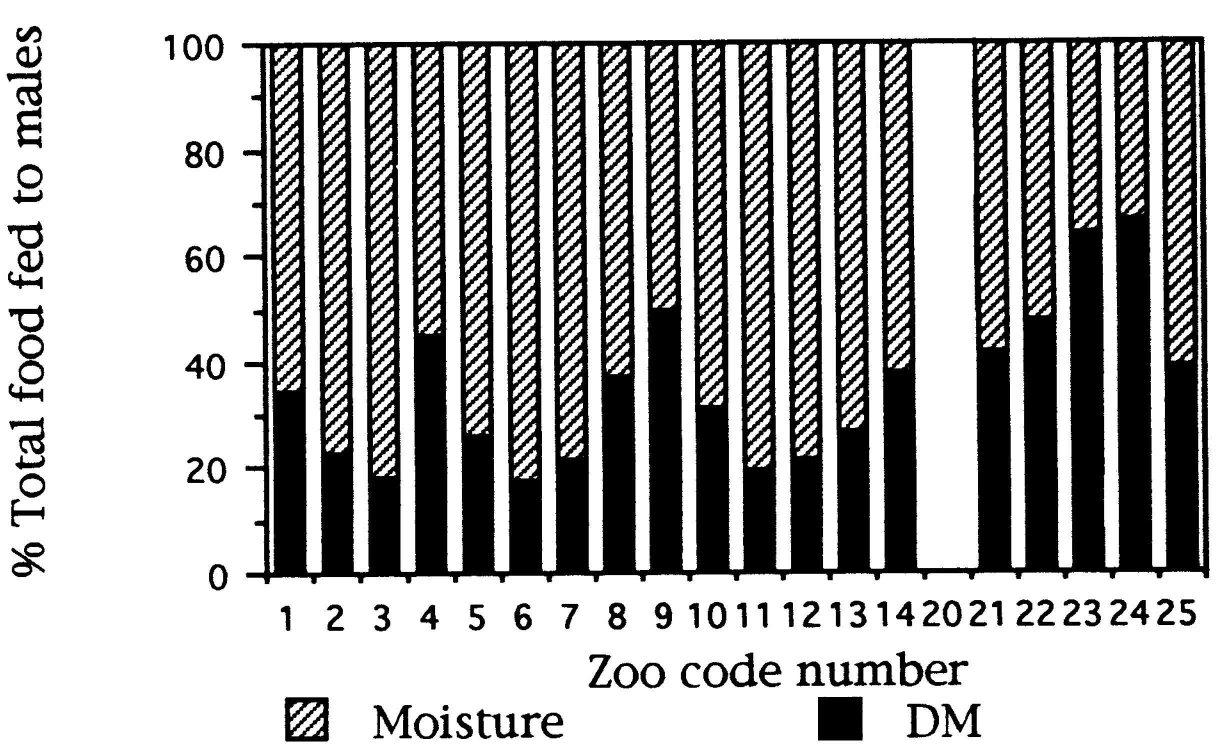

Fig. 5.3a Percentage of dry matter (DM) and moisture in the total amount of food fed to adult male babirusa in captivity.

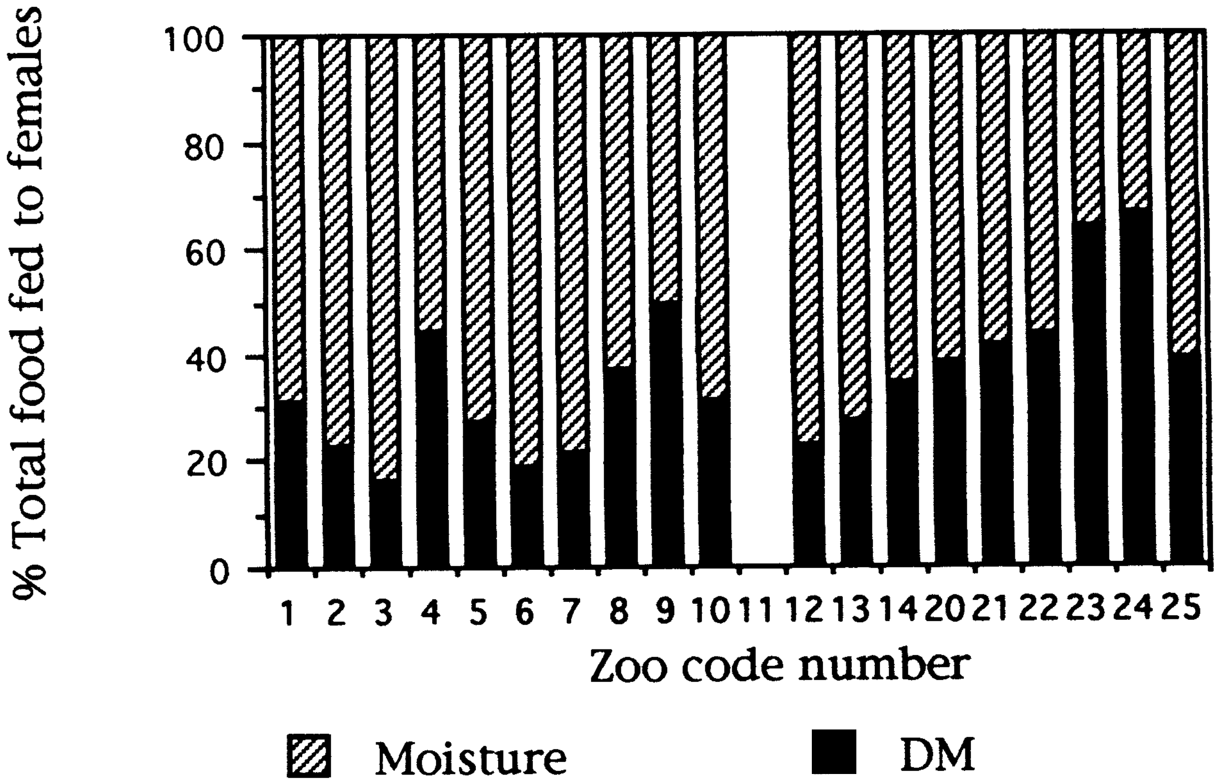

Fig. 5.3b Percentage of dry matter (DM) and moisture in the total amount of food fed to adult female babirusa in captivity.

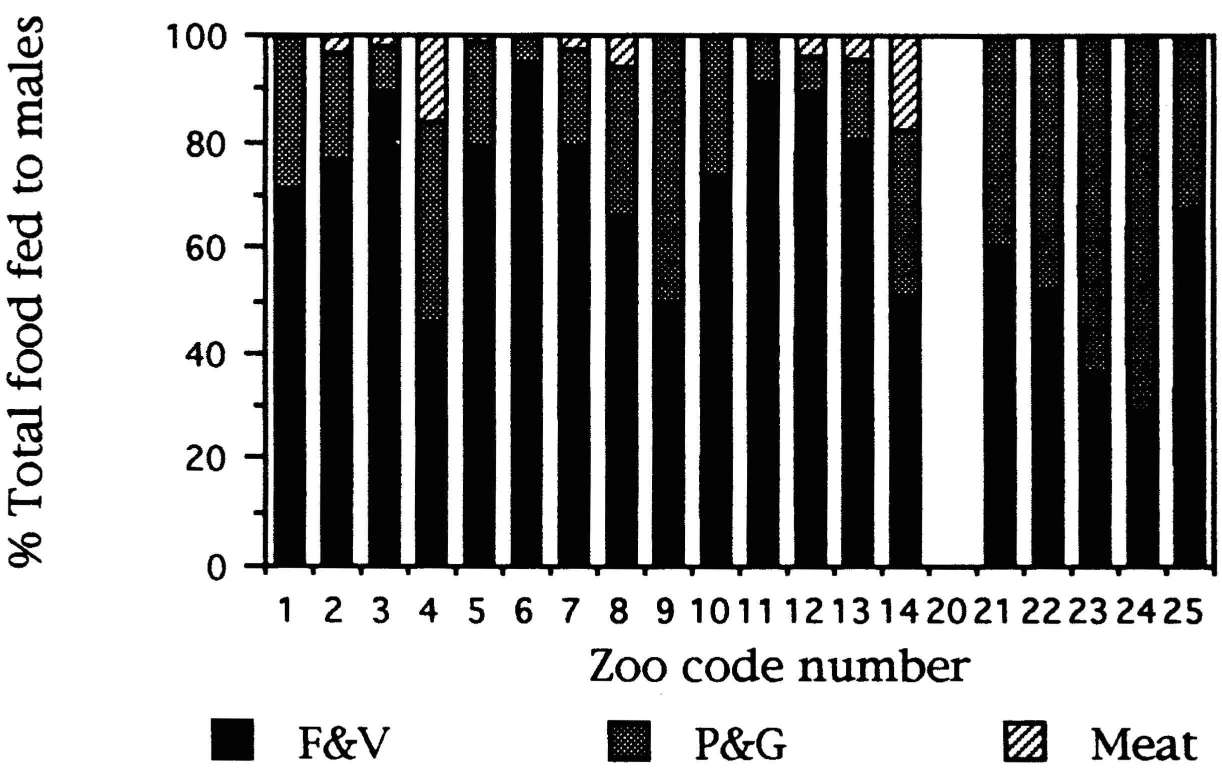

Fig. 5.4a Percentage of fruit and vegetables (F&V), pellets and grains (P&G) and Meat in the total amount of food fed to adult male babirusa in captivity

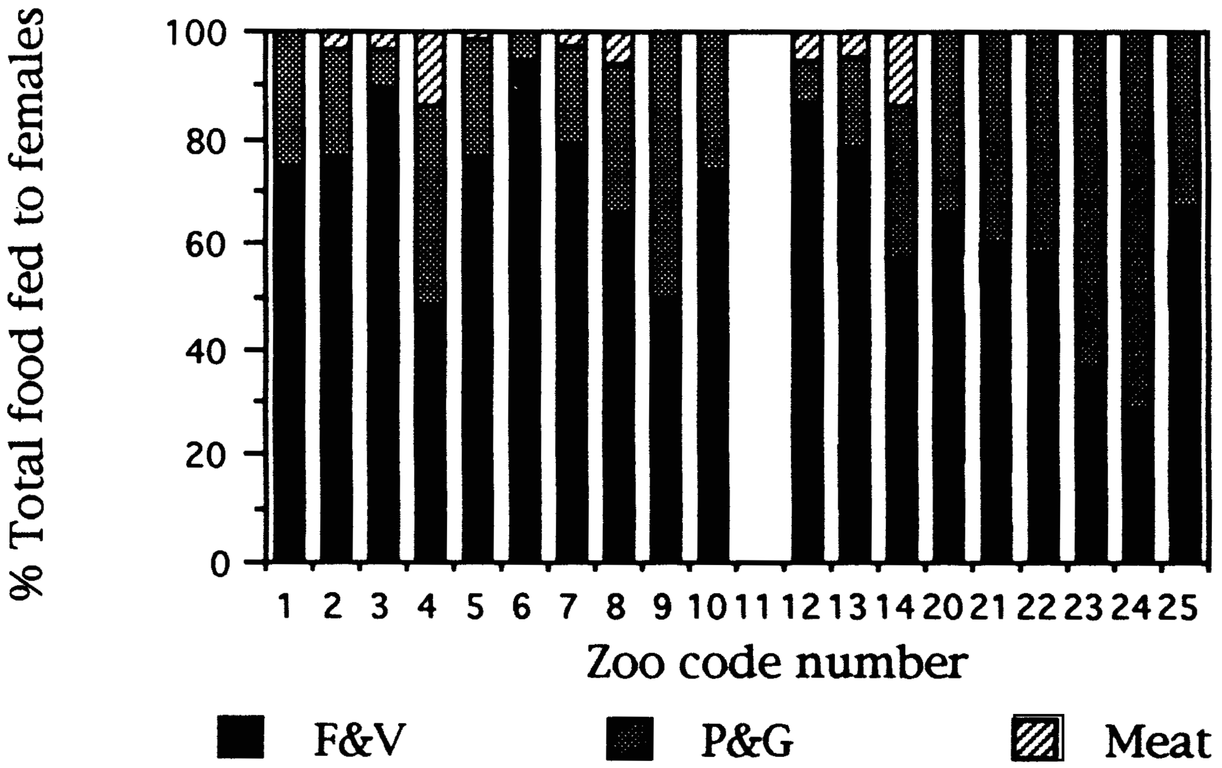

Fig. 5.4b Percentage of fruit and vegetables (F&V), pellets and grains (P&G) and Meat in the total amount of food fed to adult female babirusa in captivity

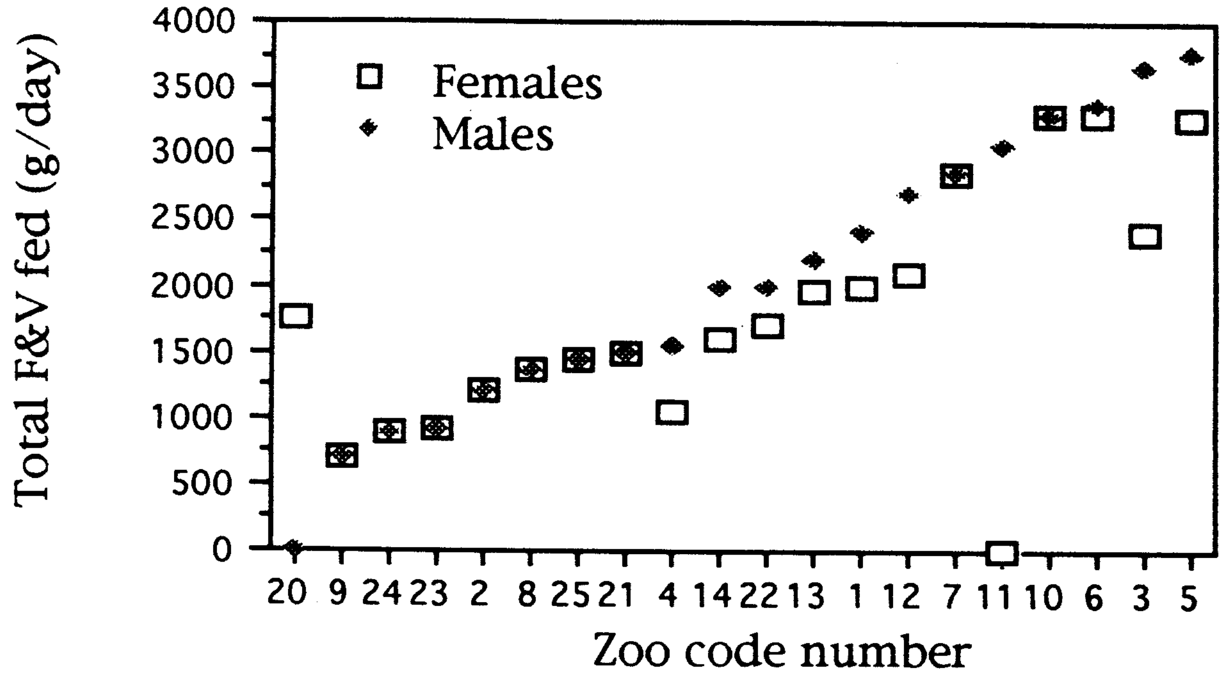

Fig. 5.5 Total amount of fruit and vegetables (F&V) fed to adult male and female babirusa in captivity.

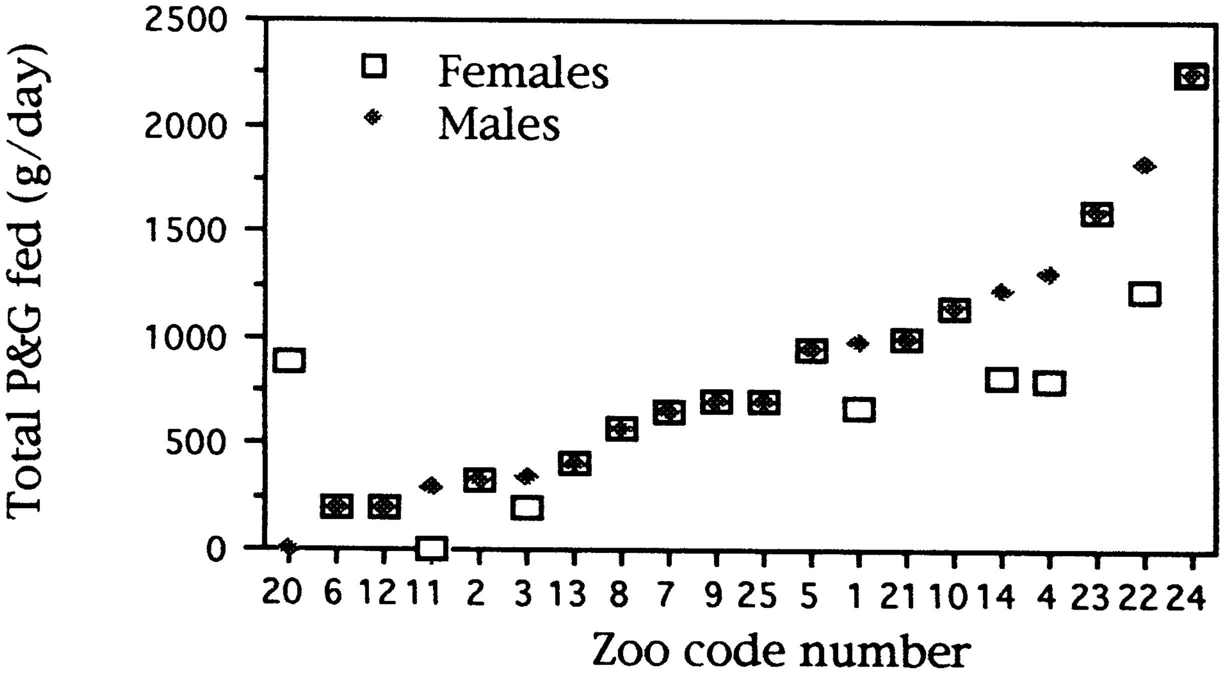

Fig. 5.6 Total amount of pellets and grains (P&G) fed to adult male and female babirusa in captivity.

figures illustrate the wide variation in the amounts fed of each category ranging from 700g - 3770g for **F&V**, 190g - 2260g for **P&G** and 50g - 680g for **Meat** with only zoos 2-5, 7-8 and 12-14 feeding their animals a regular amount of **Meat**. In nine zoos, females were receiving less **F&V** than the males whereas in only 5 of these zoos (1, 3, 4, 14, 22) females were also receiving less **P&G** than males (Table 5.1b). This is also evident from the results in Table 5.2. For the latter 5 zoos the percentage of the male ration fed to the female was larger for **F&V** than for **P&G**. Six of the nine zoos where females received different rations than males were feeding their animals regular amounts of **Meat**. In two of these zoos (4,14), females received about half the amount of **Meat** fed to the males.

The total amounts of CP fed to the animals each day varied from 43 - 399g for males and from 43g - 364g for females (Fig. 5.8 and Table 5.1c). Zoos 1, 3, 4, 14 and 22 fed their females between 59% and 66% of the CP ration of the males (Table 5.2). The same zoos fed their females less **P&G** than the males and also had the largest reduction in the total amount of DM fed. In zoos 12 and 13, females only received 5.4% - 7.1% less than the males, corresponding to the small reduction in total DM fed. Zoos 5 and 6 seemed to be feeding their females slightly less wet food, and for zoo 5 even DM, than the males, whereas the females are in fact receiving slightly more CP than the males. In all other zoos males and females were fed the same amount of CP. Fig. 5.9a, b indicate that in most zoos, **P&G** are the most important suppliers of CP. Although **Meat** is only fed in small quantities it contributes significantly to the protein ration of the animals in those zoos where it is fed.

Compared to the males, a larger proportion of the total CP in the diet of females in zoos 1, 3, 4, 14 and 22 is of **F&V** (1, 3, 4 and 14) or **Meat** (3), rather than **P&G** origin. The opposite is true for the females in zoos 12 and 13 where a larger proportion of the total CP fed to the females is of **P&G** origin. Slightly more CP is of **F&V** origin in the diets of the females in zoos 5 and 6 although this is not immediately evident from the graph.

The total amounts of fat fed to the animals each day varied from 11g - 150g for males and from 10g - 135g for females (Fig. 5.10 and Table 5.1c). Zoos 1, 3, 4, 14 and 22 fed their females between 58% and 74% of the fat ration of the males (Table 5.2). The amount of fat fed to the females in

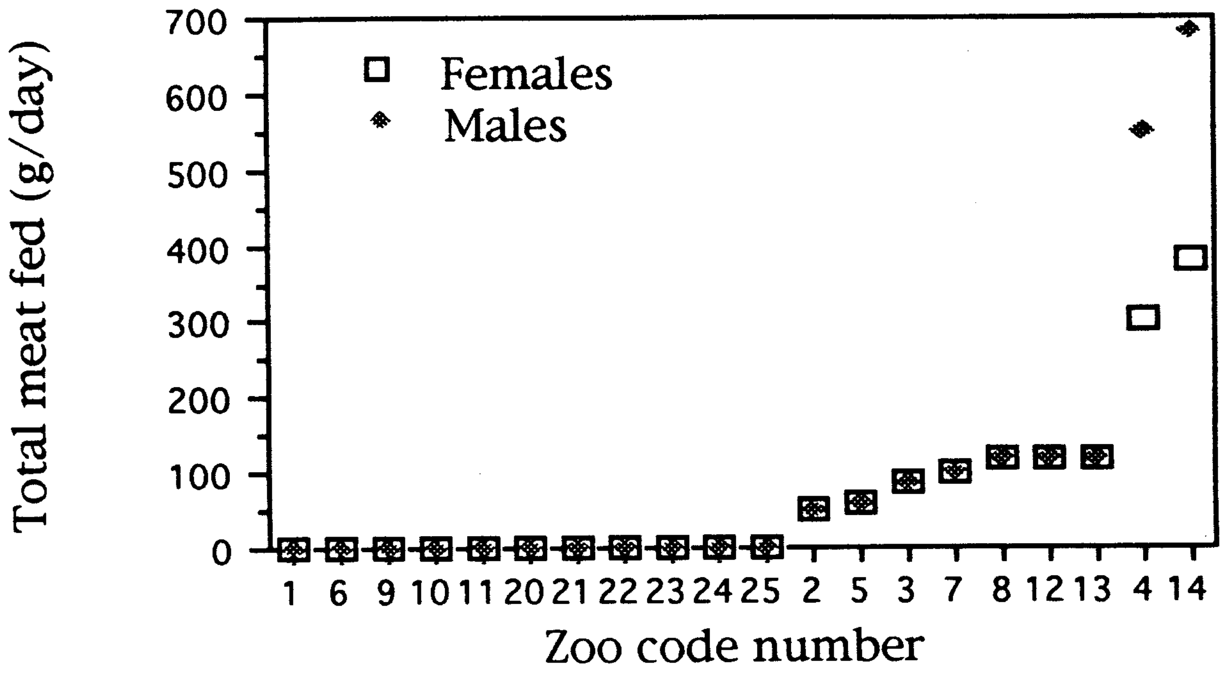

Fig.5.7 Total amount of meat fed to adult male and female babirusa in captivity.

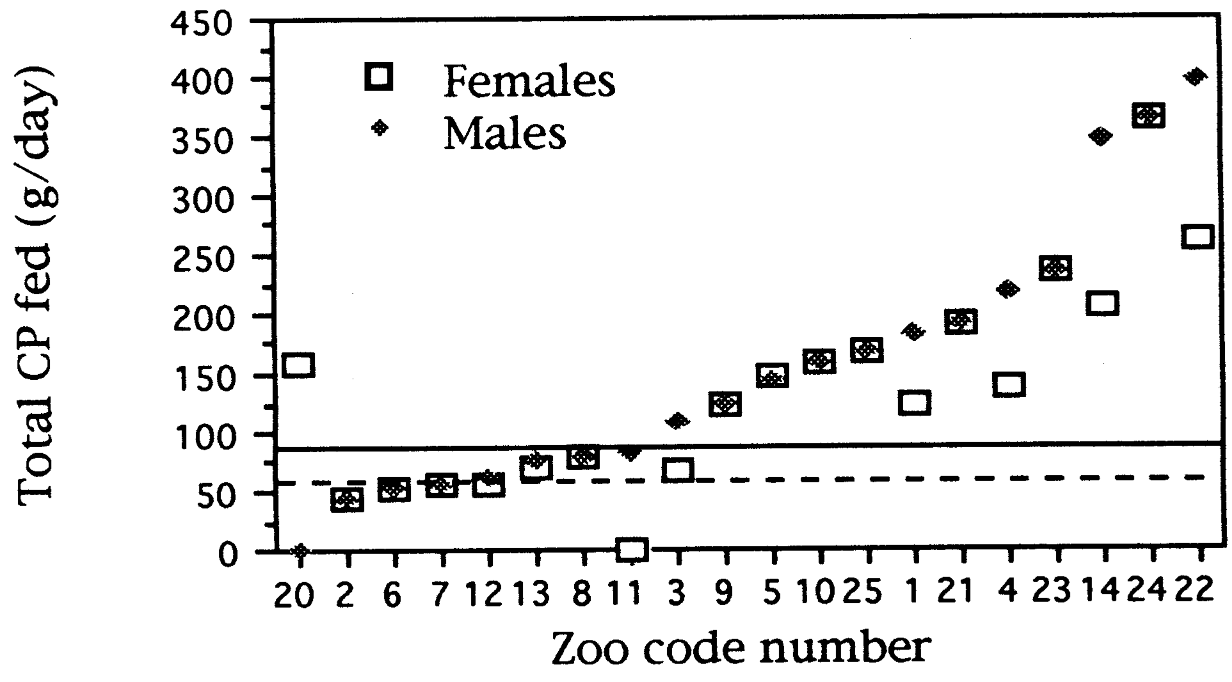

Fig.5.8 Total amount of crude protein (CP) fed to adult male and female babirusa in captivity.

full line: predicted CP requirement of males
dashed line: predicted CP requirement of females

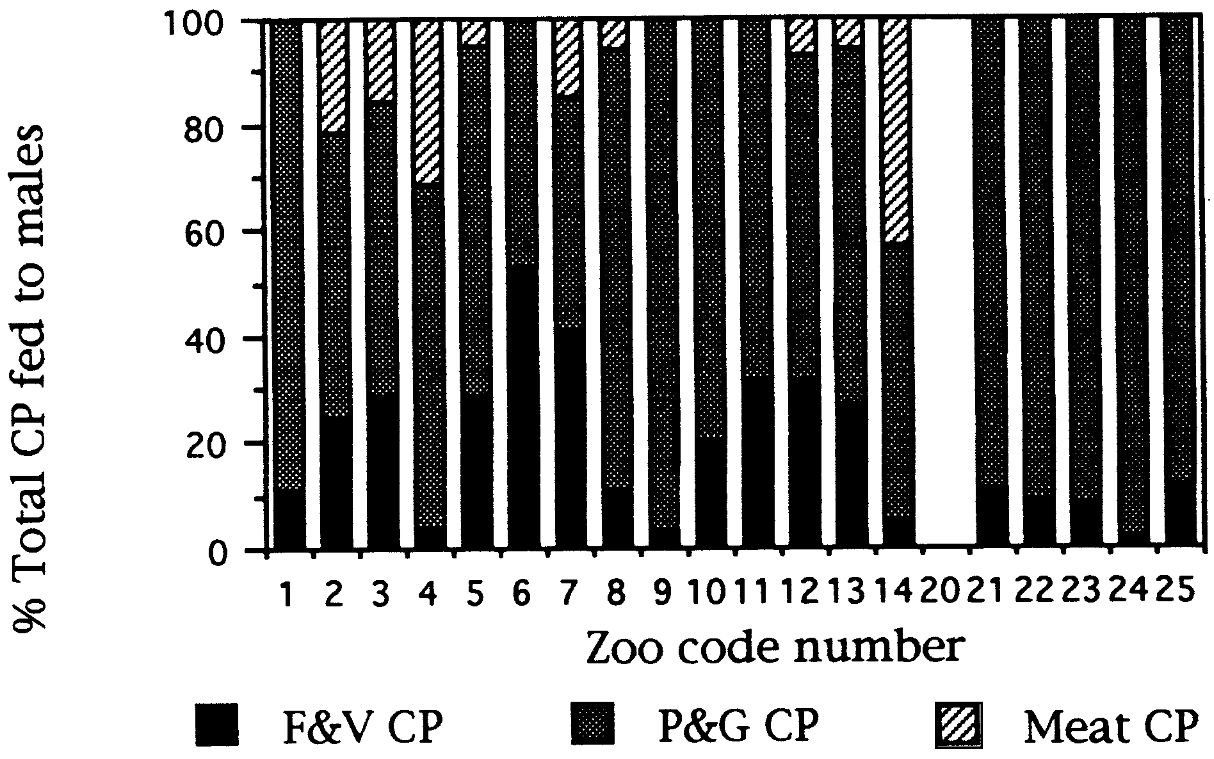

Fig. 5.9a Origin of the crude protein (CP) fed to adult male babirusa in captivity.

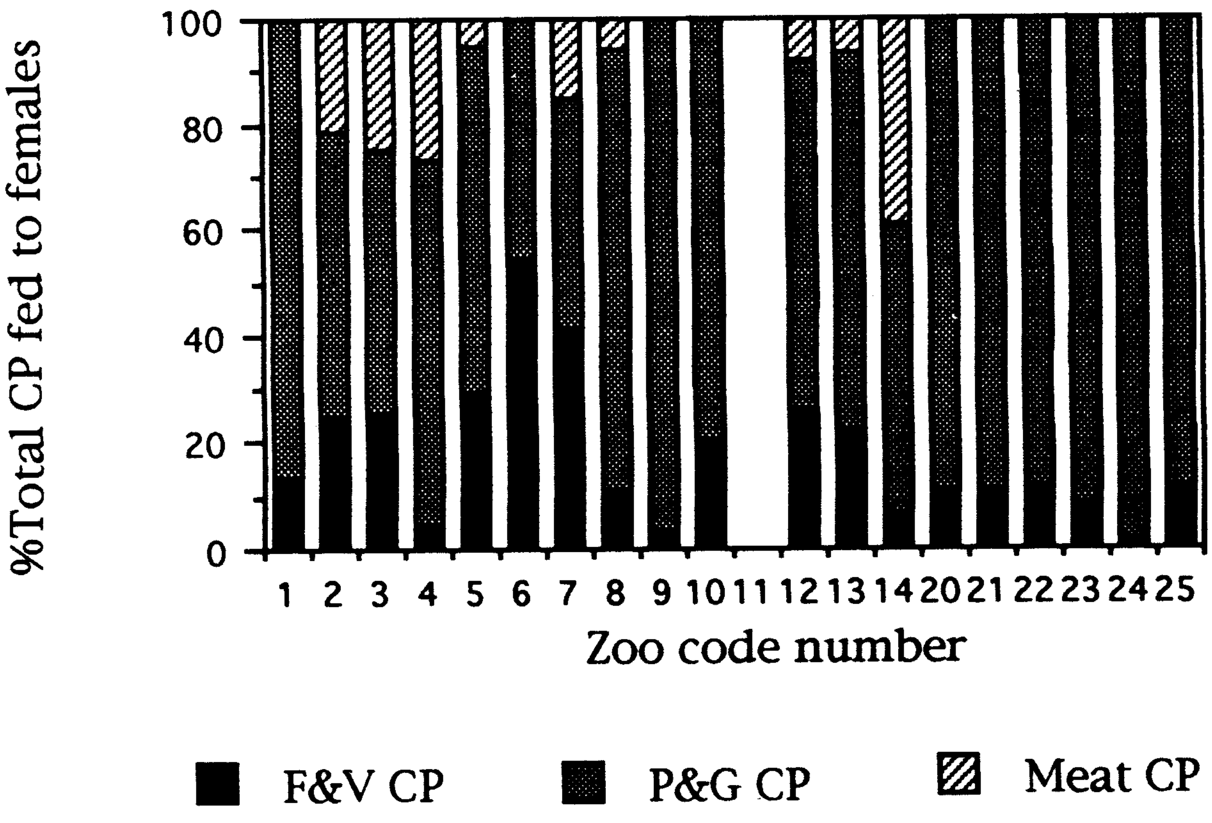

Fig. 5.9b Origin of the crude protein (CP) fed to adult female babirusa in captivity.

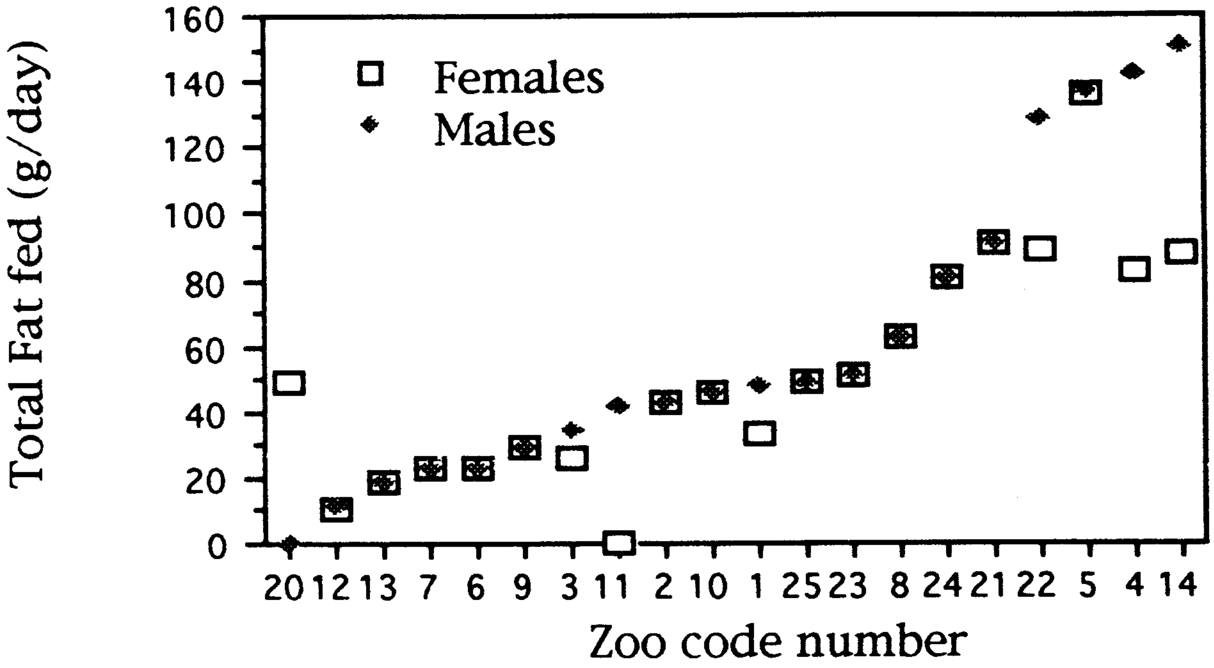

Fig. 5.10 Total amount of fat fed to adult male and female babirusa in captivity.

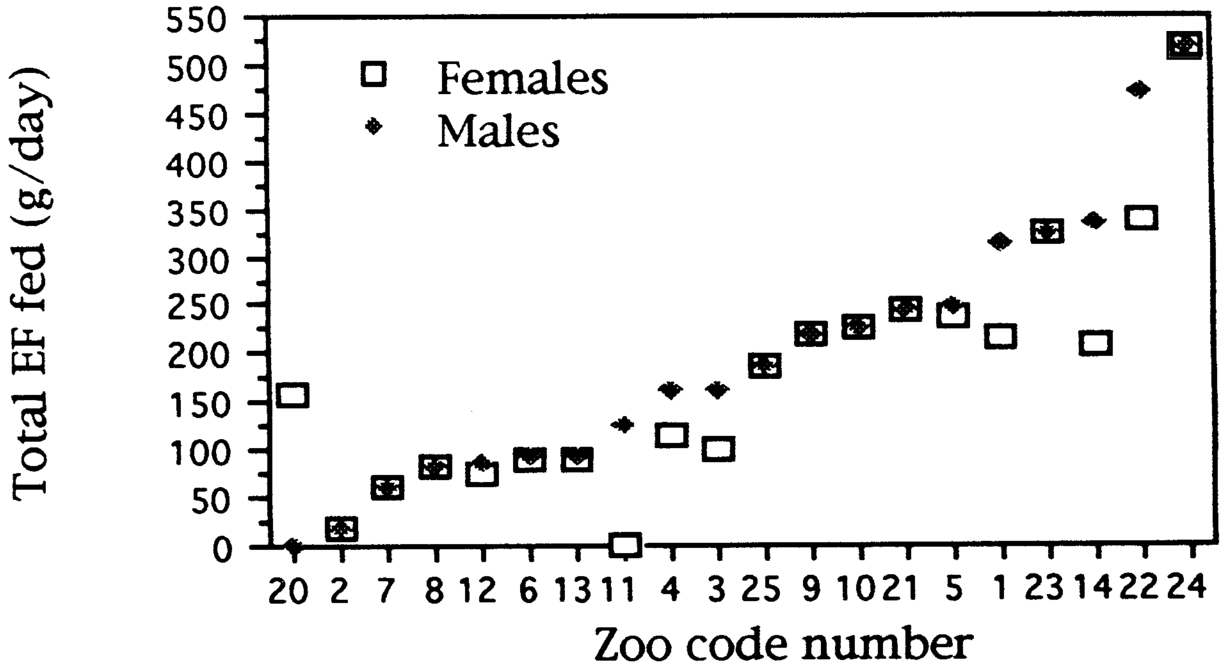

Fig. 5.12 Total amount of Englyst fibre (EF) fed to adult male and female babirusa in captivity.

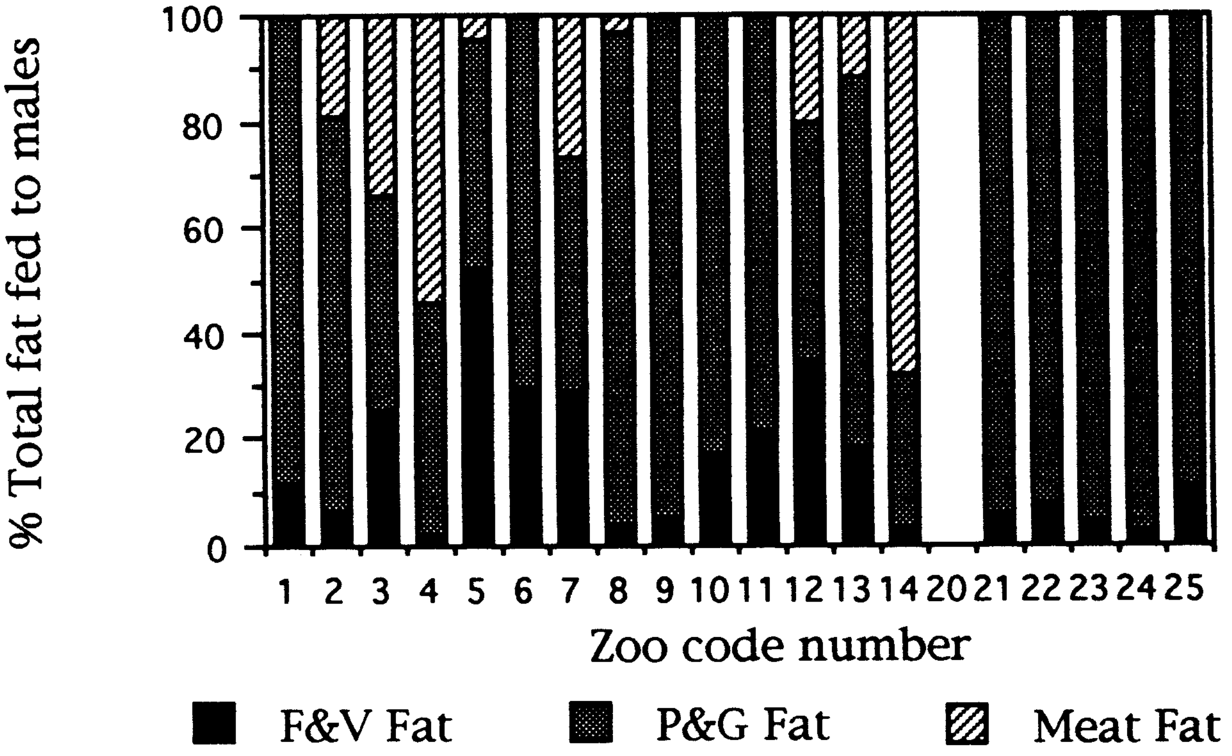

Fig. 5.11a Origin of the fat fed to adult male babirusa in captivity

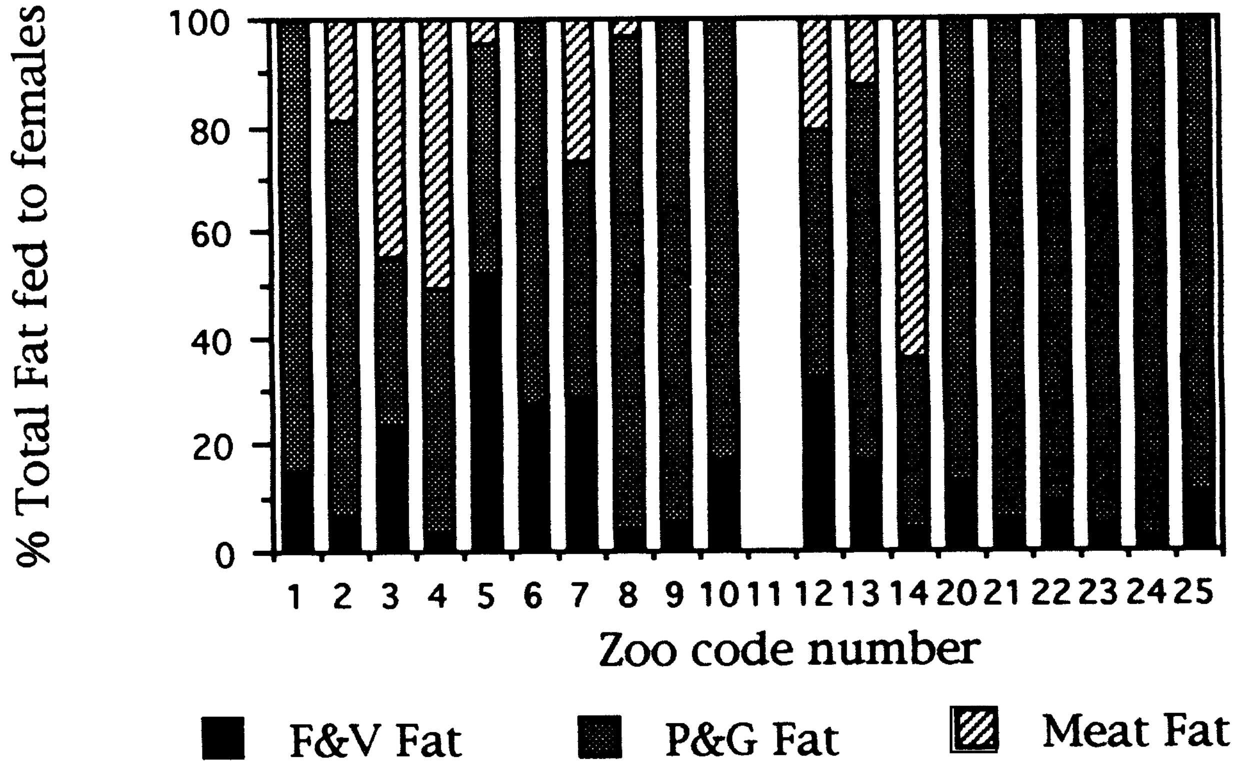

Fig. 5.11b Origin of the fat fed to adult female babirusa in captivity.

zoos 5, 6, 12 and 13 was only slightly smaller than that fed to the males, the fat ration of the females ranging between 96% and 99% of that of the males. In all other zoos males and females were fed the same amount of fat. From Fig. 5.11a, b it becomes apparent that in those zoos where **Meat** is fed, this is an important source of fat. In most zoos **P&G** supply a much higher proportion of the total fat in the diet than **F&V**. In comparison to the males, females in zoos 1, 4, 5(only slightly) and 22 obtained a greater proportion of their fat from **F&V,** whereas females in zoos 3 and 14 obtained a greater proportion of their fat from **Meat**. In the diet of females in zoo 6 slightly more fat was from **P&G** origin than in the diet of the males.

The total amounts of EF fed to the animals each day varied from 19g - 516g for both males and females (Fig. 5.12 and Table 5.1c). Females in zoos 1, 3, 4, 14 and 22 were fed between 62% and 72% of the EF fed to the males (Table 5.2). Females in zoo 12 were offered 86% of the males' EF ration whereas those in zoos 5, 6 and 13 received almost as much as the males (96%). In all other zoos males and females were fed the same amount of EF. **Meat** only contributes insignificant amounts of fibre to the diet (Fig. 5.13a, b). Comparison of Fig. 5.9a, b and Fig. 5.11a, b with Fig. 5.13a, b indicates that although **F&V** are generally not major CP and fat providers, they can form an important source of dietary fibre. In comparison to the males, females in zoos 1, 3, 14 and 22 obtained a larger proportion of their EF from **F&V**. Females in zoo 4, 5-6(slightly), 12 and 13 have a higher proportion of EF from **P&G** origin than the males.

The total amount of DE fed daily to the animals varied between 5.82 MJ and 29.12 MJ for both males and females (Fig. 5.14 and Table 5.1c). Zoos 1, 3, 4, and 22 fed their females between 54% and 71% of the amount of DE that was fed to the males (Table 5.2). Females in zoo 5, 12 and 13 were offered between 86% and 94% of the DE ration for the males. Zoo 6 seemed to be feeding its females slightly less food than the male whereas in fact she is receiving 15% more DE than the males. Comparison of Fig. 5.15a, b with Fig. 5.9a, b and Fig. 5.11a, b indicates that **F&V** can be important sources of DE even though their contribution to the CP and fat portion of the diet is usually small. Females in zoos 1, 4, 6, 14 and 22 obtained a larger proportion of their DE from **F&V** than the males in

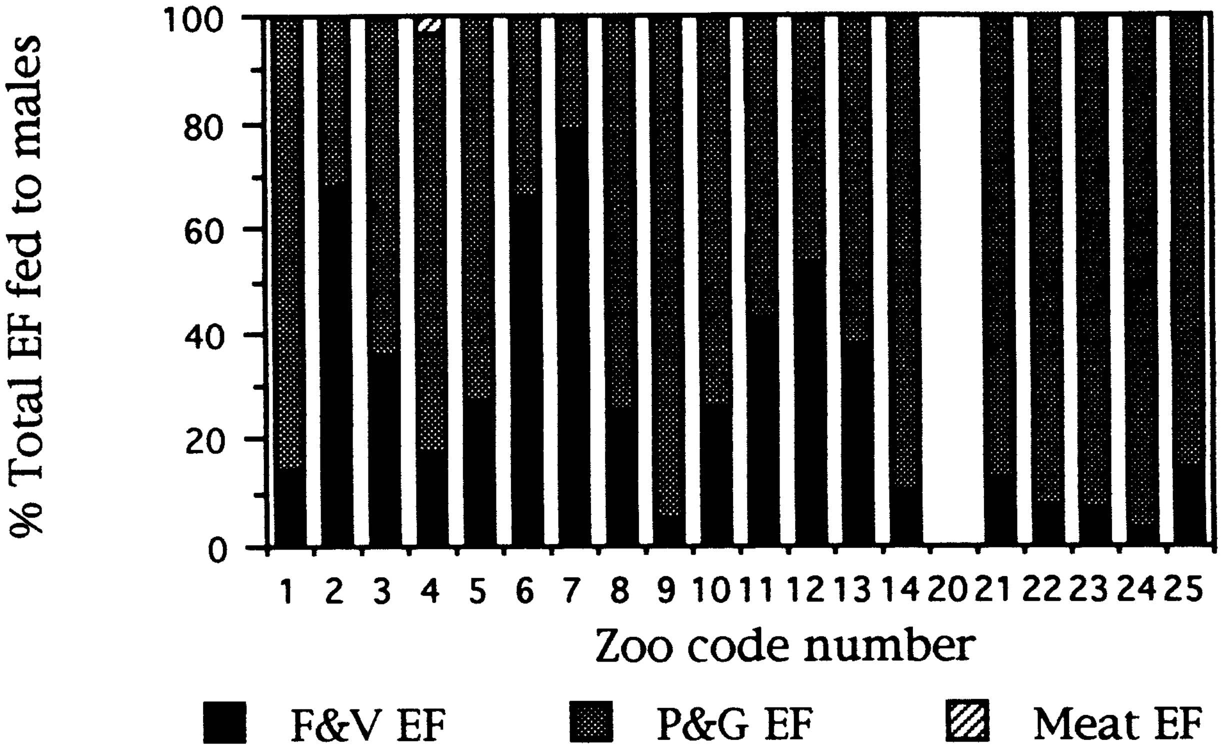

Fig. 5.13a Origin of Englyst (EF) fibre fed to adult male babirusa in captivity.

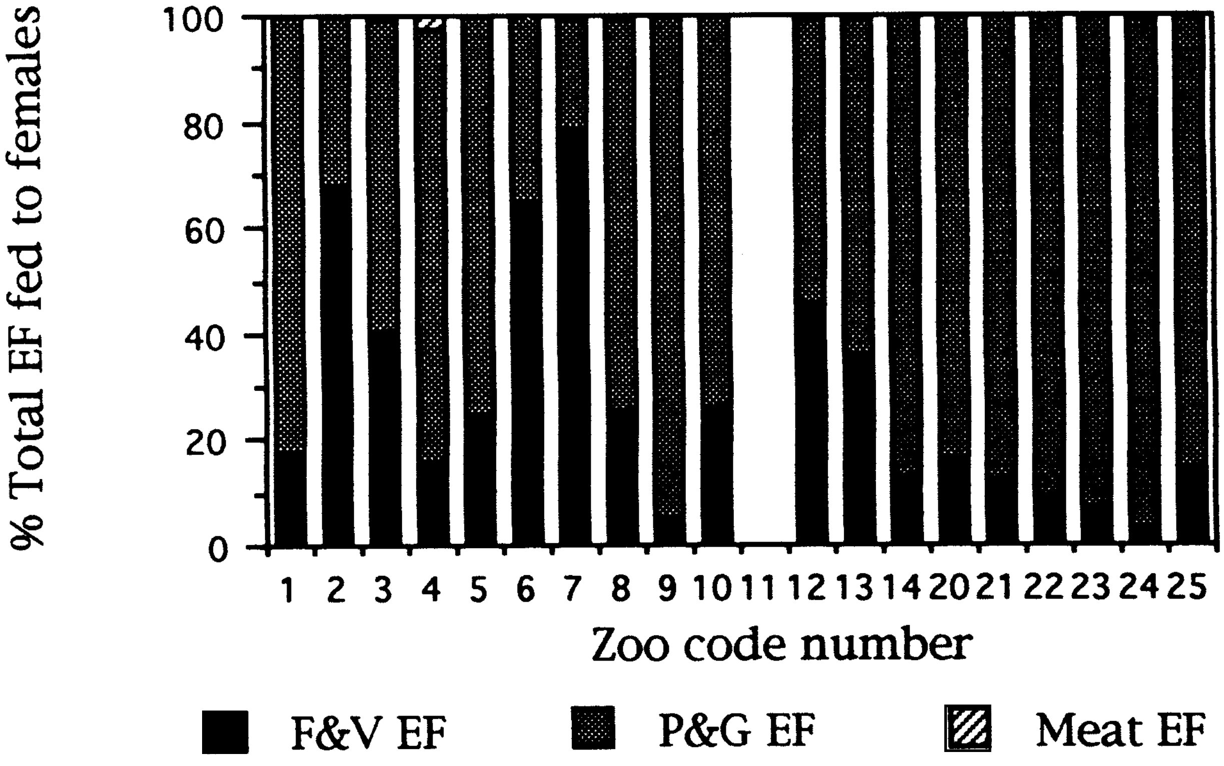

Fig. 5.13b Origin of Englyst (EF) fibre fed to adult female babirusa in captivity.

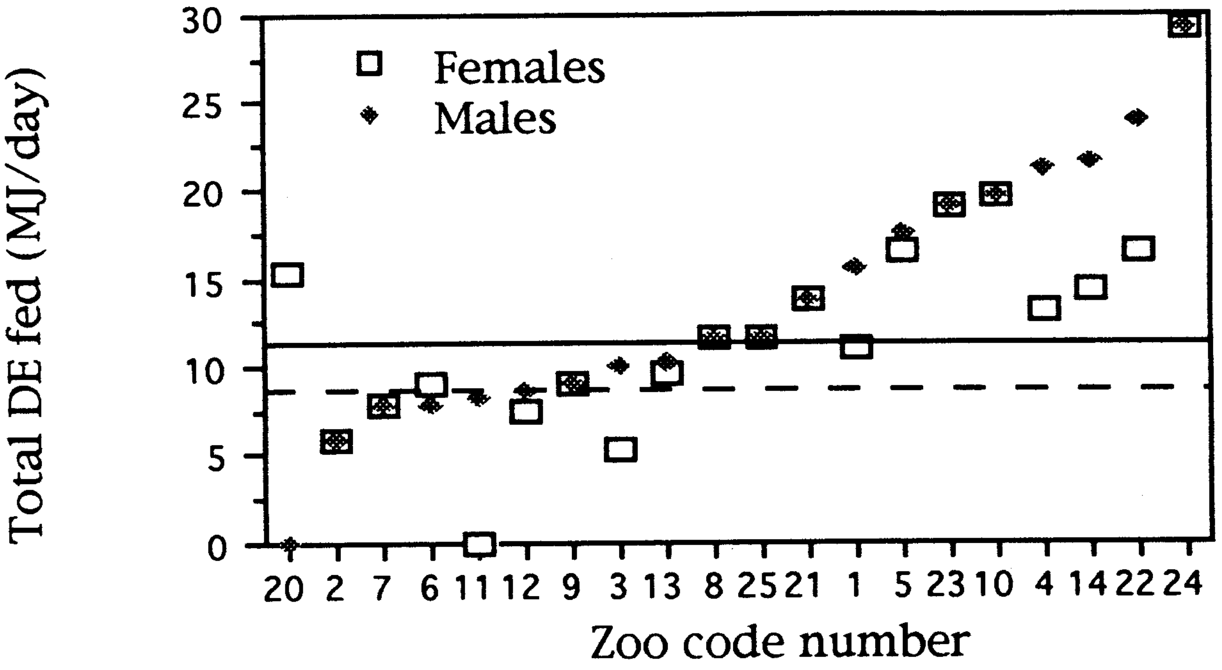

Fig.5.14 Total amount of digestible energy (DE) fed to adult male and female babirusa in captiviity.

full line: predicted DE requirement of males
dashed line: predicted DE requirement of females

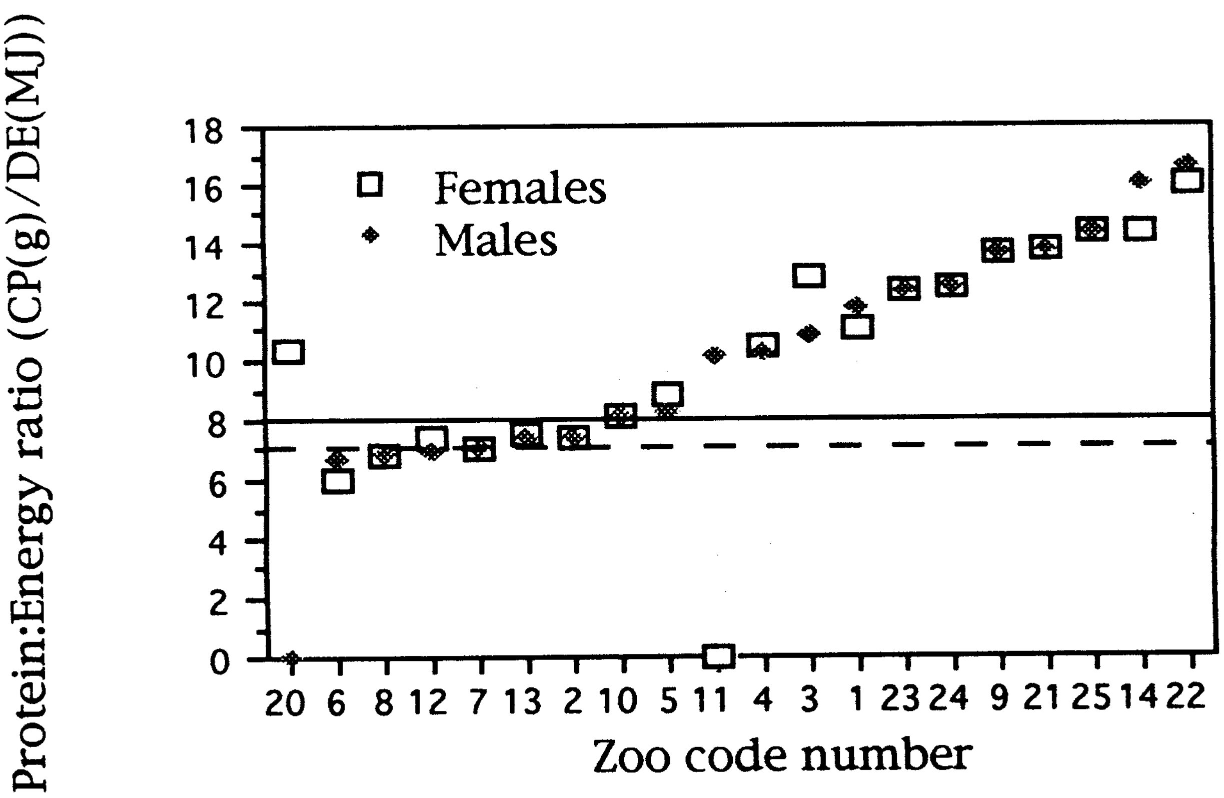

Fig.5.16 Protein:energy ratio of diets fed to adult male and adult female babirusa in captivity.

full line: predicted protein:energy requirement of males
dashed line: predicted protein:energy requirement of females

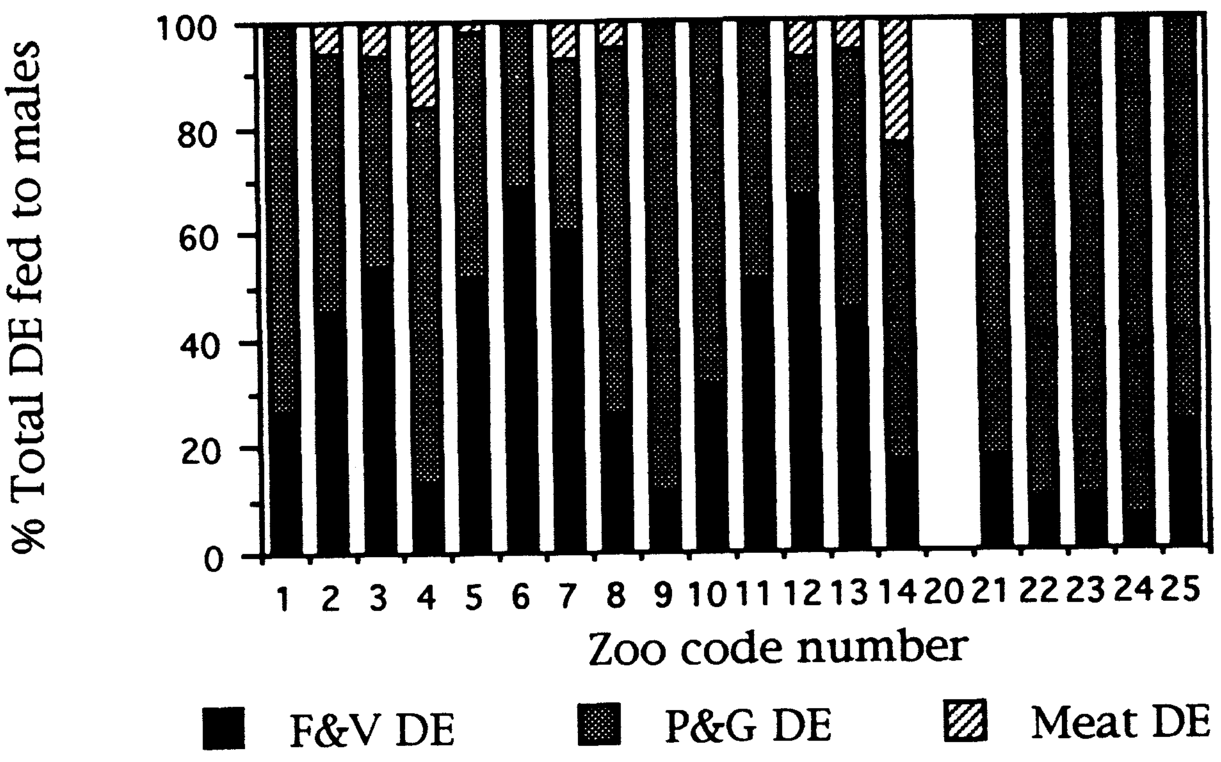

Fig. 5.15a Origin of Digestible energy (DE) fed to adult male babirusa in captivity.

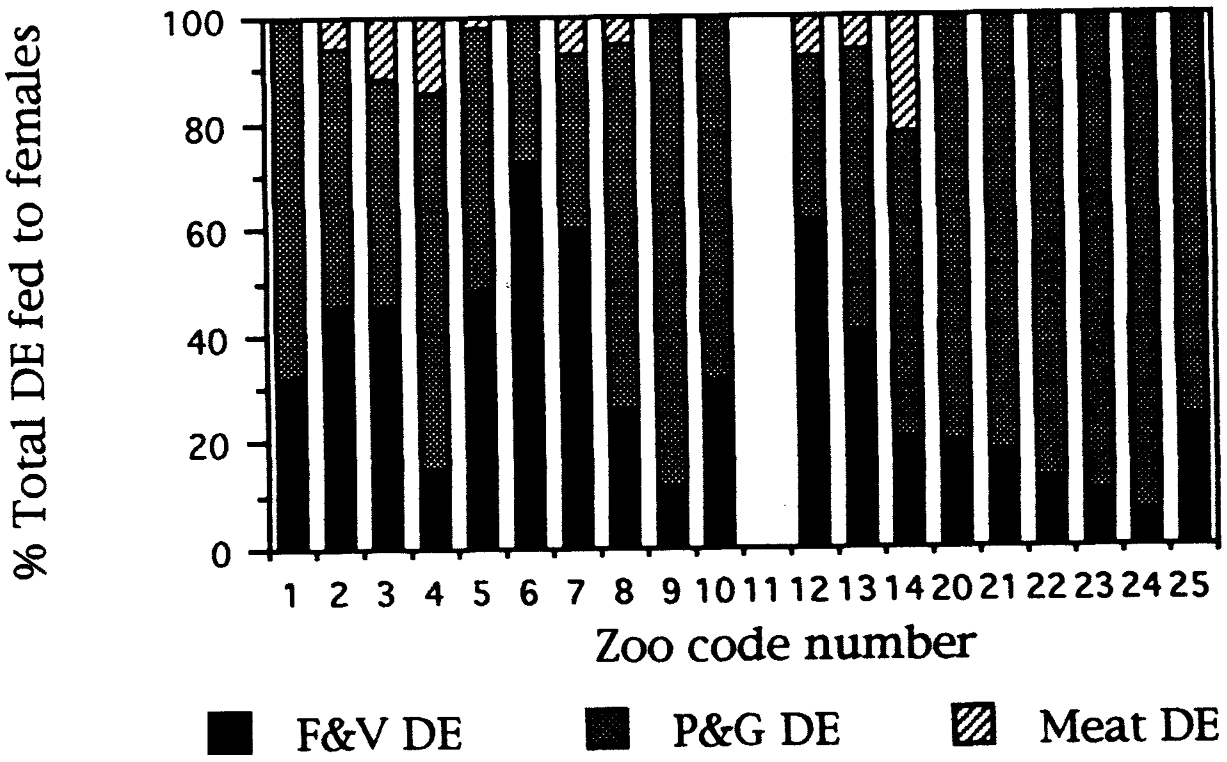

Fig. 5.15b Origin of Digestible energy (DE) fed to adult female babirusa in captivity.

these institutions. Females in zoo 3 and 12 obtained a larger proportion of DE from **Meat** and those in zoos 5, 12 and 13 from **P&G** than the males in the same institutions. When combining Table 5.1b with Table 5.1c, it becomes evident that zoos feeding the highest amounts of DM are generally also those feeding the highest amounts of CP, Fat, EF and DE.

Protein: Energy ratio:
The protein: energy ratio of the diets ranged from 6.7 to 16.6 for males and from 5.95 to 16.0 for females (Fig. 5.16 and Table 5.1c). Of the 9 zoos that were feeding male and female animals different diets, the protein: energy ratio for females in zoos 1, 6, 14, and 22 was smaller than that of the males whereas the ratio for females in zoos 3, 4, 5, 12, and 13 was larger than that for males.

Forage

Forage offered to the babirusa came in many forms and shapes. A list of all the different types of forages fed to the babirusa and the parts of these forages that are eaten by the babirusa can be found in Table 5.3. Some zoos did not specify the species of forage fed and their accounts were included under the general terms branches, grass, hay, and leaves. Most herbal material, grass, hays and corn stems were eaten completely. In some zoos alfalfa hay was eaten completely whereas others stated that the animals picked out the leaves to eat and would sometimes chew the stems but not always eat them. The babirusa were fed a very wide variety of tree branches. Leaves of these branches were most often eaten whereas bark, twigs and buds appeared to be somewhat dependant on the species although a precise account of the tree parts eaten was not always provided. Many zoos fed fresh branches and fresh grass, herbs and alfalfa during the season and fed dried branches with leaves, winter branches without leaves and hays during the winter. No information on the nutritional composition could be found in the literature for many of the forages fed. The type and amount of forage offered usually varied from season to season and the inclusion in the diet was often not on a regular basis. For all of the above reasons, detailed nutritional analyses of the forage offered to the babirusa in captivity was not possible.

Table 5.3 List of forage items fed to babirusa in captivity.

Item	Form	Parts eaten	No zoos
Branches	fresh	bark, leaves, twigs, buds	8
Grass	fresh	entirely	9
Hay	dry	entirely	4
Leaves	fresh and dry	entirely	2
Acacia	branches fresh	leaves only	3
Alder (*Alnus* sp.)	branches fresh	?	1
Alfalfa	fresh and hay	entirely	9
Alfalfa pellets	ground, dry	entirely	1
American beech (*Fagus grandifolia*)	branches fresh	?	1
American Oak (*Quercus rubra*)	dried leaves	leaves	1
Ash (*Fraxinus excelsior*)	branches fresh	bark, leaves, twigs	1
Banana (*Musa acuminata*)	leaves	?	1
Beech	branches fresh	leaves	1
Birch (*Betula pendula*)	branches fresh	bark, twigs, buds	3
Black locust (*Robinia pseudoacacia*)	branches fresh	?	1
Black willow (*Salix nigra*)	branches fresh	?	1
Clover	fresh	entirely	1
Corn stems	fresh and dried	entirely	1
Crabapple (*Malus* sp.)	branches fresh	?	1
Forsythia (*Forsythia* sp.)	branches fresh	?	1
Fragrant honeysuckle (*Viburnum* sp.)	branches fresh	?	1
Golden bamboo (*Phyllostachys aurea*)	branches fresh	?	1
Grape (*Vitis vinifera*)	branches fresh	?	1
Hackberry (*Celtis occidentalis*)	branches fresh	?	1

Table 5.3 continued

Item	Form	Parts eaten	No zoos
Hawthorn	branches fresh	leaves	1
Hazel	branches fresh	leaves	1
Hibiscus (*Hibiscus rosa*)	branches fresh	?	1
Hydroponic barley	fresh	entirely	1
Kentucky coffee tree (*Gymnocladus dioicus*)	branches fresh	?	1
Maize	stem+cobs	entirely	2
Mangrove (*Avicennia germinans*)	branches fresh	?	1
Mulberry	branches fresh and dry	leaves, bark	1
Oak	branches fresh and dry	leaves, bark	2
Poplar (*Populus euramericana*)	branches fresh	bark, leaves, twigs, buds	2
Red maple (*Acer rubrum*)	branches fresh	?	1
Silver maple (*Acer saccharinum*)	branches fresh	?	1
Sugar maple (*Acer saccharum*)	branches fresh	?	1
Sweetgum (*Liquidambar styraciflua*)	branches fresh	?	1
Sycamore (*Acer pseudoplatanus*)	branches fresh	bark, leaves, twigs	1
Timothy hay	dry	?	3
Torch ginger	?	?	1
Weeping fig (*Ficus benjamina*)	branches fresh	?	1
Weeping willow (*Salix babylonica*)	branches fresh	?	1
White mulberry (*Morus alba*)	branches fresh	?	1
White poplar (*Populus alba*)	branches fresh	?	1
Willow (*Salix alba*)	branches fresh	bark, leaves, twigs, buds	4

The potential effects of forage on the overall nutritional composition of the diet will be illustrated with four examples. Four zoos offered their animals a certain amount of a more or less fixed forage type each day. The nature and amount of the forage fed as well as the effect of inclusion of this forage onto the composition of the daily diet of the animals in these zoos is indicated in Table 5.4. It becomes evident that the inclusion of 200g grass daily has a smaller influence on the DM, CP, EF and DE content of the overall diet than the inclusion of 100g of alfalfa hay. The inclusion of 1.6kg alfalfa hay in the diet makes the DM, CP and EF content of the diet rise dramatically, especially if compared with the influence of a larger amount (1.85kg) of hydroponic barley with mixed hay. In all 4 zoos females received the same amount of forage as the males. However, because the females in zoos 4 and 22 received a smaller amount of the basal diet, a greater proportion of their DM, CP, Fat, EF and DE was now of forage origin in comparison with the males. For example, in zoo 4 the proportion of DM, CP, Fat, EF and DE of forage origin was 2.9%, 5.6%, 6.7%, 0.9%, 24.2% and 3.9% for males and 4.5%, 8.8%, 10.2%, 1.6%, 30.8% and 6.2% for females.

Feeding methods:

In 15 out of the 20 zoos, animals were generally fed singly for at least the main part of their meal. Animals would sometimes receive smaller portions of their daily rations while being together in one outdoor enclosure. Zoo 1 specified that males and females could be fed together when the female was in heat. One zoo (7) fed the male and female from two separate troughs in the same enclosure. In the remaining four zoos (5, 22, 24 and 25) pairs of animals received their meal together. In all zoos females were fed together with their piglets. Those zoos that fed the animals in pairs separated the male from the female when parturition was near.

Two zoos had one single feeding time each day. In most institutions (15), the meals of the animals were spread over two feeding times, different zoos feeding different proportions at different times. The remaining 3 zoos fed their animals over 3, 4 and more than 5 times during the day. In the latter zoo, the largest proportions of the daily diet were offered at two times during the day, the morning and the afternoon, whereas during the

Table 5.4 Influence of the inclusion of forage items on the overall nutritional composition of the diet of babirusa in captivity.

Zoo No.	Sex	Forage		Total food (g)	DM (g)	CP (g)	Fat (g)	EF (g)	DE (g)	%DM
4	M	100 g alfalfa hay	-F	3390	1539.42	217.75	142.25	160.22	21.25	45.41
			+F	3490	1630.82	233.29	143.55	211.40	22.11	46.73
	F	100 g alfalfa hay	-F	2140	948.94	137.29	82.23	115.34	13.11	44.34
			+F	2240	1040.34	152.83	83.53	166.52	13.97	46.44
7	M&F	200 g grass	-F	3617	788.91	55.11	23.13	60.97	7.77	21.81
			+F	3817	818.90	60.12	24.13	75.91	8.03	21.45
22	M	1600 g alfalfa hay	-F	3825	1827.50	398.50	129.09	472.10	23.98	47.78
			+F	5425	3289.90	647.10	156.89	1291.06	37.73	60.64
	F	1600 g alfalfa hay	-F	2925	1275.80	262.20	89.29	337.34	16.43	43.62
			+F	4525	2738.20	510.80	117.09	1156.30	30.18	60.51
23	M&F	1000 g HP+ 425 g alfalfa hay+ 425 g timothy hay	-F	2520	1618.67	235.50	51.38	325.10	19.04	64.23
			+F	4370	2475.12	364.62	68.48	812.43	26.41	56.64

-F = Composition of the daily diet without the inclusion of forage.
+F = Composition of the daily diet with the inclusion of forage.
M = male, F = female.

rest of the day the animals were allowed to search for smaller amounts of finely cut food items which were scattered around at least three times each day. Babirusa in the zoo with 4 feeding times also received their food scattered in the enclosure. In most zoos forage was not fed at a regular time and remained available to the animals for the entire day and sometimes night.

In 7 out of 20 zoos the food was offered on the ground whereas in 9 institutions it was offered in troughs or tubs. The food was offered on a bed of grass or hay in 4 institutions and it was specified that this was not always eaten. One zoo (22) offered the food on a bed of alfalfa (1.6kg, see above).

Preferences and dislikes

When zoos were asked if the babirusa showed a preference for certain food items, the following items were mentioned (Table 5.5).

The most favoured items seemed to be fruits and especially apples and bananas, although these were also more often included in the diet (Table 5.1). Note that only two vegetables were recorded as a favoured item, and then only once each. Forages were also not mentioned often. However, forage items were usually available all day long, whereas the basal diet tended to be fed at fixed times in fixed places. It can be assumed that the animals will concentrate on the basal diet items during these feeding times, so that a preference between forage and these items may be hard for the keepers to establish. One zoo (3) mentioned a particular liking by the babirusa for alfalfa since the animals would spent 30-60 minutes sorting out and eating the best leaves.

When asked if the animals showed any dislikes for certain items (shown by them being not eaten, not always eaten, eaten last or regularly left over) the following items were mentioned (Table 5.6).

Table 5.5 Reported babirusa preferences for individual food items

Items	Times mentioned
Fruit:	
Apple	15
Banana	14
Grapes	2
Orange	2
Pear	2
Cherries	1
Coconut	1
Melon	1
Peach	1
Tomatoes	1
Fruits (undefined)	4
Vegetables:	
Carrots	1
Lettuce	1
P&G:	
Maize	3
Nuts	3
Seeds	1
Boiled rice	1
Bread	1
Meat:	
Chicks	1
Eggs	1
Grasshoppers	1
Mice and rats	1
Forage:	
Fresh leaves	2
Alfalfa (sort out leaves)	1

Table 5.6 Food items in zoos reportedly disliked by babirusa.

Items	Times mentioned
Fruit:	
Tomatoes	3
Vegetables:	
Celery	5
Cabbage	5
Raw carrots	5
Boiled potatoes	2
Broccoli	2
Fodder beet	2
Aubergines	1
Black salsify	1
Boiled yams	1
Brussels sprouts	1
Cauliflower	1
Leek	1
Onion	1
Spinach	1
Green vegetables	1
P&G:	
Pellets	2
Dog chow	1
Rolled oats	1
Grain except corn	1
Meat:	
Crickets	1
Forage:	
Timothy hay	1
Alfalfa	1

Apart from tomatoes, not a single fruit was mentioned as a disliked item. Tomatoes seem to be a special item, since they were especially favoured by some animals and absolutely rejected by others. In contrast with the preference list (Table 5.3) a lot of vegetables were mentioned as disliked items, especially members of the cabbage family (Brassicaceae) such as cabbage, brussels sprouts, cauliflower and broccoli and roots or tubers such as carrots, potatoes, yam, fodder beet and salsify. It is also remarkable that of the **P&G** category, maize and nuts seemed the more preferred items whereas the commercial pellets and other grains seemed less popular. In the one zoo where crickets were fed, animals would take these into the mouth every now and then but spit them out whole thereafter. After a few attempts the animals lost all interest in the crickets. No other meat items were mentioned as disliked, whereas some were mentioned as preferred items.

Weights:
In general, animals in zoological collections are not routinely weighed and when asked for weights of the adult babirusa in their collections not many zoos were able to reply. Table 5.7 gives all the weights reported by the zoos. Because of the scarcity of information from different collections no relation could be made between the weight of the animals and the different diets fed in different zoological collections. For further calculation purposes (see discussion) the average weight of adult male babirusa will be taken as 95kg and that of adult females as 65kg.

4. Discussion

The wide range of amounts of total food fed, and the lack of a straight relationship between total food fed and DM fed can be explained by the differences in the proportions of the various food categories (fruit and vegetable; pellets, grains, bread, nuts and oils; and meat fish and eggs) within the diet. Because of the relatively high water content of fruit and vegetables, zoos feeding large amounts of this category may be perceived to be feeding their pigs a large amount of food. A lot of the weight fed to these animals is however water. Similarly, when a large proportion of the diet is made up out of commercial pellets (which usually have a water content of only 13%) the zoo may be perceived to be feeding their

Table 5.7 Weight and age at time of weighing of adult babirusa in different zoological collections. (?? = animals imported from Indonesia at an unknown age).

Zoo No.	Sex	Age (years)	Weight	
1	M	?? (>6)	100kg	
	M	?? (>6)	118kg	
	M	3	70kg	
	F	16	62kg	
	F	?? (>6)	62kg	
	F	5.5	72kg	
4	M	14	105kg	
5	M	12	110kg	(estimated)
	M	4	80kg	(estimated)
	F	10	80kg	(estimated)
	F	5	70kg	(estimated)
22	F	5	41kg	(estimated)
	M	5	84kg	(estimated)

animals only a small amount of food. But in fact, the animals are receiving a lot more nutrients than when they would be fed an equal weight of fruit and vegetables. Particular caution should be taken in the feeding of pellets and grains since small amounts of these items fed can represent a large proportion of the total amount of DM and therefore protein, fat, EF and DE that the animal is receiving.

All pigs will include a certain proportion of animal matter in what they eat. Babirusa in captivity have been observed to catch mice, rabbits, ducks and pigeons (Leus et al., 1992) and the animals observed in the semi-natural enclosure at St Martin la plaine eagerly investigated and sucked at old bones they found. It is likely, therefore that the babirusa, like the other pigs, supplements it's diet with animal matter. For these reasons the feeding of animal matter to babirusa in captivity is to be encouraged, however, it should also be taken into account that meat-products are generally high in protein and fat. A small amount of meat in the diet will therefore contribute a relatively large amount of protein and fat and the amount of P&G (which contain a large amount of these nutrients) should therefore be adjusted accordingly.

Similar caution should be taken when offering certain forage types. Because they are dried, hays contain more dry matter per unit weight than fresh forage. Replacing a certain weight of fresh forage offered in the summer with an equal weight of dried forage in the winter therefore causes significant alterations in the animals' diet. Alfalfa hay also has a higher protein and DE content than other hays. Therefore, caution should again be taken when feeding alfalfa hay since small amounts fed will represent important contributions to the total DM-, protein- and DE intake of the animal.

In those zoos where females received a different diet from the males, the females received less food than the males although the percentage reduction differed widely between zoos ranging from 2% less to 35% less. In only one zoo was the female diet created by a more or less proportional reduction in each food category (**F&V, P&G, Meat**). In some zoos females only received less **F&V** than the males and not less **P&G** or **Meat,** whereas in others, the reduction in **P&G** was larger than that in **F&V.**

Because of the high water content of **F&V**, a reduction in **F&V** alone caused only a minor decrease, and sometimes even an increase, in the total amounts of DM, CP, Fat, EF and DE fed to the females. However, a reduction in the amount of **P&G** fed, on the contrary, did cause a significant reduction in the total amounts of DM, CP, Fat, EF and DE fed. When creating the diet of the female by reducing the amounts fed to the males, caution needs to be taken to reduce each category by an equal proportion. This way, the female will receive an equal proportion of DM, CP, Fat, EF and DE in the diet as the males, and within each nutrient, the proportions of **F&V**, **P&G** or **Meat** origin will be equal to those of the male.

This is important since nutrients of the same category but of different origin often have a different digestibility rate. For example, it is well known that the digestibility of a diet not only depends on the total amount of fibre in the diet but also upon the balance of the different fibre components (i.e. lignin, cellulose and hemicellulose) within this total amount (Stanogias and Pearce, 1985; Morgan, 1989; Whittemore et al., 1993). Proteins of different origins have different amino acid make up and are of different value to the animals (McDonald et al., 1981; Whittemore et al., 1993). For example, the spectrum and balance of amino acids of plant origin is less easily utilised by the pig than that of meat origin (Whittemore et al., 1993). A reduction in the amount of plant matter fed to the female without a reduction in the amount of animal matter can therefore still result in too much protein being fed to the female. Vegetable oils are generally high in unsaturated fatty acids of long chain length and are easily absorbed whereas fats high in saturated fatty acids of medium chain length are poorly absorbed (Whittemore, 1993). Also, protein, fat, fibre and starch all contribute different proportions to the overall DE value of the diet (Morgan et al., 1984). One hundred grams of protein, fat, fibre and starch contributes 1.9, 3.5, 0.1 and 1.6 MJ DE per kg DM respectively (Whittemore, 1993). A proportionately unequal reduction of the amounts of the different food categories fed to the male as a diet for the female can therefore result in a disproportionate change in the DE content of the females' diet. For example even when a female is receiving less total food intake than the male, she may still be receiving more DE if her diet is proportionately higher in fat than that of the male.

Experience with domestic pigs suggests that the range of values for the different nutrients in the babirusa diets is too wide for all the diets to be adequate for their requirements. The exact nutritional requirements of the babirusa remain as yet unknown, but a number of estimates can be made based upon studies carried out on the domestic pigs. The maintenance DE for a Large White pig of 95kg can be calculated as being 14 MJ/day from the equation: ME maintenance $=1.75Pt^{0.75}$, with Pt = protein weight in the body (16% of the body weight for a Large White pig) (Whittemore, 1993). ME = metabolisable energy or the digestible energy minus the energy contained in the urine and in that excreted gasses. It has been established that DE and ME relate to one another in the following fashion: DE=ME/0.96 (Whittemore, 1993) and DE can therefore be estimated from the ME value. The maintenance state relates to a state where the body is neither anabolising nor catabolising body tissues and the formula can therefore be used to predict the requirements of adult, non-growing, non-gestating and non-lactating animals. Taking into account that the babirusa has a smaller mature size and is a non-developed pig, its Pt can expected to be lower than that of a Large White pig. If we estimate the Pt of the babirusa to be 12% of the body weight, and if we take 95kg as the body weight of an average adult male (see Table 5.7) then its maintenance DE would be 11.3 MJ/day. The DE for a female babirusa of 65kg would then be 8.5 MJ/day compared to 10.6 MJ/day for a 65kg Large White.

In a similar way we can estimate the maintenance requirement for crude protein in the diet. The amount of ideal protein for maintenance can be calculated from the formula: 0.004Pt (Whittemore, 1993). The balance of the different amino acids in the food is generally different from that in pig protein, but pigs still need to transfer food proteins into pig proteins. It is therefore not just the total amount of protein that indicates the quality of the diet but rather the amount and balance of those amino acids that are necessary for the construction of pig protein. That part of the total protein intake that contains the right spectrum and balance of the amino acids essential for the functions of maintenance and production is called "ideal protein" (Whittemore, 1993). Using the same Pt values as above, the ideal protein requirements for maintenance for Large White and babirusa respectively amount to 61g and 46g, and 42g and 31g for 95kg and 65kg (male and female) animals respectively. In order to derive from this the requirements for CP intake, we need to divide these amounts by the protein score (= the proportion of the dietary protein that is ideal) and the digestibility (the proportion of the ideal protein that will be digested). If we estimate the protein score to be 0.7 and the digestibility 0.75 (Whittemore, 1993), then the required amount of crude protein in the diet for maintenance is 116g and 88g for 95kg Large White and babirusa respectively and 80g and 59g for 65kg Large White and babirusa respectively.

When we apply the estimated values for the babirusa to Fig. 5.8 and Fig. 5.14, then a number of zoos appear to be feeding their babirusa below the maintenance values and the animals would theoretically not be able to survive. This discrepancy could be explained in a number of ways: by the feeding of forage which could not be calculated into the total; the reporting of incomplete information in the questionnaire; or the extra feeding of the animals by the public. Two of the favourite items fed to the animals in a zoo by the public are peanuts and bread, both of which are high in energy. For example, 50g of peanuts (=1/2 of the average packet of shelled peanuts for sale) contributes 46.9g DM, 12.8g crude protein, and 2.21MJ DE and 100g bread contributes 60.5g DM, 8.5g crude protein, 0.96MJ DE. Even small amounts of these items fed by the public can therefore have an important impact on the total daily diet.

It is also not known at this moment whether the babirusa would be less dependent on the amount and quality of the dietary protein than the domestic pig. The reason for this being that one of the advantages of foregut fermentation is that the micro-organisms will ferment dietary amino acids into ammonia and will then utilise this ammonia for the production of bacterial protein, the balance and spectrum of amino acids of which can be much more suitable to the host than that of the dietary protein (Moir, 1965 and 1968; Bauchop, 1978; McDonald et. al., 1981). In other words, the micro-organisms will transform low quality dietary protein into good quality microbial protein. The ability of the micro-organisms to use non-protein nitrogen also means that the nitrogenous degradation product of protein, urea, could be recycled if it is transported back to the stomach instead of excreted in the urine (Moir, 1965 and 1968; Bauchop, 1978; McDonald et al., 1981). If one or both of these mechanisms are of some importance in the babirusa then we could expect their requirements for the total amount and quality of the dietary protein to be less than that of a domestic pig with equal protein weight in its body. Further studies are needed to look into this possibility.

A number of zoos seem to be feeding their animals up to four times the requirement for protein and up to twice the requirement for DE, which will result in the animals putting on weight. Personal observations confirmed that obesity is a problem in a number of captive babirusa. The relation between obesity and reproductive success remains unclear at the moment. There are clear differences in breeding success between the zoos but among those institutions with regular breeding (for example zoos 1, 2, 12 and 13) animals are being underfed as well as overfed according to the predicted values for CP and DE. The effects of feeding on reproductive success are likely to be masked by substantial differences in management of males and females among the different zoos. Proteins and amino acids fed in excess to the animals requirements will be deaminated and will either form precursors for the formation of body fats or will be excreted in the form of urea. The deamination of proteins is a very inefficient process and is a large drain on the animals energy supply (Whittemore, 1993). Fats make the greatest contributions to DE and the transfer of diet fats to body fats is a very efficient process costing the animals very little energy (Whittemore, 1993). Mature animals have a smaller need for protein because there is no longer any above maintenance lean tissue growth but have a higher need for energy to sustain body maintenance activities (McDonald et al., 1981; Whittemore et al., 1993). Mature animals will therefore have a smaller protein: energy ratio than young growing animals. A protein: energy ratio of 13g CP/MJ DE is considered to be appropriate for pregnant adult female domestic pigs or growing domestic pigs above 80kg (Whittemore, 1993). We can therefore expect the required protein: energy ratio for an adult non-gestating, non-lactating babirusa to be lower than that. If we calculate the ratio of the predicted requirement for protein and energy (see above) then we become

8 and 7g CP/MJ DE for 95 and 65kg babirusa respectively. When fig 5.16 is consulted, however, it appears that in 12 institutions both male and female animals have higher protein: energy ratio than 8g CP/MJ DE. This means that the animals are receiving too much protein in relation to energy which is a large strain on the animals deamination system.

When asked for favourite items consumed by the babirusa, much more fruits than vegetables were mentioned whereas the opposite was true when asked which items were disliked by the animals. A preference for fruits was expressed by most wild pig species and tropical rain forest peccaries in their natural environment (Skinner et al., 1976; Briedermann, 1976, 1990; Howe et al., 1981; Breytenbach and Skinner, 1982; Kiltie, 1981; Jones, 1984; Pfeffer and Caldecott, 1986; Baber and Coblentz, 1987; Seydack, 1990; Caldecott, 1991a, b) except the warthog which is predominantly a grazer (Field, 1970; Cumming, 1975; Mason, 1982; Rodgers, 1984). Compared with non-reproductive plant material, fruits contain a high concentration of nutrients which could explain why they are favoured by the wild pig species. Most fruits contain a high proportion of carbohydrates such as starch and especially sugar but often have a CP content of less than 0.5% of the wet weight (Thomas, 1984; Whitten et al., 1987). This fits well with the observation in the present study that fruit and vegetables tended to be less important in the contribution of CP and fat to the diet but more important in the contribution of fibre and DE. It has also been shown that domestic pigs have a marked preference for sweet substances which might again contribute to this preference for fruits (Kennedy and Baldwin, 1972). In most of these wild pig species roots and tubers became the most important items in those periods that fruits were scarce (Field, 1970; Cumming, 1975; Howe et al., 1981; Mason, 1982; Breytenbach and Skinner, 1982; Jones, 1984; Rodgers, 1984; Seydack, 1990). The reason why carrots, potatoes, yams and fodder beets appear on the list of items more disliked by the babirusa may be that the fruit supply of the captive babirusa is generally a very stable supply, and in most zoos the babirusa are not forced to consume underground plant parts to meet their nutritional demands in the way that the animals in the wild may be. Alternatively, the dislike for roots and tubers may be more fundamental, and could be linked to the fact that, unlike most other wild pigs, babirusa have never been observed to root in compact ground. The possibility therefore exists, at least during certain seasons, that roots do not form as large a part of the diet of the wild babirusa as they do in the diets of other wild pigs.

Cabbage, brussels sprouts, cauliflower and broccoli all belong to the Brassicaceae or cabbage family which is characterised by a particular set of flavours caused by the inclusion of sulphur volatiles and isothiocyanates (Eskin, 1979). Both the flavour caused by these substances as well as their potential toxicity may explain why they were not among the favoured food items of the babirusa. This type of poisoning is well known in ruminants fed on large quantities of kale. The most important toxin in the cabbages, S-methylcysteine sulphoxide is transformed by the rumen micro-organisms into dimethyldisulpide, which has a haemolytic action and causes loss of appetite, haemoglobinuria, jaundice and anaemia (Rook and Thomas, 1983).

A preference for fruit and the consumption of a wide variety of tree leaves, buds, twigs and bark fits well within the hypothesis of the babirusa being a non-ruminant forestomach fermenting frugivore/concentrate selector as was proposed in chapter 2. Fruits and above-ground dicotyledonous plant parts are relatively nutrient rich food items. They can be digested and fermented efficiently during the fairly brief passage through the stomach, where the micro-organisms perform an important role in the digestion of mechanical plant defence components, the detoxification of chemical defence components, the utilisation of non-protein nitrogen and the production of vitamins which are then available to the host (Moir, 1965, 1968; McDonald et al., 1981; Bodmer, 1990). The findings of the inter-zoo study also support the findings of the study in which two babirusa were observed foraging in a semi-natural enclosure. The animals mostly consumed bramble leaves and cherries and did not ingest much herbal material. Babirusa in captivity and in semi-natural condition also demonstrated the ability to carefully select and manipulate certain plant and fruit parts. Captive babirusa were seen to shell peanuts, peal bananas, pick alfalfa leaves off the stems and to eat different parts of a range of leafy branches offered to them. The babirusa in a semi-natural environment selected the leaves of one grass species, the ears of another grass species and the flowers of a certain herb

(*Sanguisorba minor* Scop.). These observations suggest that the babirusa would be able to select and separate out the more easily digestible plant parts. Studies combining the diet composition of babirusa in the wild with the nutritional composition of the items they selected would shed much further light on this phenomenon.

The behaviour of the babirusa in the semi-natural enclosure indicated that babirusa mainly forage by walking around with their nose close to or on the ground surface; that next to sleeping, the animals spent more time foraging and eating than any other behaviour. The technique, employed by a limited number of zoos so far, of scattering the food around in the enclosure at many different times of the day is therefore completely in line with the animals natural behaviour and should be encouraged. The observation in Surabaya Zoo that babirusa will stand on their hind legs without support to eat the leaves of trees in their enclosure can also be brought into practise in captivity when feeding tree branches to the animals (Macdonald et al., 1993). Suspending the branches high enough above the animals but just within reach should elicit such behaviour.

In both Antwerp and Surabaya Zoo it was observed that males tend to monopolise the food when animals are fed together (Leus et al., 1992). Males in Antwerp zoo only allowed the females to eat beside them when the female was in oestrus (Leus et al., 1992). Therefore, in those zoos where males and females are fed together, caution should be taken to avoid the male monopolising the food; such a behaviour has been seen to form a major source of stress to the female at feeding times. All zoos fed females and their young together. When the feeding is done on the floor it makes the food immediately available to the youngsters which have been observed to start nibbling at solid foods as soon as one week of age (Leus et al., 1992). A number of zoos remarked that pregnant and lactating females required more food to keep the same body weight. Pregnant and lactating females will specifically need a higher protein: energy ratio because of the increase in protein catabolism either for the growth of the piglets or the production of milk (Whittemore, 1993).

Even though at first glance the diets fed to animals in captivity may seem to be very similar, large differences can appear when the nutritional composition of the diet is calculated. The range of composition of the diet fed to adult babirusa in captivity was so wide that it was impossible for all of these diets to be within the requirements of the animals. Since the present study is the first to look into these nutritional requirements, no stock of knowledge on this species was available which could indicate whether the prediction equations (developed for the domestic pig breeds) also held for the babirusa.

One of the priorities with regard to the babirusa is therefore the measurement of their requirements for protein and energy. This would be expected to be of major benefit to the captive breeding program of the species. In recent years a technique of diet selection for pigs was developed; it was shown that when pigs were given a choice between two foods that differ in their crude protein content, they were able to select a diet that met their requirements for maintenance, growth and fattening (Kyriazakis et al., 1990, 1991; Bradford and Gous, 1991a and b). When this technique was tested with two different pig breeds (an improved pig breed: F1 hybrid Large White x Landrace, and an unimproved pig breed: purebred Chinese Meishan) it was shown that when given a choice between an appropriate pair of foods that differ in their crude protein content, pigs of different breeds were able to select a diet that met their requirements and allowed them to express the growth and carcass characteristics typical for their breed (Kyriazakis et al., 1993, see reprint at end of thesis). It was suggested that the same technique might be useful to determine the protein requirements of other animal species where these were unknown as is often the case with wild animals kept in captivity (Kyriazakis et al., 1993). A short study was therefore undertaken, with as its aim a test of the feasibility of determining the protein requirements of the babirusa by means of this food selection technique.

5. Feasibility study of the use of the diet selection technique for the determination of the protein requirements of the babirusa.

Material and methods

Animals and housing

Animals of two different institutions were used in this study, corresponding to zoo code numbers 1, 12 and 13 (one institution had two slightly different diets for babirusa in different places within the zoo). The age of the animals used and the diet they normally received can be found in Table 5.8. All animals were housed individually and each pen was provided with two round metal food bowls connected by a metal strap. A heavy concrete beam was positioned on top of the metal strap in between the two food bowls so that these could not be turned over. Spillage was carefully collected from the concrete floor and weighed with the food refusals.

Foods

Two foods with similar calculated digestible energy contents, but different crude protein (CP) concentrations were formulated and fed as coarsely ground meal:

Low protein diet (L):

Maize + Commercial vitamin and mineral mixture (50g/1000kg).
886g dry matter(DM)/kg food.
104g CP/kg DM.
92g CP/kg food.

High protein diet (H):

2/3 Maize + 1/3 Soya Bean Meal(toasted)+ Commercial vitamin and mineral mixture (50g/1000kg).
890g dry matter (DM)/kg food.
198g CP/kg food.

Chinese Meishan pigs between 21 and 34kg selected a diet of 144g CP per kg food whereas Large White x Landrace pigs of a similar weight selected 194g CP. Chinese Meishan pigs are an unimproved pig breed with a

Table 5.8 Studbook number, age at time of study, normal diet (indicated by the zoo code number referring to chapter 5) and treatment for animals used in the food selection study. (??= animal of unknown age when it arrived in Europe from Indonesia)

Institution 1:

Animal	Sex	Age (years)	Diet	Treatment	
0044	M	10	12	HLHLHL	L right
0057	M	7	12	LHLHLH	L left
0031	M	12	13	HLHLHL	L left
0058	F	7	12	HLHLHL	L right
0067	F	6.5	12	LHLHLH	L left
0069	F	6.5	13	LHLHLH	L left

Institution 2:

Animal	Sex	Age (years)	Diet	Treatment	
0047	M	?? >9	1	LHLHLH	L left
0049	M	?? >9	1	HLHLHL	L right
0155	M	2.5	1	LHLHLH	L left
0174	M	0.5	1	HLHLHL	L left
0048	F	?? >9	1	LHLHLH	L left
0050	F	?? >9	1	LHLHLH	L right
0066	F	6.5	1	HLHLHL	L left
0143	F	2.5	1	LHLHLH	L left
0158	F	1.5	1	HLHLHL	L right
0157	F	1.5	1	HLHLHL	L right

slower growth rate and lower mature body weight than the improved pig breeds (Cheng, 1983, 1984). Babirusa are an unimproved pig species with an even lower mature body weight than the Chinese Meishan pigs (~100kg v. 250kg for male babirusa and Chinese Chinese Meishan respectively (Cheng, 1983, 1984; Leus et al., 1992)). Most babirusa used in the study were non-growing adult or slow growing subadult animals and not young fast growing juveniles as was the case in the previous study with Chinese Meishan and Large White x Landrace pigs (Kyriazakis et al., 1993). It was therefore expected that the protein requirements of the babirusa would be even lower than those of the Chinese Meishan.

It was not possible to offer the babirusa the same diets as had been offered to the Chinese Meishan and Large White x Landrace pigs since the pigs would not have been able to select a diet with a CP content lower than 130g /kg food. In order to offer the animals a 'low protein' diet that was as low in protein concentration as possible, a maize diet was selected. Since soya and maize have got a very similar DE content, the inclusion of soya in the maize diet created a high protein diet with similar energy concentration as the low protein maize diet. Since the amount of CP selected by pigs decreases as the pigs grow heavier and older (Kyriazakis et al., 1990, 1993), it was considered that the babirusa with a lower adult body weight than the Chinese Meishan would not select a diet that was much higher than 144g CP/kg food. The two diets used in this study therefore provided the babirusa with a very wide range of CP concentrations (from 92 to 198 CP/kg food). Maize based diets had the added advantage that maize was often said to be one of the favourite food items of the babirusa. It was expected that this would reduce the chance of rejection by the animals. The diets were intended to be adequate for vitamins and minerals and a commercial vitamin/mineral mixture was therefore included.

Design
The experiment consisted of two periods.

Period 1 (Learning period):
The babirusa were allowed to sample independently the two foods that subsequently were going to be offered as a choice according to the method established by Kyriazakis et al. (1991). Food L and H were offered alone and *ad libitum* on alternate days for a period of 4 days, while on day 5 one food was offered in the morning and the other in the afternoon. The starting diet was distributed among the animals as indicated in Table 5.8.

Period 2 (Choice feeding period):
For a period of 7 days the babirusa were given free and continuous access to both foods L and H as a choice. The position of the feed troughs for food L and H was distributed as indicated in Table 5.8. For all animals in institution 1 except 0049, 0048 and 0174 the position of the troughs was reversed for two days after the first 7-day choice period.

Both during periods 1 and 2, the daily feed refusals were measured to the nearest 1g at the same time each morning. Spillage was carefully collected from the concrete floor and weighed with the refusals.

Statistical analyses

Results were analysed using oneway analyses of variance and t-test on minitab statistical package.

Results

Learning period

The amounts ingested by the animals during the adaptation period can be found in Table 5.9. Two animals in institution 1 (0044 and 0058) and two animals in institution 2 (0048 and 0174) did not consume significant amounts of any of the foods during the first three days and had to be taken off the experiment. All animals showed initial hesitation to the diet, whether it was L or H and did not eat much during the day-time of day 1. Some animals, however (0066, 0157, 0158, 0049, 0155, 0143) had eaten all the available food by the morning of day 2. Animal 0031 never sampled food H on the first day. On day 2, all animals which received food H on day 1 ate larger amounts of food L on day 2. This included animal 0031 which only ate 100g of food L but had not eaten anything from food H and had very low intakes compared to the other adult male pigs for the remainder of the adaptation period. The reactions to food H shown by those animals which had been fed on food L during day 1 were variable, some eating larger amounts of food H, others eating much smaller amounts of food H. Except for animal 0031, all animals fed on food L during day 2 ate less of food H during day 3, the amounts of food H eaten during day 3 being smaller than those eaten of the same food during day 1, except for animal 0049. Animals fed on food H during day 2 ate larger portions of food L during day 3, except for animal 0047 which had eaten large amounts of food H during day two. On day 4 animals fed food L ate larger amounts of it than they had of food H during the previous day and of food L during day 2. Animal 0049 was an exception to the latter which may be explained by the fact that he had eaten a large amount of food H during day 3 and was therefore likely to be less hungry than the other animals which had eaten only small amounts of food H during day 3. All animals fed food L during day 3 ate smaller amounts of food H during day 4, animal 0050 by now showing a true aversion for food H. Generally, during day 5 smaller amounts seemed to be eaten of both foods but it must be remembered that exposure time to each of the food was only half that of the previous day since the foods were changed in the middle of day 5. However, not only babirusa 0031, 0066, 0158 and 0157 which first received food H on day 5, but also babirusa 0069 and 0050 which first received food L on day 5 only ate little to almost nothing of food H.

Table 5.9. Intake (grams) of food L and H by the babirusa during the learning period. The first part of the table contains the results of the animals that received the high protein food (H) on day 1 and the second part those that received the low protein food (L) on day 1.

Animal	Day 1	Day 2	Day 3	Day 4	Day 5	
	H	L	H	L	H	L
0031	0	100	137	680	10	666
0049	1250	2752	1666	1912	622	1670
0066	1000	2398	70	2718	4	986
0158	1000	1220	318	1731	40	1124
0157	1000	1100	46	1590	8	958
	L	H	L	H	L	H
0057	545	98	2455	932	1488	850
0067	560	1348	1680	1264	464	880
0069	290	72	1210	540	525	20
0047	2300	2936	2608	1004	1880	944
0050	1596	400	1456	6	1140	6
0155	2000	1447	1878	1068	868	730
0143	1500	1500	2250	588	1704	122

Choice feeding period

When given the choice between foods L and H simultaneously, only 4 animals (0057, 0067, 0155 and 0049) consumed significant amounts of both foods whereas the other animals almost completely ignored food H. Animal 0047 consumed 372g of food H on the first day of the choice feeding period but only ate very small amounts (6-12g) or nothing at all of food H during the other days. A similar result was obtained for animal

0158 which consumed 256g of food H during day 1 but only 2-14g on the other days. Animals 0031, 0069, 0066, 0143, 0157, 0050 only sampled food H on some days, eating not more than 16g. All of the latter animals, except 0143 already showed an aversion to food H during the adaptation period. Those animals that did eat significant amounts of both foods during the choice feeding period (0057, 0067, 0049 and 0155) had also eaten relatively large amounts of food H during the learning period.

For animals 0057, 0067 and 0155, the mean amounts of food L consumed were significantly different from the mean amounts consumed of food H ($p<0.001$), a larger amount being consumed of food L than of food H. This indicates that the animals did have a preference for one of the foods. The eating pattern of animal 0049 was very irregular in both the total amount eaten and the proportions of the two foods eaten, some days consuming more of food L, and on others more of food H. The animal refused to eat at all during day 7 and showed some clinical distress, the reason believed to be constipation. No significant difference could be found between the mean amounts of food L and H consumed during the previous 6 days and since a clinical condition may have interfered with the results this animal was not included in further analyses.

The results for animals 0057, 0067 and 0155 are shown in Table 5.10. The total amounts of food ingested were significantly different from one another ($p<0.001$). There was also a significant difference between the total amount of CP ingested each day for 0057 and 0067, and for 0057 and 0155 ($p<0.001$). The total amounts of crude protein ingested each day by 0067 and 0155 were not significantly different from one another. There was no significant difference in the proportion of crude protein in the diet selected, the overall average for the three animals being 130 ± 11g CP/kg fresh food selected. Equally, no significant difference was found between the proportions of food H in the selected diets, the overall mean for the three animals being 356 ± 107g food H/kg fresh food selected. This indicates that the three pigs selected a diet similar in composition but ate different amounts of this diet which caused the differences in the amount of CP ingested each day.

Table 5.10 Daily food intake, CP intake, amount of CP in the diet selected and amount of food H in the total food intake for the choice feeding babirusa. (Data = mean±stan. dev.)

Animal	Sex	Inst.	Total food intake (g/day)	Total CP intake (g/day)	Amount CP in diet selected (g/kg food)	Amount food H in total intake (g/kg food)
0057	M	12	2365±269	303±38	128±10	344± 89
0067	F	12	1553±117	211±17	136± 5	416± 49
0155	M	1	1795±179	223±31	125±15	309±144
Significance			***	***	NS	NS

Inst. = Institutes where animals were housed are indicated with zoo code numbers refering to chapter 5.
M= Male
F=Female
*** = p<0.001

Since all other animals only consumed insignificant amounts of food H, the percentage CP in the diet selected (92.7±1.0g CP/kg food) was similar to the percentage of CP in food L (92g CP/kg food). The total amount of food eaten, and therefore the total amount of CP ingested each day was very variable with no trends obvious between animals of the two institutions or between animals of different age or sex (Table 5.11). The amount of food selected by animal 0047 became smaller as the study period progressed (from 1500g to 337g) which explains the large standard deviation for this animal. Animal 0143 ate significantly more food than any other animal ($p<0.001$) except 0047 whereas animal 0050 ate significantly less food than any other animal except 0031. No other statistical differences were found between the intakes of the animals. Since almost nothing of food H was consumed, the total amount of CP ingested each day largely reflects the total intake of the animals.

Table 5.11. Total food intake and total CP intake of those animals that only consumed insignificant amounts of the high protein food (H) during the choice feeding and therefore almost exclusively consumed the low protein food (L).

Animal	Sex	Inst.	Total food intake (g/day)	Total CP intake (g/day)
0031	M	13	992±357	91±33
0069	F	13	1242±245	114±23
0050	F	1	694±241	64±22
0066	F	1	1447±331	134±31
0143	F	1	2594±270	239±25
0158	F	1	992±357	130±28
0157	F	1	1110±174	102±16
0047	M	1	2088±891	198±94
Significance			***	***

Inst. = Institute where animals were kept indicated with zoo code numbers refering to chapter 5.
M= Male
F=Female
*** = $p<0.001$

Those animals for which the position of the two food troughs was reversed for two days after the first 7-day choice feeding period showed the same preferences as they had done before the change. This indicates that their choice was not made on the bases of the position of the food troughs.

Discussion

In order for food selection experiments of this nature to work it is not only important that the two diets are nutritionally of the right composition, but also that they posses different organoleptic properties which the animals can associate with this difference in nutritional composition (Rose and Kyriazakis, 1991). The incorporation of a learning period in food selection experiments is essential since it gives the animals the time to associate the smell and taste of the new foods with their nutritional composition (Gous et al., 1989; Kyriazakis et al., 1990; Rose and Kyriazakis, 1991). Babirusa in both institutions normally receive mostly succulent fruits and vegetable matter as the bulk of their food with pellets and grains as a supplement. A diet composed wholly of coarsely ground meal was therefore very strange to them, which may explain the initial hesitation towards both foods L and H during day 1, as well as the fact that 4 animals refused to eat significant amounts of either diet for a period of three days. Another condition for food selection experiments to be successful is that both diets offered are equally palatable to the pigs. Since maize was often mentioned as one of the favourite foods of the babirusa, it was expected that both diets would be palatable. In practise however, four pigs ate much less (or almost nothing) of food H after day three than they had done on day one or two, even though it was the only food offered during that day. By day five a total of six pigs consumed 20g or less of food H and were therefore avoiding the food. The same six pigs together with animals 0047 and 0143, which also showed a sharp decline of the amount of food H consumed over the study period, did not eat significant amounts of food H during the choice feeding period. This suggests that to these eight pigs food H was not as palatable as food L, that this was learned by the pigs during the learning period, and that the choice made during the choice feeding period was not one based on protein content of the diet but on the palatability of the food.

Palatability has been defined as the degree of readiness with which a food is selected and eaten (McDonald et al., 1991). Smell, touch and taste are important factors in determining the palatability of a food (McDonald et al., 1991). Food L and H were both coarsely ground meals but food H smelled and tasted different (to the observer) from food L. It is possible that food H had a smell and/or taste which was not acceptable to all babirusa. Soya bean meal contains goitrogenic and anticoagulant substances as well as protease inhibitors which have an inhibitory action on protein digestion. These inhibitors can however be deactivated by heating, and toasted soya bean meal is often included in the diet of domestic pigs (McDonald et al., 1991). In the present experiment also, toasted soya bean meal was used and it is not clear at this moment which of the soya bean meal characteristics was/ were responsible for the aversion to food H. Post-ingestive cues may also have influenced the palatability of food H; for example some nutrients create a feeling of satiety sooner than others.

The three pigs that did eat both food H and L when given the choice and did not show any signs of clinical distress, selected a diet with a statistically equal proportion of CP. The total CP intake each day was different since the three pigs ate different amounts of the diet selected. Previous studies indicated that younger pigs select a diet with a higher crude protein concentration than older pigs (Kyriazakis et al., 1990; Kyriazakis et al., 1993) and that growing female pigs select a diet that is lower in CP concentration than growing male pigs (Kyriazakis and Emmans, 1991; Rose and Kyriazakis, 1991). These findings appear to be at odds with the results of the present study since all three pigs, although of different age and sex selected the same diet. However, it must be remembered that these three pigs belonged to different institutes and were thus being fed different diets. Animals 0057 and 0067 belonged to the institute with code number 12 and animal 0155 belonged to the institute with code number 1. Within zoo number 12, males and females were also fed different diets. Table 5.12 presents the composition of the daily diet previously fed to each of the three animals.

Table 5.12 Composition of the daily diet previously fed to the choice feeding babirusa (g/day).

Animal	Sex	Inst.	Total wet weight	DM	CP	Fat	EF	DE
0057	M	12	3000	641	60	11	87	8.7
0067	F	12	2400	548	56	11	75	7.5
0155	M	1	3375	1175	181	48	313	15.5

In contrast to the choice feeding studies with domestic pigs, the babirusa in this study had a different nutritional background, animals in institution 1 being fed a diet with a much higher DM and CP content than those in institute 12. Studies with domestic pigs showed that they were able to select a diet that corrected previous mis-feeding. Pigs previously underfed CP selected a diet with a higher CP concentration than pigs previously fed too much CP (Kyriazakis and Emmans, 1991). This may explain why the diet selected by the younger male babirusa, 0155, was not higher than that selected by the adult male 0057. Male 0155 had been receiving a diet which was much higher in CP than male 0057, and depending on where the true CP requirements of the babirusa lie, either or both of these animals may have been compensating for previous misfeeding. The same applies to the lack of difference in the CP content of the diet selected by the male and female, the female having previously received a diet with a DM content which was 85% of that of the male with a CP content that was 93% of that of the male.

The calculated daily CP requirements for a 95kg and a 65kg adult babirusa were 88g and 59g respectively. These values contrast sharply with the daily amounts of CP ingested by the choice feeding babirusa which were much higher (303, 211 and 223g CP/day). The latter may be a reflection of previous underfeeding in CP in zoo 12 when the animals were youngsters and would have required a lot of protein for growth, and/or it may reflect the younger age of animal 0155 which was still growing and therefore had a protein requirement not only for maintenance but also for growth. Alternatively it may indicated that for a thus-far unknown reason, babirusa have a higher protein requirement than the Large White domestic pig.

From the above observations it is clear that a number of problems have been identified and that these need to be solved before the technique of choice feeding can be applied to the babirusa.

There is a need for the identification of a set of diets which offer a very broad range of protein concentration. These diets not only need to be equally palatable to the babirusa, but also can be fed to this species for a prolonged amount of time without eliciting abnormal clinical effects. The very variable food intake of the animals which were not consuming both foods L and H suggests that even if a diet is palatable there may still be a number of other factors influencing the food intake. One of these is gut fill. Animals may be stimulated to eat more food than they require in order to obtain the appropriate gut fill (Whittemore, 1993). Although it is reasonably well known for domestic pigs what the appropriate amount of food is to obtain this gut fill, this is still an unknown factor in the babirusa. Another factor that needs to be resolved before reliable estimates of CP requirements of the babirusa can be obtained from the choice feeding technique is the different nutritional background of the animals under study. As was clear from the first part of this chapter, adult male babirusa receive very different diets in different zoos; within one zoo, adult female babirusa were sometimes fed a diet which was different from the males not only in quantity but also in quality. Adult female babirusa receive different diets in different zoos and, although this was not part of the scope of the present study, it may be expected that the diets fed to the young growing animals show the same variation in amount and composition as those fed to the adult animals.

These different nutritional backgrounds could be overcome if two equally palatable and suitable diets can be defined for the babirusa. In this fashion, the diet selection of the babirusa with different nutritional background and of different age and sex could be followed over a longer time-span in which the animals would be able to correct any misfeeding that may have occurred in the past and could demonstrate their true CP requirements, thereby defining what is characteristic for their species, age and sex.

6. Conclusions

Fruits were the items most favoured by babirusa in captivity. The animals also readily consumed a wide variety of leaves, buds and twigs from branches. The nature of the items fed to babirusa was not very different from zoo to zoo but the proportions of the different food categories fed were very variable. The range in the amounts of total food, dry matter, crude protein, fat, fibre and digestible energy fed to the animals was so large that it was impossible for all diets to be appropriate with respect to the requirements of the babirusa. According to prediction equations established for domestic pig breeds the energy requirements for the babirusa were estimated to be 11.3 MJ/day for males and 8.5 MJ/day for females. In a similar way the protein requirements of the babirusa were estimated to be 88g CP/day for males and 59g CP/day for females. Some zoos fed their babirusa below these requirements whereas others appeared to be overfeeding their animals. Thus babirusa in different zoos had very different nutritional backgrounds. The latter was identified to be one of the problems blocking the application of a recently developed technique of diet self-selection as a way of revealing the protein requirements of babirusa. There is a need for greater control over the diets of babirusa fed in different zoos in order to measure the true CP requirements of babirusa by means of this food selection technique.

CHAPTER 6 DISCUSSION OF THE DIET OF BABIRUSA IN ITS NATURAL HABITAT.

1. Introduction

Information on the diet of babirusa in the wild is scarce and anecdotal in nature. Valentijn wrote in 1726:

> "De spijs van dit dier is niet dezelve, als die van de andere Bosch verkens, die canari (een soort van Indiaanse amandelen) eeten; maar alleen, of gras, of wel bladeren van de waringin en andere wilde bomen. Men heeft van't zelve ook niet te vrezen, dat het, gelijk andere verkens, de thuinen verwoesten, de heiningen doorwroeten, en't gezaaide, of geplantende verderven zal, alzoo't zich meest met boombladeren behelpt, en geen quaad ter wereld doet."
> (The food of these animals is not the same as that of the other forest pigs, which eat canari, a sort of Indian almond; but they only eat grass or leaves of the waringi and other wild trees. One should also not fear that they, like other pigs, will ravage gardens, uproot fences and destroy that which is planted, whilst they only feed themselves with tree leaves and don't do any harm at all.)

He also adds that animals kept in captivity in local gardens were generally fed on rice, batata (= sweet potato), leaves, canari, padi and fish, including the intestines. It later appeared that Valentijn's descriptions were not based on his personal observations but were a summary of an unpublished and now missing manuscript by Rumphius (1628-1702) entitled "Amboinsch Dierboek" (Polman, 1983).

During the following centuries, basically the same information (with a few additions here and there) has been repeated over and over again in encyclopaedic works by Halle (1757), Batsch (1788) Desmarest (1820) Goldsmith (1822), Schreber and Wagner (1835), Tjeenk Willink (1905) Haltenorth (1963), Morris (1965) and others. Some of these additions, such as the inclusion of water plants, fruit and invertebrates in their diet, appear to be extrapolated from first hand reports by Lesson and Garnot (1825), Wallace (1870), Sarasin and Sarasin (1905) and Deninger (1910). Other additions, however, appear to be based on reports of food items fed to babirusa in captivity such as fish (Valentijn, 1726) and roots (Geoffroy Saint-Hillaire and Cuvier, 1842).

More recently, new information was obtained by Selmier (1978, 1983) who visited Sulawesi and the Togian islands in search of babirusa. Residents of Lore Kalamanta (Sulawesi) reported to her that babirusa and *Sus celebensis* ate the same greens and acorns, but that they had different preferences. Both in Lore Kalamanta and on the Togian islands *Elatostema* (Urti.*) was reported as a favourite babirusa food. The babirusa on Pangempan, one of the Togian islands, were observed to eat fruits (e.g. mango and coconuts) and various fungi. They would also visit the small village gardens in search of maize, millet, sweet potatoes, sugar cane and small herb-trees among others.

Since Selmier (1983), the only first hand information to be published on the diet of babirusa in the wild was a note by Whitten et al. (1987) stating that the major fruit eaten by the babirusa in the west of the Dumoga-Bone National Park was said to be the pangi fruit *Pangium edule* Reinw. (Flac.).

The above information represents all that is available on the composition of the diet of babirusa in the wild. From the results of the previous chapters however, a number of assumptions can be made. Babirusa are likely to be non-ruminant foregut fermenters specialised in the fermentation of cell solubles and the more easily digestible cell wall fractions. These substances are most abundant in fruits and dicotyledonous plant parts rather than the monocotyledonous plants such as grasses. When given access to a semi-natural enclosure, the babirusa mostly selected leaves (bramble leaves) and fruits (unripe cherries). Likewise, in captivity, the animals showed a preference for fruit items and readily consumed the leaves, buds and twigs of a wide variety of trees. From these observations we can assume that fruit and leaves will probably form important ingredients in the babirusa diet, supplemented with smaller quantities of herbs, grass, roots and animal matter.

This chapter will investigate some of the trees and plants available to the babirusa of Sulawesi (*B. b. celebensis*) with special reference being paid to the fruiting trees and the type of fruits they produce. The nature of the plants available to the babirusa will of course depend on the habitats and forest types frequented by them. For this reason, a short description of the forest types of Sulawesi will be presented first together with notes on the likelihood of babirusa being found in these forests.

2. The forest types of Sulawesi

Lowland evergreen rain forest:

Lowland evergreen rain forest occurs in ever-wet, well drained inland locations up to about 1200m altitude. It is characterised by a very dense, lofty green vegetation with very high trees (up to 45m) (van Steenis, 1950). The Sulawesi lowland rain forest is markedly different from those of Borneo and other islands on the Sunda Shelf. Lowland rain forests on the Sunda Shelf are often dominated by trees of the Dipterocarpaceae family (Lack and Kevan, 1984; Whitmore, 1984a; Whitmore and Sidiyasa, 1986). East of the Wallace Line this family is not so common, and there is a much more diverse floral composition (Whitten et al., 1987). More information with respect to the plants of lowland evergreen rain forest in Sulawesi may be found in the papers by Hickson (1889), Steup (1931, 1932, 1933, 1935, 1939a, b), Verhoef (1938), Bloembergen (1940), Meijer (1974), Lack and Kevan (1984, 1987), Soewanda et al. (1984), Whitmore et al. (1984b), Whitmore and Sidiyasa (1986), Whitten et al. (1987) and Whitmore et al. (1989). There have been several reports of the presence of babirusa in the lowland evergreen rainforest (Macdonald, pers. comm.; Selmier, 1978, 1983; Patry and Capois, 1989; Patry, 1990) although recent reports suggest that the babirusa may have now largely moved from the lower lying coastal areas to the more inland, higher and less accessible regions (Macdonald, 1993).

Fresh water swamp forest:

Fresh water swamp forest occurs on land subjected to occasional flooding with mineral rich fresh water (≥ pH6) (Whitmore, 1984a). The floral composition of fresh water swamps can vary with the local soil and drainage conditions but travelling from the edge of the open water to the drier areas one typically finds grassy vegetation followed by palms and pandans followed by a forest very much like dryland lowland forest with shrubs and trees (Whitmore, 1984a; Whitten et al., 1987). Further information about fresh water swamp forest plants in Sulawesi may be found in the papers by Bloembergen (1940), Whitten et al. (1987) and Whitmore et al. (1989). There have been several reports, mostly in encyclopaedic works, stating that babirusa tend to live in swampy and marshy areas and along rivers (Lesson and Garnot, 1826; Jennison, 1927; Temminck, 1835; Boitard, 1851; Haltenorth, 1963).

Peat swamp forest:

The only major peat swamp in Sulawesi is the Rawa Aopa swamp, 100km west of Kendari (Whitten et al., 1987; Zwahlen, 1992). The vegetation in the swamp itself includes water plants in various forms and shapes whereas the swamp forest can be found towards the edges of the swamp where, although the soil is still flooded for a large part of the year, the water is less deep (Zwahlen, 1992). Information additional to that found in the papers by Whitten et al. (1987) and Zwahlen (1992) may be obtained in Whitmore et al. (1989). The presence of the babirusa in the Rawa Aopa peat swamp forest has recently been verified (Zwahlen, 1992).

Mangrove forest:

The typical tropical coastline mangrove forests have become rare in Sulawesi. Mangrove trees are tolerant of saline conditions but can also grow in fresh water conditions and will therefore sometimes be found more inland along rivers. A typical mangrove forest contains practically no understorey vegetation and contains trees provided with specially developed root systems to cope with the regular flooding of saline sea water (Whitten et al., 1987). Babirusa have been reported to swim and dive in the sea (Valentijn, 1726; Selmier, 1983) but it is more likely that they, like rats, macaques, other pigs and lizards, visit the edges of the mangrove forest to forage for fruits and various animal products (Whitten et al., 1987). Further information about the mangrove forests of Sulawesi may be found in the paper by Whitmore et al. (1989)

Riverine forest:

The riverine forest is usually not very distinct from the surrounding lowland forest and not many of the trees recorded in riverine forest are restricted to it (Whitten et al., 1987). Additional information on riverine forest plants in Sulawesi may be found in the papers by Steup (1933) and Whitmore and Sadiayasa (1986). Video recordings have been made of babirusa visiting salt licks alongside a river in the north of Sulawesi (Patry and Capois, 1989; Patry, 1990)

Forest on ultrabasic soils:

When considering the exceptional soil conditions formed over ultrabasic rocks (low silica and a high iron and magnesium content), it might be expected that most of the plants found in these areas are more or less restricted to them (Whitmore, 1984a; Whitten et al., 1987). It is generally agreed that low densities of vertebrate animals are found living in regions with ultrabasic soils in Sulawesi. Whether this is related to low productivity, high levels of defence compounds in the leaves, or an imbalanced nutrient and mineral concentrations in the plant parts is not yet known (Whitten et al., 1987). There is no information on the presence of babirusa in the forests on ultrabasic soils of Sulawesi.

Forest on limestone:

A limestone landscape is very rugged with steep slopes, vertical walls, crevices, overhanging precipices and only very few gentle sloping surfaces (Whitmore, 1984a; Whitten et al., 1987). Soils on limestone are particularly rich in calcium and magnesium (Whitten et al., 1987). The plant species found in limestone areas require a tolerance of high levels of calcium and have been selected by their ability to cope with both this and the physical nature of the landscape. The result is a very specific community of trees which are found mainly in the gentler sloping areas. The steep cliffs and rock faces are colonised with a distinctive, more herbaceous flora (Whitmore, 1984a; Whitten et al., 1987). More information for Sulawesi may be found in Bloembergen (1940). The babirusa are hunted by the people of Toradja land, a limestone rich area in Central Sulawesi (Bloembergen, 1940). Babirusa are therefore certainly present in this area but their presence on particular sites is likely to related to the accessibility of the terrain (steepness of slopes etc.).

Monsoon forest:

Tropical rain forests are replaced by monsoon or seasonal forests in those regions where water is periodically seriously limiting to the vegetation (Whitmore, 1984b). Most monsoon forests are largely deciduous. Little monsoon forest remains in Sulawesi because of its susceptibility to fire. Repeated burning of a monsoon forest eventually turns the vegetation into grassland (Whitten et al., 1987). Additional information on the monsoon forest plants of Sulawesi may be found in the papers by Sarasin and Sarasin (1905), Steup (1929, 1939a, b), Bloembergen (1940) and Whitten et al. (1987). It is conceivable that the babirusa will venture into the monsoon forests, if only during the wetter months. Since recent investigations have indicated that babirusa tend to disappear from a region as soon as the forest disappears (Whitten et al, 1987), it is unlikely that they will frequent the dry grassy savannahs.

Montane forest:

Above the lowland forest the lower montane forest is found with shorter, less massive trees, epiphytes and orchids. At higher altitudes the trees become even shorter with small, relatively thick leaves. This is called the upper montane forest. At even higher altitude, the trees are shorter still, with smaller leaves, epiphytic lichens but practically no orchids. This is the subalpine forest. In valleys and water-logged places in this zone there are virtually no trees but a covering of shrubs, herbs and tough grasses (Robbins and Wyatt-Smith, 1964; Whitmore, 1984a; Whitten et al., 1987). The altitudes at which the different montane forest types occur are mainly governed by temperature and cloud level. A useful altitude scheme suggested by Whitten et al. (1987) for Sulawesi is:

lowland and hill forest	0 - 1500m
lower montane forest	1500 - 2400m
upper montane forest	2400 - 3000m
subalpine forest	>3000m

Additional information on montane forest composition on Sulawesi is contained within the papers by Steup (1931, 1939a, b), Bloembergen (1940), Wemmer and Watling (1986) and Whitten et al. (1987). According to Deninger (1910) the babirusa on Buru were mainly confined to the mountainous regions and are present at altitudes of at least 1000m.

Bloembergen (1940) visited the forests in the region of the Lindu-lake at 1000m altitude and reported that the local people hunt wild pigs, babirusa, deer and anoa in this region. More recent studies of the Lore Lindu reserve in Central Sulawesi indicated that only 10% of the land lies below 1000m whereas about 70% of the reserve lies between 1000-1500m (Wemmer and Watling, 1986) and the babirusa are therefore likely to be present at these heights. No further information on the altitudinal zonation of the babirusa is available in the literature. It can be expected that they will frequent the lower montane forest if only because of the important food source represented by the fruits of the Fagaceae trees which often dominate this forest type (Wemmer and Watling, 1986; Whitten et al., 1987). From the lower montane forest upwards, their occurrence remains an open question.

For more detailed information on the nature and composition of the vegetation in these regions the reader is referred to the references linked with each forest type and to Appendix 1. The latter gives a detailed annotated list of most of the tree species reported from the Sulawesi forests, together with information on the appearance, habitat, fruits and local use of some of the trees. Both the different forest types and the appendix will be referred to throughout this chapter. A lot of the more recently gathered information on the composition of the Sulawesi forests is to be found in unpublished reports, mostly to Institutions of the Indonesian Government, and are not readily accessible. Nevertheless, some of the information from these reports has been assembled and discussed by Whitmore (1984b), Whitten et al. (1987), Whitmore et al. (1989) and Zwahlen (1992) and it is these references that have been consulted for the purposes of this thesis.

* All genus and species names of the plants of Sulawesi mentioned in this chapter will be followed by a 4-letter abbreviation of the family they belong to. More information about these plants can be found in Appendix 1 which is organised in alphabetical order according to the plant families.

3. The diet of wild babirusa

The diet of babirusa in the wild can be summarised as consisting of herbs, leaves, roots, fruits, cultivated plants from gardens and animal material(Valentijn, 1726; Lesson and Garnot, 1825; Wallace, 1870; Sarasin and Sarasin, 1905; Deninger, 1910; Selmier, 1978, 1983).

In the herbal category, grass, water plants and *Elatostema* (Urti.) were mentioned. In common with other tropical rain forests, few herbs can be found on the forest floor. However, herbs do appear in forest gaps during the younger phases of forest development (Whitmore, 1984a; Whitten et al., 1987). Grasses are especially dominant in those regions which are frequently subjected to fires (Whitten et al., 1987). The grassy patches in the enclosures of captive babirusa tend not to show signs of extensive grazing, but animals have been observed eating from the grass in their enclosure and will eat fresh grass that is offered to them (Leus et al., 1992; Chapters 4 and 5). When given the opportunity, captive babirusa include grass and herbs in their diet, but not to such an extent that they can be described as grazers. It was also shown in Chapter 3 that the babirusa are less able to digest cellulose and lignin of grass origin than the domestic pigs. Grass is therefore unlikely to be one of the main constituents of the babirusa diet.

The herb *Elatostema* is a non-stinging member of the nettle family (Urticaceae) and generally grows on rocks, in streams or under shrubs (Ridley, 1924). It is said to be one of the favourite foods of the babirusa in Lore Kalamanta (Sulawesi) as well as on the Togian islands (Selmier, 1978). In most of the European zoos that were visited for this study, the common nettle *Urtica dioica* L. (Urti.) was found to grow untouched inside the enclosures of the animals. Only once did I observe a young female in Antwerp Zoo eating some leaves of this plant. Since the common nettle has the stinging hairs typical of the nettle family, this character may be an important deterrent against the selection of this plant as a source of food in Europe.

A well known water plant which is consumed as a vegetable by man *Ipomoea aquatica* Forsk. (Conv.), is better known in Indonesia as "kangkung" (Ooststroom, 1948; Hanerwald, 1991). There are four reasons why kangkung is likely to be consumed by the wild babirusa:

1) it can form very dense masses in marshy areas such as at the delta of the Djenemaedja river, south of Palopo in Sulawesi (Ooststroom, 1948)
2) it forms an important part of the diet of the babirusa in Jakarta and Surabaya Zoo, Indonesia, and is readily eaten by those animals
3) it is a regular food of wild pigs in Malaya (Ooststroom, 1948) and
4) babirusa are known to frequent swampy habitats.

In 1825 inhabitants of Buru reported to Lesson and Garnot that the babirusa in the interior of the island "se plait au milieu des joncs et des plantes aquatiques" (amuse themselves in the middle of rushes (or rattans) and water plants). Since then there have been several reports, mostly in encyclopaedic works, stating that babirusa tend to live in swampy and marshy areas and along rivers (Jennison, 1927; Temminck, 1835; Boitard, 1851; Haltenorth, 1963). Babirusa are reported from the Rawa Aopa peat swamp, 100km west of Kendari (Zwahlen, 1992) and recent observations and video recordings of wild babirusa in the north of Sulawesi show animals in a muddy, swampy environment as they come to drink and wallow at a salt lick (Patry and Capiod, 1989; Patry, 1990). Tropical rain forests in general are relatively wet places and can quickly turn into a muddy and marshy environment especially during the rainy season. Babirusa are known to make use of such temporarily flooded areas for wallowing (Deninger, 1910; Selmier, 1978). The babirusa in Jakarta and Surabaya zoo, Indonesia, also make ready use of temporarily flooded areas of their enclosure and the concrete water pools provided (Fig. 1.1). A babirusa in Surabaya zoo was observed swimming in the little canals inside the zoo after escaping from its pen (Harwono, pers. comm.). Babirusa are also said to swim large distances, and even to dive in the sea (Valentijn, 1726; Selmier, 1983). Considering their affinity for mud and water, as well as their ability to swim, it seems likely that babirusa will frequent marshes and swamps of various types and will consume plant material growing in these areas.

According to Valentijn (1726) and Desmarest (1820) wild babirusa eat leaves of trees such as those of the "waringi" and banana trees (*Musa*).

The consumption of a variety of tree leaves by the wild babirusa would not be surprising considering the selection of bramble leaves by the animals in the semi-natural enclosure (Chapter 4) and the enthusiasm with which babirusa in captivity eat the leaves, buds and twigs of trees and branches (Chapters 5). Female babirusa in Surabaya Zoo would go to great lengths to reach the leaves of the few trees in their enclosure. They would raise themselves off the ground and balance on their hind legs without support while stretching out to reach the leaves with their mouths (Macdonald et al., 1993). Valentijn (1726) reported that wild babirusa would stand on their hind legs with their front legs leaning against a tree, even though the function given to this behaviour by him was "the sampling of smells of approaching enemies". I have often observed captive babirusa standing on their hind legs while leaning against uprights of their zoo enclosures in order to reach the leaves of suspended branches, or food items offered over the fence by the public. This seems a more likely explanation for the behaviour of the animals in the wild than that mentioned by Valentijn (1726). This type of foraging behaviour is better known from the African Gerenuk (*Litocranius walleri*) (Antilopini) which, unlike any other antelope, is able to stand unsupported on its hind legs while feeding on the leaves, shoots and flower buds of thorny trees and shrubs (Estes, 1992; Kingdon, 1982). This is made possible through several adaptations in its anatomy among which the wedge shaped hooves, robust lower limbs and modified lumbar vertebrae seemed most important (Estes, 1992). The ability of the female babirusa in Surabaya to stand on her hind legs unsupported while browsing is therefore quite remarkable. Furthermore, babirusa not only stand upright to forage on leaves, but the adult males also fight with one another while standing on their hind legs (Macdonald et al., 1993). The lumbar skeletal structure of the babirusa has not yet been compared with that of the Gerenuk or of the other wild pigs; it is therefore not yet known whether the vertebrae of the babirusa are modified in any way to facilitate this use of their hind limbs.

The babirusa's inability to root in compact ground has been confirmed several times in recent years (Selmier, 1978; Macdonald et al., 1989, 1993; Leus et al., 1992; Leus, 1993). Hunters and guides of Lore Kalamanta even claim to be able to distinguish between furrows made by *Sus celebensis* and those produced by babirusa. Babirusa are said to make shallow, straight-lined furrows whereas *Sus celebensis* dig deeper and thrust their snouts in lines that radiate from one spot (Selmier, 1978). Both in captivity and in the wild babirusa were only seen to turn over soil in areas where it comprised loose sand or wet mud (Patry, pers. comm.; Macdonald, 1990; Leus et al., 1992; Leus, 1993; Chapter 4). These observations make subterranean plant parts less likely food items for the wild babirusa, perhaps with the exception of roots from plants growing in loose, muddy or sandy soils.

Wild babirusa are said to eat fruit, but the only fruits specified were "canari, a sort of Indian almond" (Valentijn, 1726), acorns (Selmier, 1978), "pangi" (*Pangium edule* Reinw. (Flac.)) (Whitten et al., 1987), mangos (Selmier, 1983) and coconuts (Sarasin and Sarasin, 1905; Selmier, 1978, 1983).

The name "canari" most likely refers to the seeds of the fruits produced by trees of the genus *Canarium* (Burs.); possibly *Canarium vulgare* Leenh. (Burs.) or *Canarium indicum* L. (Burs.), the almond-like seeds of which are edible to man. There are approximately 11 species of *Canarium* (Burs.) on Sulawesi (see Appendix 1). Since the plum-shaped fruits are reasonably large (often about 3 by 2 cm) and usually have a fleshy pericarp (Leenhouts, 1956), it seems likely that the babirusa will eat the entire fruit and not just the seeds. *Canarium* (Burs.) trees can become locally abundant (Leenhouts, 1956) and are therefore a potentially important food source for the babirusa, especially since the seeds are very oily (Leenhouts, 1956) and therefore energy rich.

Oaks (*Lithocarpus* (Faga.)) and chestnuts (*Castanopsis* (Fag.)) are important components of especially the lower montane forest of Sulawesi, where they can come to dominate the forest (Steup, 1931; Bloembergen, 1940; Wemmer and Watling, 1986; Whitten et al., 1987). For example, recent studies of the Lore Lindu reserve in Central Sulawesi (which has a picture of the babirusa as its logo) indicated that only 10% of the land lies below 1000m whereas about 70% of the reserve lies between 1000-1500m. As a consequence, the dominant forest type in the reserve is the lower montane forest (between 1000 and 2650m) with especially *Castanopsis* (Faga.) and *Lithocarpus* (Faga.) as the dominant tree species (Wemmer and Watling, 1986). Because of the high nutritional contents of the starch and/or oil-rich fruits and because of their long or frequent fruiting seasons, the Fagaceae often represent an important part of the diet of many vertebrates living in Fagaceae containing forests around the world. They are thought to be of great importance to the Sundaic bearded pigs (*Sus barbatus barbatus* and *Sus barbatus oi*) (Caldecott, 1991a, b). Acorns are also one of the favourite food items of the European wild pig (*Sus scrofa*) (Briedermann, 1976, 1990; Groot Bruinderink, 1977; Genov, 1981). For example, during good fruiting years, between the months of October and February, acorns and beechnuts can come to represent around 80% of the food components in the diet of this species (Briedermann, 1990). Chestnuts (*Castanea* (Faga.)) are often ignored by these animals, the reason for which is thought to be the presence of saponins in the nuts (Briedermann, 1990). Considering the dominance of Fagaceae trees in the Lore Lindu reserve, it is very likely that oaks and chestnuts will also be part of the staple diet of the babirusa in the reserve. Babirusa in captivity are often offered small quantities of acorns (*Quercus* (Faga.)) and chestnuts (sweet chestnut *Castanea sativa* Miller (Faga.)) during the fruiting season. These are readily eaten (chapter 5). The babirusa in Antwerp Zoo also eat the horse-chestnuts (*Aesculus hippocastanum* L. - of the separate family of Hippocastanaceae) that fall into their enclosure from the tree alongside the fence. The horse-chestnut contains a saponin glucoside called aesculin. Ingestion of large amounts of the fruits has been known to cause inflammation of the mucous membranes, vomiting (where possible), weakness, lack of co-ordination, muscular twitching, stupor and paralysis in cattle, horses, pigs and man (Cooper and Johnson, 1984). So far, no negative effects following ingestion of the horse-chestnuts were observed in the Antwerp babirusa.

The major fruit eaten by babirusa in the west of the Dumoga-Bone National Park is said to be the large pangi fruit, *Pangium edule* Reinw. (Flac.) (Whitten et al., 1987). It grows in a wide variety of habitats mainly below 300m but sometimes reaching up to 1000m (Sleumer, 1954; Appendix 1). It is not known whether the babirusa eat just the soft and mushy pericarp, or the entire fruit including the seeds with their arils.

The seeds contain high concentrations of gynocardin, a cyanogenic glucoside. Cyanogenic glucosides release hydrocyanic acid (HCN) when they are broken down by an enzyme system within the plant itself (Sleumer, 1954; Burkill, 1966; Cooper and Johnson, 1984). This enzyme system is normally kept separated from the cyanogenic glucoside but breakdown of the plant cells during mastication or after ingestion brings the enzymes and the cyanogenic glucoside in contact with one another so that HCN is produced.

Many fruits employ chemical defence compounds in order to avoid predation of seeds before they are ripe (Whitten et al., 1987). The concentrations of these compounds usually reduce as the fruit ripens (Whitten et al., 1987). However, it is not uncommon for some fruits to retain their defensive compounds even after the fruit is ripe. This is one of the mechanisms by which fruits actively protect their seeds from being eaten or destroyed by non-disperser animals or micro-organisms such as bacteria and fungi (Herrera, 1982). Some animals demonstrate an ability to avoid toxic foods behaviourally, and others have the ability to detoxify some of the compounds via a number of metabolic pathways (Freeland and Janzen, 1974; Klaassen et al., 1986). Furthermore, whether or not a potentially toxic compound will have an adverse effect on a certain animal depends on a wide range of factors. These include: the amount of the toxin ingested; whether or not there was previous experience with the toxin; the energy content of the food item; the nature and amount of the other nutritional components of the food item and the abilities and efficiency of the animal's detoxification system (which varies from species to species and from individual to individual). (Freeland and Janzen, 1974; Klaassen et al., 1986). It is therefore not possible to reject a certain fruit as a potential food item for the babirusa based solely on the presence of a potentially hazardous substance.

The other fruits reported to be eaten by the babirusa were the mango (*Mangifera indica* L. (Anac.) and the coconut (*Cocos nucifera* L. (Palm.)) (Sarasin and Sarasin, 1905; Selmier, 1979, 1983). The mango tree was native to South Asia but is now extensively cultivated in the tropical regions of Asia, Africa and America (Hill, 1952). Although it is mostly found in cultivation or as a village tree, it can become naturalised in lowland forests (Ding Hou, 1978). Young mangos are astringent, acidic and rich in vitamin C. As the fruit grows, starch is accumulated in both peel and pulp. During the ripening process, this starch is converted into sucrose so that ripe mangos taste sweet (Nagy and Shaw, 1980). Mangos, together with fruits produced by trees of the same genus, or indeed the same family (Anacardiaceae), are well known to provide a source of food for many animals such as birds, squirrels, monkeys, pigs and elephants (Ding Hou, 1954; Appendix 1). It is highly likely that babirusa will eat the fruits produced by the wild Anacardiaceae trees. They may also visit village borders and plantations to feed on the fruits of the cultivated trees. Babirusa are known to visit coconut groves and village gardens in search for food items such as coconuts, maize plants, sweet potatoes (*Ipomoea batatas* (L.) Lamk. (Conv.)), sugar cane and small herb trees (Sarasin and Sarasin, 1905; Selmier, 1978, 1983). The babirusa are not able to break open intact coconuts and will only feed on coconut pieces or germinating nuts. They are therefore not regarded as pests, and their presence in the plantations is reported to be tolerated by the (Muslim) coconut farmers (Selmier, 1978, 1983). Because of the continuous flowering and fruiting of the cocos palm (Hill, 1952) and the high oil content (and therefore energy value) of the nut endosperm (Holland et al., 1991), the coconut is a potentially important item in the diet of the wild babirusa. It may also form an important "backup food" during times when wild forest fruits and greens are scarce. Inhabitants of the Togian islands believe that babirusa prefer to eat wild forest foods and will only come to the coconut groves when the wild food is in limited supply (Selmier, 1978).

The literature does not supply any further information on specific fruits eaten by the babirusa. From Appendix 1 it becomes clear that there is still an enormous array of other fruits being produced in the Sulawesi forest, all of which could potentially be consumed by the babirusa. However, each fruit is not eaten by the same range of animals. Whether or not a certain fruit is consumed by a certain animal will depend on its nutritional composition, accessibility and morphological characteristics among other factors. The three specified factors will be discussed briefly below.

Fruits tend to be divisible into two groups, "cheap" fruits and "expensive" fruits, according to the seed dispersal strategy used by the plant (McKey, 1975; Howe and Smallwood, 1982). Most plants employ the first strategy which is to produce large numbers of "cheap" fruits which will attract a wide variety of animals many of which are seed predators. These "cheap" fruits generally contain a lot of carbohydrates (typically sugar) but often contain less than 0.5% protein in their wet weight (Thomas, 1984). Figs (*Ficus* (Mora.)) are often considered as examples of cheap fruits (Whitten et al., 1987). They are said to be abundant, rich in sugar, containing no secondary compounds in their fruits and they are fed upon by practically every fruit-consuming vertebrate in the tropical forest (Janzen, 1979). Recent studies have however indicated that figs are not necessarily sugary, a number of them having quite a low sugar and metabolisable energy content and a relatively high fibre content (Conklin and Wrangham, 1994). Only a limited number of plants employ the second seed dispersal strategy which is to produce a limited number of "expensive" fruits which are searched for by obligate frugivore seed dispersers. These expensive fruits generally have a high lipid content and offer up to 6%-7% protein in their wet weight (Thomas, 1984). Examples of expensive fruits include nutmegs (Myristiceae) and laurels (Lauraceae) (Whitten et al., 1987). One Sulawesi tree which produces particularly protein rich fruits is the introduced pioneer tree *Piper aduncum* L. (Pipe.) which produces fruit with up to 10% protein (Whitten et al., 1987).

Obligate frugivores need to find fruits that will provide them with an adequate diet balanced in protein, lipids and carbohydrates and they therefore need to specialise in selecting the so-called expensive fruits (Thomas, 1984; Whitten et al., 1987). As was discussed above, babirusa are known to ingest plant material other than fruits. They also include invertebrates in their diet (Deninger, 1910; Selmier, 1983) and captive babirusa have proved to be efficient hunters of small mammals and birds (Leus et al., 1992). Because of this ability to supplement their diet with other plant material as well as animal products, it is likely that babirusa will exploit both "cheap" and "expensive" fruits and will not to be limited to the latter.

An animal can only feed on a particular fruit if it is accessible to it both in time and space. For example, one of the most important food items for the Sundaic bearded pigs (*Sus barbatus barbatus* of Borneo and *Sus barbatus oi* of Malaya and Sumatra) are the oil rich seeds of the Dipterocarpaceae (Caldecott, 1991a, b). The dipterocarps strongly influence food availability because they dominate the lowland rain forest of islands on the Sunda shelf and they all tend to fruit together at long but irregular intervals of five to seven years (Whitten et al., 1987; Caldecott, 1991b). The Sundaic bearded pigs have adapted to this scarce and unpredictable food supply in a number of ways among which the ability to travel (large body, long legs, swimming ability), flexible foraging behaviour (variable group size and the use of predictable food sources through migrations) and a vigorous response to food supply opportunities (potentially high growth rates, early maturation, relatively large litter size and short gestation length) (Caldecott, 1991a). None of the dipterocarp trees contributing to the diet of the bearded pigs (Caldecott, 1991b) are present on Sulawesi. In their stead are seven species all of which produce rather small, long winged nuts adapted for wind dispersal (Appendix 1) (Symington, 1943-1974; Ashton, 1984; Whitmore and Sidiyasa, 1986; Whitmore et al., 1989). The seeds of these Dipterocarp species are therefore unlikely to be a staple food for the babirusa.

The place of the dipterocarps in Sulawesi is taken by trees that do not appear to fruit gregariously (Whitten et al., 1987). We can therefore expect fruit supply to be less scarce and more continuous. The smaller litter size and longer gestation length of the babirusa seems to fit within this schema. It is not clear when and how often babirusa in the wild tend to give birth and it is therefore not known whether this is related to food supply. Recent reports suggest that babirusa live in small family groups of a few adult females with their offspring, while the large adult males appear to be more solitary (Patry and Capois, 1989; Patry, 1990). However, there is no information on the composition, stability and movements of these groups and the relation of these factors to food supply. Even though babirusa do seem to have the ability to travel (they have been reported to be good swimmers (Valentijn, 1726; Selmier, 1983) and runners, and are able to jump over obstacles in their way (Selmier, 1978; Leus, unpubl. obs.)), there are no reports of mass migrations such as those known for the bearded pigs. Should fruit shortages occur, then migration is not the only possible solution to this problem. Another strategy which is typical for animals with a fixed home range, comprises a change in diet composition whereby fruits are replaced by other food items such as animal matter (Whitten et al., 1987). The omnivorous nature of the babirusa suggests the latter strategy as the more likely solution to a limited fruit supply. Other "backup foods" for the babirusa could include cultivated fruit and vegetables collected from local village gardens and plantations.

Although some fruits, such as the rather fleshy fruits of the Moraceae (figs) and Rubiaceae, are consumed by most fruit eating vertebrates (Janzen, 1979; Gautier-Hion et al., 1985), studies investigating the dispersal of seeds by tropical forest animals have indicated that certain categories of frugivores tend to select fruits with specific morphological characteristics (Ridley, 1930; van der Pijl, 1957, 1969; McKey, 1975; Gautier-Hion et al., 1985; Dubost, 1986). None of these studies, however, included pigs and a syndrome of "pig-fruits" is as yet undescribed. "Bird and Monkey fruits" (= brightly coloured, often sweet tasting fruits with succulent flesh containing arillate seeds e.g. Apocynaceae, Anacardiaceae, Lauraceae, Lecythidaceae, Meliaceae, Myristicaceae and Sapotaceae (Appendix 1)) are known to be eaten by ground dwelling animals such as pigs after they have been partially eaten and discarded by the birds and monkeys (Ridley, 1930; Ng, 1972; Whitmore, 1973; Gautier-Hion et al., 1985; Corner, 1988; Kochummen, 1989; Durrell, 1993; Appendix 1). Those parts of the fruits available to the terrestrial animals are usually the skins and seeds with some remaining pieces of flesh (Ng, 1972; Whitmore, 1973; Corner, 1988; Kochummen, 1989). Recent video recordings of babirusa in Northern Sulawesi showed babirusa and Sulawesi macaques (*Macaca*) in close proximity to one another (Patry and Capiod, 1989; Patry, 1990; Patry, pers. comm.). Since fruits are an important component in the diet of the Sulawesi macaques, the possibility exists that the babirusa will feed on fruit remains discarded by these foraging primates. Fruit species eaten by the macaques include figs (*Ficus* (Mora.)), *Dracontomelum* (Anac.), *Syzygium* (Myrt.), *Spondias pinnata* (L. f.) Kurz (Anac.) and *Pangium edule* (Flac.) (Whitten et al., 1987; Watanabe & Brotoisworo, 1982). Other arboreal fruit eaters making fruits and seeds available to terrestrial mammals are squirrels (Sciuridae), fruit bats (Pteropodidae) and civets (Viverridae). For example, bearded pigs in Sarawak, Borneo, have been observed feeding on the remains of *Dracontomelum* (Anac.) fruits that were dropped by squirrels after they had eaten part of the pulp (Ding Hou, 1978).

Fruits falling off the trees without the interference of arboreal animals tend to be either young, unripe aborted fruits or very ripe fruits. Many of the ripe fruits that fall to the ground have already lost, or will quickly loose, their bright colours, turn brown and start to rot (Gautier-Hion et al., 1985). Fallen fruits nevertheless forms an important part of the diet of many terrestrial animals.

This chapter has indicated which food items and for the fruits, which type of fruits are available to the babirusa in Sulawesi. Hypotheses have been put forward regarding the likely importance of each of the food categories, fruits, leaves, herbs, grasses and animal matter within the diet of the babirusa, based on the results of the studies in the previous chapter. These hypotheses now need to be tested in the field. A detailed study of the diet of the babirusa in the wild is required. The babirusa in northern Sulawesi could be observed fairly easily as they came to drink at a salt lick, but they were never observed to eat in that area (Patry and Capois, 1989; Patry, 1990; Patry, pers. comm.). Both the vigilant nature of the babirusa (they will run into cover at the least sound (Patry, pers. comm.)) and the dense vegetation in the jungle will make it almost impossible to follow the animals closely enough to allow detailed observations of what exactly they are eating. Analyses of faecal material could be complicated by the fact that the habitat of the babirusa is shared with that of the other wild pig species on Sulawesi, *Sus celebensis*. Nevertheless, faeces of even relatively closely related species can often be distinguished by smell, differences in diets, the presence of protozoa, differences in body size of the producer etc. The detailed list (Appendix 1) of the species of trees of Sulawesi, the habitat in which they occur and the type of fruit they produce will form an important basis for this type of study.

4. Conclusions

The results of the previous sections of the thesis suggest that the main items in the diet of wild babirusa are fruits and leaves supplemented with smaller amounts of herbs, grass, roots and animal matter. The available literature suggests that the babirusa are present in most forest types of Sulawesi and that the trees in these forests produce a wide range of fruits which appear suitable for babirusa.

GENERAL CONCLUSIONS

The very large area covered by cardiac glands in the stomach of the babirusa, together with the presence of micro-organisms and a pH suitable for their survival led to the hypothesis that the babirusa was a non-ruminant foregut fermenter specialised in the fermentation of cell solubles and more easily digestible fibres. The finding that the babirusa was less able to digest Acid Detergent Fibre from dried grass than the domestic pig, but could digest Neutral Detergent Fibre and organic matter of the total diet better than the domestic pig fitted well with this hypothesis. The hypothesis was also supported by the results of the foraging study; the babirusa demonstrated an ability to carefully select certain plant parts when eating herbs and showed a preference for eating leaves and fruit when allowed to forage in a semi-natural enclosure. This suggested that wild babirusa have the ability to select those plants and plant parts which are more easily digestible. Captive babirusa also showed a preference for fruit. The range between zoos in the amounts of total food and nutrients fed was too wide for all these diets to meet the nutritional requirements of the babirusa. Equations predicting the requirements for digestible energy and crude protein of domestic pigs were applied to the babirusa and suggested digestible energy requirements of 11.3 MJ/day for males and 8.5 MJ/day for females, and crude protein requirements of 88g/day for males and 59g/day for females. Greater control over the composition of the diets fed to captive babirusa and more fundamental research into the palatability of the constituents is needed before the technique of diet self-selection can be successfully applied to the babirusa for the determination of its crude protein requirements. The results reported in the thesis, together with the information gathered from the literature, support the view that the main items in the diet of wild babirusa are likely to be fruits and leaves supplemented with smaller amounts of herbs, roots and animal matter. Potential sources of fruit are indicated in the appendix.

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APPENDIX 1: SOURCES OF POTENTIAL PLANT FOOD FOR BABIRUSA IN SULAWESI

An annotated checklist of the trees, palms and some shrubs and herbs of the Sulawesi forests was prepared together with additional notes on the habitat, physical appearance, fruits and local usage of some of the genera and species. The foundation of this list was a checklist published by Whitmore et al. (1989), and information from this source is indicated in bold type face. The species names which they enclosed by brackets referred to small trees, shrubs, climbers and herbs, and this convention has been retained for all the information from this source. Additional information was collected on the occurrence of other relevant genera and species from Hickson (1889), Bloembergen (1940), Steup (1931, 1932, 1933, 1935, 1939a, b), Meijer (1974), Dransfield (1981), Ashton (1984), Lack & Kevan (1984 & 1987), Soewanda et al. (1984), Whitmore and Sidiyasa (1986) and Whitten et al. (1987). A number of other botanical works were consulted for descriptions of fruits and these are indicated in the list. Data gathered from sources other than Whitmore et al, (1989) are indicated in plain type face. The list is organised alphabetically by family and within families alphabetically by genus and species. Where mentioned, the colour of the fruit is that of the mature fruit unless otherwise indicated. A short explanation of the botanical terms used in the list follows below (from: Tootill, 1984 and Sugden, 1992):

The term Malesia occurs a number of times in the text and refers to "the phytogeographical region which stretches the whole length of the Malay archipelago and beyond the Bismarck archipelago east of New Guinea, from 95°E to 153°E." (Whitmore, 1984).

pericarp:	the whole wall of the ripe fruit consisting out of the exocarp, mesocarp and endocarp.
exocarp:	the outer layer of the fruit.
mesocarp:	the layer between the exocarp and endocarp; often fleshy or succulent.
endocarp:	inner layer of the fruit surrounding the seeds.
stone:	a hard endocarp containing the seed.
carpel:	the female reproductive unit of a flower.
berry:	a juicy fruit usually with many small seeds (e.g. tomato).

drupe:	fruits with an often fleshy mesocarp and a hard stony endocarp (e.g. peach).
dehiscent:	splitting open
indehiscent:	not splitting open
capsule:	a dehiscent dry fruit usually with many small seeds.
nut:	an indehiscent dry fruit with a hard wall containing one seed.
cupule:	the kind of spiny husk enclosing a chestnut or the cup-like structure surrounding an acorn.
pod:	long, thin, dry, dehiscent fruit structures well known from the pea-family (Leguminosea).
achene:	a dry fruit with one seed.
samara:	a small dry fruit (achene) with wing-like outgrowths.
aril:	an extra seed envelope which is often coloured and fleshy.
endosperm:	tissue in the seed performing the function of food storage for the seedling.
cotyledons:	part of the embryo of a seed plant which are either thin and become the first photosynthetic organs of the seedling, or are thick and take over the role of the endosperm as food storage in the seed.
hypocotyl:	that part of the seedling positioned below the cotyledons. If the cotyledons leave the seed at germination and become photosynthetic organs, the hypocotyl is that part of the seedling between the cotyledons and the root. If the cotyledons have a storage function and stay in the seed at germination, the root is the actual hypocotyl.
calyx:	the remains of the outer layer of the flower bud.
receptacle:	the top of the stalk of a flower.
crustaceous:	brittle
sclerenchym:	strengthening tissue with thick, often lignified cell walls.
globose:	round
subglobose:	almost round
deciduous:	shedding their leaves at least once a year.
liana:	woody climber.
epiphytic:	non-parasitic plants without roots in the ground but growing on the stems and branches of other plants. The obtain their nutrients from the air, rain water and debris on their supports.

ANNOTATED LIST OF TREES AND PALMS OF THE SULAWESI FOREST

ACERACEAE

Acer caesium (Reinw.ex Bl.) Kosterm. = *A. laurinum*
Acer laurinum Hassk.

> Sole Indonesian member of the Aceraceae (sycamores and maples) (Bloembergen, 1948; Whitmore et al., 1989). The up to 48m high tree produces 8-13mm light winged fruits adapted for wind dispersal (Bloembergen, 1948). **Mainly primary forest, 750-2250 m.**

Acer niveum Bl. = *A. laurinum.*

ACTINIDIACEAE

Saurauia lepidocalyse
Saurauia oligolepsis

> Its fruits are pushed into the ground by the flower-bearing shoots (=geocarpy) (van Balgooy and Tantra, 1986).

ALANGIACEAE

***Alangium griffithii* (Clarke) Harms**

> **Tree, 25m. Lowlands and thicket 60-400m.**

***Alangium javanicum* (Bl.) Wang**
***Alangium miliense* Bloembergen**

> **Tree, 30m. Lowland forests. Endemic.**

(*Alangium salvifolium* (L. f.) Wang.)

AMARANTHACEAE

Alternanthera
"Erect, ascending, trailing, creeping floating or clambering herbs" (Backer, 1948a).

ANACARDIACEAE

Fruits of this family are drupaceous with generally a thin exocarp, a fleshy and resinous mesocarp (sometimes waxy or oily) and a hard endocarp or stone. Some fruits are eaten by birds, squirrels, monkeys, pigs, elephants and other animals. In Sarawak (Borneo) it has been observed that squirrels would eat part of the pulp of Dracontomelon fruits, dropping the remains on the ground. These fruit remains were readily eaten by the pigs which acted as dispersers because the seeds they ate mostly stayed in tact (Ding Hou, 1978).

Buchanania arborescens (Bl.) Bl.
A mainly lowland tree (4-35m), **primary and secondary forest** growing in a variety of habitats. Its fruits are sublentiform drupes about 1cm in diameter with a thick woody or bony stone.

Campnosperma
The fruits are fairly small (< 1cm) drupes with hard and woody endocarp which are eaten by birds (especially pigeons) (Ding Hou, 1978).

***Camnosperma auriculatum* (Bl.) Hk.f.**
Tree 38m. Lowland forest, sometimes swamps, sometimes secondary forest.
***Campnosperma brevipetiolatum* Volkens**
Tree, 48m. Primary and secondary forests, to 450m.

Dracontomelum
The trees are sometimes planted in villages because the fruits have a thin layer of sour, juicy pulp around a big stone (Ding Hou, 1978). The fruits are also known to be eaten by the macaques on Sulawesi (Anon, 1980; Bismark, 1982; Watanabe and Brotoisworo, 1982).
Dracontomelum dao (Blanco) Merr. & Rolfe
A deciduous tree, **43-(55)m** confined to forests in high rainfall areas at low altitudes. The edible fruits are drupes, measuring about 2.5cm in diameter and containing a stone 1cm in diameter (Ding Hou, 1978).

***Gluta papuana* Hou**
Tree 31m. Lowlands, swamps and riverine forest.

Gluta renghas L.
A large tree **(50m)** mostly found at low altitudes in swampy coastal regions and peat swamps. The pinkish-brown subglobose fruits measure 3.5-5cm in diameter and the seed they enclose can be eaten after roasting (the cashew *Anacardium occidentale* is of the same family). Other tree parts, such as the raisin of leaves and branches, are poisonous and can cause itching (Ding Hou, 1978; Burkill, 1966).

Koordersiodendron pinnatum Merr.
A tall (45m) lowland **(to 460-800m)** forest tree producing yellowish, broadly ellipsoid drupes measuring about 2.5-4 by 1.5-2.5cm. The endocarp around the 2.5 by 1.5cm large seed is cartilaginous. The species is also present on the Sula islands (Ding Hou, 1978).

Mangifera
The fruits are resinous drupes with often a thick and fleshy mesocarp (especially in cultivated species e.g.. the mango: *M. indica* L.) and a lignous or fibrous stone (endocarp) (Ding Hou, 1978).

Mangifera altissima Blanco

A 12-35m tall tree found primarily in inland primary forest at low altitudes **(to 400m)**. It fruits from April to December. The green-yellowish drupes are variable in shape and measure about 5.5-8 by 4-6cm. The mesocarp is rather fibrous, resinous and acid. In the Philippines the fruits are used for pickles (Ding Hou, 1978).

Mangifera foetida Lour.

This 10-40m high tree is widely cultivated throughout Malesia and sometimes occurs as village tree. It can also be found naturalised in dry lowland forest. The ovoid 8-10 by 6-7cm large drupe has a fleshy, fibrous, juicy, savoury and fragrant mesocarp. The fruits are used in curries and pickles and the sweet variety can be eaten raw (Ding Hou, 1978).

Mangifera indica L.

The mango tree reaches 10-**45**m in height and is mainly found in cultivation and as village trees below 500m but it can occur naturalised in lowland forests up to 1700m. The mango is a drupe very variable in shape, size and colour. It is usually ovoid-oblong in shape, measuring about 4-25 by 1.5-10cm, and coloured in shades of green, yellow and red. The fleshy and juicy mesocarp is bright red or orange in colour and contains a thick and very hard stone (Ding Hou, 1978).

Mangifera minor Bl.

An 18-32 m high tree found in lowland primary and secondary forest **(400-750m)** and planted in villages. The oblong drupe measures 5-10 by 4-6.5cm but the mesocarp is thinner and not as fleshy. There is one large fibrous stone (Ding Hou, 1978).

Mangifer timorensis Bl.

An up to 30m tall tree found in forests at altitudes between 300 and 1000m. The hard, non-edible yellowish drupes are globose or subglobose in outline and measure 3.5-4.5cm in diameter (Ding Hou, 1978).

***Pleiogynium timoriense* (DC.) Leenh.**

Tree 36(-48)m. Lowlands to 560m, rarely 750-970m.

Rhus

The fruits are fairly small drupes (< 1cm) with a leathery, brittle or bony endocarp.

(*Rhus nodosa* Bl.)

Scandent Shrub,, or liana, up to 15m. Lowland primary forest, to 1400m.

***Rhus taitensis* Guill**

Tree, 30m. Primary forest.

Semecarpus
The fruits are fairly large drupes (around 2 cm) with a fleshy exocarp and mesocarp full of acid resins, and a crustaceous endocarp. (Ding Hou, 1978)

Semecarpus cassuvium **Roxb.**
Tree, 4-27m. Lowland primary and secondary forests, to 600m.
Semecarpus cuneiformis **Blanco**
Tree, 20m. Primary and secondary forests, 600-700m.
Semecarpus forstenii **Bl.**
Tree, 8-40m. Lowland forest to 800m.
Semecarpus heterophyllus **Bl.**
22m. Lowlands to 1800m.
Semecarpus longifolius **Bl.**
Tree, 20m. Lowland forests to 300m.

Spondias pinnata (L. f.) Kurz
A 20-25m tall tree of primary, mixed and secondary forest up to 500m. It flowers from May to January and fruits from February to November. The edible yellow-orange drupes are ellipsoid in shape and measure about 3-5 by 2.5-3.5cm (Ding Hou, 1978). The fruits are eaten by the macaques on Sulawesi (Anon, 1980; Bismark, 1982; Watanabe and Brotoisworo, 1982).

ANNONACEAE

Cananga
Oblong pulpy fruit carpels with several seeds in two rows.
Cananga odorata (Lamk.) Hk.f. & Thoms.
An up to 30m tall tree of **disturbed and secondary lowland** forest, forest edges and villages. The oily, black oblong-ovoid fruits (2.5 by 1.8cm) are eaten by squirrels, bats and monkeys which act as dispersers (Kochummen, 1972a). The fruits are also eaten by macaques on Sulawesi (Anon, 1980; Bismark, 1982; Watanabe and Brotoisworo, 1982).

Cyathocalyx

Desmos

Meiogyne

Miliusa

Orophea
Shrubs or small trees with globose to elongate fruits (Kochummen, 1972a).

Pheanthus

Platymitra

Polyalthia
Mainly lowland forest understorey trees or shrubs with few to many fruits (Kochummen, 1972a).
Polyalthia lateriflora (Bl.) King
A medium sized tree rarely exceeding 30m with red ovoid-elliptic fruits measuring 3-3.5cm (Kochummen, 1972a).

Pseuduvaria

Sageraea

Saccopetalum horsfieldii Benn.

Stelechocarpus

Xylopia

Apocynaceae

Alstonia angustifolia Wall. ex A. DC.
A small **(to 10(15)m.)** lowland tree usually found in seasonal swamps. Its fruits are two long (50-70cm) slightly woody follicles filled with small seeds provided with silky hairs (Whitmore, 1973a).
***Alstonia pneumatophora* den Berger**
To 39m. Sometimes swamps.
***Alstonia scholaris* (L.) R. Br.**
To 36m. Lowlands, Primary and secondary forest.
***Alstonia spectabilis* R. Br.**
Tree, 40m. Lowlands, up to 450m.
Alstonia villosa* Bl. = *A. spectabilis

Dyera
A large to huge tree with fruits in the form of a pair of large woody follicles enclosing 12-24 airborne seeds (Whitmore, 1973a).
***Dyera costulata* (Miq.) Hk. f.**
Giant emergent Tree, 60m. Lowlands, occasionally swamps.

Kibatalia
A small to big tree with fruits are in the form of two follicles filled with airborne seeds (Whitmore, 1973a).
***Kibatalia wigmani* (Koord.) Merr.**
Tree. NE Sulawesi. Endemic.

Rauvolfia
Shrubs or small trees with fruits in the form of black, oval, up to 1cm long drupes enclosing 1-2 warty stones (Whitmore, 1973a).
(*Rauvolfia amsoniifolia* DC.)
Primary and Secondary forests.
(*Rauvolifa samarensis* Merr.)
Tree, to 18m. Lowlands
(*Rauvolfia sumatrana* Jack)
Tree, to 20m. Lowlands to 1350m.

Wrightia
Shrubs or small trees in the form of two woody follicles with lots of tufted, airborne seeds (Whitmore, 1973a).
***Wrightia pubescens* R. Br.**
Tree, to 35m.

AQUIFOLIACEAE

Ilex.
Trees or shrubs, lowlands to mountains, c. 20 species in Indonesia of which a few sometimes reach timber-size.

ARACEAE

Aglaonema sp.

Pothos hermaphroditus Merr.

Scindapsus sp.

ARALIACEAE

Cephaloschefflera blancoi* (Merr.) Merr. = *Schefflera blancoi

***Gastonia serratifolia* (Miq.) Philipson**

Heptapleurum insularum* Seem. = *Schefflera insularum

(*Polyscias cumingiana* (Presl) F-Vill.)
Shrub or small tree, 5m.
***Polyscias nodosa* (Bl.) Seem.**
Tree 25m. To 1000m.
(*Polyscias scutellaria* (Burm.f) Fosb.)
Shrub or small tree 6m. To 800m.

(*Schefflera actinophylla* (Endl.) Harms)

Large shrub or tree, often much-branded when mature. Sometimes cultivated as an ornamental.

Schefflera confinis auctt. non(Miq.)Vig. = *S. nodosa*

(*Schefflera elliptica* (Bl.) Harms)

Sprawling or climbing shrub or hemi epiphyte or liana with long slender canes. To 700m. Primary and secondary forest, sometimes open places and swamps.

(*Schefflera minahassae* Harms)

Epiphyte, possibly also terrestrial, tree or shrub. Forest. Minahasa, 500-700m.

Schefflera nodosa F.M. Muller

Probably at lower elevations. Endemic (Minahassa).

(*Schefflera* sp. aff. *gracilis*)

300-1050m. Sulawesi Selatan

(*Scefflera* sp. aff. *scandens*)

Gorontalo, Riedel s.n.

(*Schefflera "calcophila"*)

Much-branched shrub up to 2m. Limestone shrub 600-800m. Tana Toraja.

(*Schefflera sarasinorum* Harms)

Shrub up to 4m or climber (or both). On chalk or on riverbanks. 600-1500m. Endemic.

(*Schefflera* sp. aff. *burkillii*)

Shrub 3m, or liana; sometimes epiphytic. Montane forest. 700-2300m. Sulawesi Selatan.

Schefflera aromatica auctt. non (Bl.) Harms = *S. serrata*

(*Schefflera* sp. aff. *catensis*)

Climber to 3m. Forest over 1000m, sometimes with *Agathis*. Sulawesi (Selatan, Tengah).

Schefflera digitata (Blanco) Merr. non Forst. & Forst. f.=*S. insularum*

(*Schefflera insularum* (Seem.) Harms)

Terrestrial or epiphytic shrub 3-4m, or climber up to 25m. Forests and shrub, especially near rivers and in damp places, low to medium elevations.

(*Schefflera serrata* (Miq.) Vig.)

Lowlands. Sulawesi Selatan.

(*Schefflera* sp. aff. *gigantifolia*)

Tree to 7-8m (once reported as 15m, 24cm.), or liana; sometimes epiphytic. Forest, sometimes on limestone, 250-1000m. Sulawesi (Utara to Selatan, but not in extreme south).

(*Schefflera* sp. aff. *insularam*)

600m. Tana Toraja, Kjellberg 2963.

(*Schefflera* sp. aff. *minahassae*)

Half-climber, 4-5m; also a treelet to 3m. Forest; also on riverbanks. 700m. Tana Toraja.

(*Schefflera blancoi* Merr.)

Forests, rocky areas, stream depressions, or exposed ridges. Low to medium elevations.

(***Schefflera koordersii*** **Harms)**

Epiphytic tree. Forest, 450-1000m or over. Minahassa.

(***Schefflera "bellavena"***)

Tree to 6m, terrestrial or epiphytic. Forest, 780-120m. Minahassa.

(***Schefflera "calophylloides"***)

High-climbing liana. Forest, uncommon 1800-2300m. Tana Toraja.

(***Schefflera "magniligulata"***)

Shrub or treelet, 3-4m. Riverbanks, 1100m. Tana Toraja.

ARAUCARIACEAE

Agathis alba Jeffrey = *A. celebica*

Agathis beckingi **Meijer Drees =** ***A. dammara***

Agathis celebica **(Koord.) Warb. =** ***A. dammara***

Agathis dammara (Lambert) L.C. Rich

Agathis dammara is the only *Agathis* found on Sulawesi. The huge conifer tree (up to 65m) is reasonably wide spread on the island, occurring in the lowland rain forest of Central Sulawesi and up to 2000m in the mountains of the peninsulas (not the south-east peninsula) **where it may form extensive forests.** The winged seeds are produced oval seed cones which disintegrate when mature (de Laubenfels, 1986a).

Agathis hamii Meijer Drees = ***A. dammara***

Agathis loranthifolia Salisb. = ***A. dammara***

Agathis philippinensis Warburg = ***A. dammara***

Dammara = *Agathis*

BIGNONIACEAE

Deplanchea bancana Steen.

The fruits are pod-like capsules filled with winged seeds (van Steenis, 1974).

Deplanchea glabra (Steen.) Steen.

Tree 1.5-22m. 10-7000(-100)m. The fruits are pod-like capsules filled with winged seeds (van Steenis, 1974).

Dolichandrone spathacea (L. f.) K. Sch.

Tree 5-20m. The fruits are pod-like capsules filled with winged seeds (van Steenis, 1974).

Millingtonia hortensis L.

Tree 25m. Below 750m. The fruits are large pod-like capsules filled with winged seeds (van Steenis, 1974).

Radermachera pinnata (Blanco) Seem.

Tree 20m, 15-40cm. Lowlands to 600m. The fruits are pod-like capsules filled with winged seeds (van Steenis, 1974).

BOMBACACEAE

Bombax

Deciduous trees with fruits in the form of a large woody capsule enclosing small seeds provided with a dense wool-like floss to aid wind dispersal (Kochummen, 1972b). The generic name *Gossampinus* has been replaced with *Bombax* (Whitmore et al., 1989).

Bombax valetoni Hochr.

An up to 42m tall deciduous tree of primary and secondary rain forest producing 13-15cm large woody capsules enclosing small wind borne seeds (Kochummen, 1972b).

Bombax ceiba L.

Sometimes referred to as *Gossampinus malabrica* or *Salmalia malabrica.* (Whitmore et al., 1989) **Tree 30-35m.**

Bombax malabarica **DC. = *B. ceiba***

Camptostemon philippinense **Becc.**

Tree. Mangrove forest.

Durio zibethicus Murray

A large tree (over 30m) widely cultivated throughout the Asian tropics for its edible fruit better known as "durian". The green-yellow fruit is approximately ovoid in shape and 25 by 20cm large. It is in fact a woody capsule covered with 1cm long spikes, that encloses seeds which are completely covered in soft, white or yellowish sweet aril. The fruits tend to fall unopened and only split open later (from top to base) (Kochummen, 1972b).

Gossampinus* = *Bombax

Salmalia malabarica Schott. & Endl.= ***Bombax ceiba***

BORAGINACEAE

Cordia blancoi **Vid.**

Tree 25m. Endemic.

Cordia myxa **L.**

Bush or tree, sometimes 20m.

(*Cordia monoica* Roxb.)
Small tree 3-7m.
(*Cordia strigillosa* Miq.)
Small tree 8m. Endemic.
Cordia subcordata Lamk.
Tree 15m. Coasts.

Ehretia laevis Roxb.
Tree 15m.
(*Ehretia microphylla* Lamk.)
Treelet or shrub.

BURSERACEAE

Canarium
Mainly large trees (but occasionally shrubs) of primary and secondary rain forest at low altitudes, sometimes also found in monsoon or open forest. They flower mainly during the dry season and fruit mainly during the wet season, though some species apparently flower and fruit throughout the year. The fruits (often around 3 by 2cm) are usually drupe-like, plum-shaped and blue-black when ripe. The pericarp is usually fleshy and the single stone stony. The fruits, and especially the oily seeds of many species are in some way used as food (Leenhouts, 1956).
Canarium acutifolium **(D.C.) Merr.**
Tree 20(-40)m. At 250-400m.
Canarium asperum **Benth.**
Tree 8-35m. Lowlands to mountains.
Canarium balsamiferum **Willd.**
Tree 17-28m. From lowlands to 700m.
Canarium decumanum **(Rumph.) Gaertn.**
Tree 30-60m. Lowlands.
Canarium hirsutum **Willd. ssp. *hirsutum***
10-(48)m. Lowlands.
Canarium indicum L.
An up to 40m tall tree found in rain forests at low altitude, although they can be planted at altitudes up to 600 m or more. The ovoid seeds measure 3.5-6 by 2-3cm and usually contain one seed. The seeds of the tree are used as those of C. *vulgare* but are of less importance (Leenhouts, 1956).
Canarium maluense Hout.
Tree 15-40m. From lowlands to 1000m.
Canarium oleosum **(Lamk.) Engl.**
Tree 20(-30)m.
Canarium trigonum **H. J. Lam**
Tree 20-28m. Lowlands. Endemic.
Canarium vrieseanum **Engl.**
Tree 15-25(-31)m. To 500m.

Canarium vulgare Leenh.

This up to 45m tall tree can be locally abundant and is found mostly in primary forest on limestone. Its ovoid fruits measure 3.5-5 by 0.5-3cm and contain 1-3 seeds. The tree is widely cultivated in tropical regions for its almond-like, oil-rich seeds. It is closely related to C. *indicum* and used to be regarded as the same species for a long time (Leenhouts, 1956).

***Dacryodes incurvata* (Engl.) Lam**

10-30m. Low, dryland and swamps.

Dacryodes rostrata (Bl.) Lam.

A 5-35m tall tree of primary, sometimes secondary, and rarely swampy, forests at altitudes up to 600m. It flowers mainly from March to October and the fruiting months are mainly March to September. Its edible fruits are ovoid to oblong in shape and measure 1.75-3.5 by 0.75-1.5cm. The pericarp is fleshy and rather thick. There is one seed (Leenhouts, 1956).

Garuga floribunda Decne.

Primary to secondary rain- and monsoon forest tree (up to 35m) especially found in periodically dry regions. **To 400(-1200)m.** It flowers mainly between July and November and fruits mainly between October and April. The edible fruits are drupaceous, obliquely pear-shaped, and measure 5-9 by 5-12mm. Its pericarp is fleshy (Leenhouts, 1956).

Haplolobus celebicus H.J. Lam

Tree reaching 20-30m in height and found in primary forest up to 250m. It flowers between October and November and fruits in March. The fruits are drupaceous, ovoid or slightly oblique in shape, measuring 12-16 by 7-11mm. Their pericarp is thin and dry the stone paper-like. There is one seed (Leenhouts, 1956).

***Santiria apiculata* Benn.**

6-(40)m.

Santiria laevigata Bl.

Tree, 15-30(-45)m, mostly found in forests up to 1200-1500m but sometimes also present in lowland peat forest. It flowers mainly between July and December and fruits mainly between July and February. The edible fruits are drupaceous, obliquely globular (to oblong) in shape and measure 1.5-2 by 1.25-2cm. Their pericarp is rather thin and solid, the endocarp crustaceous and thin (Leenhouts, 1956).

var. *laevigata*

var. *glabrifolia* (Engl.) Lam

1.5-(45)m. Sometimes in peat swamp forest.

Santiria apiculata Benn.

A 6-20(-40)m tree, occurring in primary forests, usually on dry ground at lower altitudes (rarely up to 1200m). It flowers from February to May and again from August to November. The fruits are present from May to June and from October to January. Its fruits are drupaceous, very oblique, globose or ellipsoid and measure 10-18 by 6-13mm. Their pericarp is rather thin and solid, the endocarp crustaceous and thin (Leenhouts, 1956).

Scutinanthe brevisepala Leenh.

This primary forest tree grows up to 48m high and is found at altitudes up to 350m. It flowers in November. The fruits of this particular species are unknown but the fruit characteristics for the genus are: drupaceous fruits with fleshy pericarp, hard and bony pyrene and a single seed. Some fruits are eaten (Leenhouts, 1956).

CACTACEAE

Opuntia nigricans Haw.

Prickly pear cactus form South America. Also found at the southern end of the south west peninsula (Steup, 1929).

CAPPARIDACEAE

Capparis
Shrubs with fruits in the form of leathery berries. (Whitmore, 1973b).

Crateva
Small trees producing fruit in the form of large berries with a tough wall which are probably water dispersed (Whitmore, 1973b).
Crateva religiosa Forst. f.

Tree 5-15(-30)m. Lowlands, 100-700m. Produces round to ovoid fruits measuring 5-6cm in diameter provided with a tough wall and probably dispersed by water (Whitmore, 1973b).

CAPRIFOLIACEAE

(*Viburnum amplificatum* Kern)
Small tree. Mountain forest.
***Viburnum odoratissimum* Kern)**
Small tree. Mountain forest.
***Viburnum odoratissimum* Ker**
Shrub or small tree, sometimes to 20m. Mountains 1000-2000m.
(*Viburnum sambucinum* Bl.)
Shrub or small tree, 10-(15)m. Lowland to Mountain forests.

CASUARINACEAE

Very conifer-like trees or shrubs in which the function of leaves has been taken over by green, deciduous needle-twigs. The resemblance with conifers is carried through in the structure of the fruits which are compound cone-like structures enclosing winged fruitlets (Ng, 1978a).

Casurina celebica **L.A.S. Johnson (unpublished)**
Endemic.
Casuarina equisetifolia J.R. & G. Forst
Medium tree. Sandy coasts.
Casuarina sumatranum **Miq. =** ***Gymnostoma rumphianum***
Casuarina sumatrana Jungh.
Casuarina rumphiana **Miq. =** ***Gymnostoma rumphianum***
Gymnostoma rumphianum (Miq.) L.A.S. Johnson (= *G. sumatranum* Miq.)
Medium tree.
Gymnostoma sumatranum (Jungh. ex de Vriese) L.A.S. Johnson (she-oak)

CELASTRACEAE

(*Euonymus acuminifolius* Blakelock)
Shrub to 3.5m. 700-3200m.
(*Euonymus cochinchinensis* Pierre)
To 12m. Lowlands to 1300m.
(*Euonymus impressus* Blakelock)
Small tree, 6m. Along streams, 1100m. Endemic.
(*Euonymus Japonicuas* Thunb.)
Shrub or to 8m. (600-)1000-2950m.
Euonymus javanicus **Bl.**
Tree 23m. Lowlands to 1500m.

Lophopetalum javanicum **(Zoll.) Turcz.**
To 45m. Sometimes swamp or peat swamp, lowland to 1000-1500m.
Lophopetalum torricellense **Loes.**
Tree 29m. Primary forests 1000-2200m.

Siphonodon celastrineus **Griff.**
Tree 35m. Lowlands, to 1375m.

CLETHRACEAE

Clethra canescens **Reinw. ex Bl. var.** ***canescens***
Tree 20m. Mountains.
(*Clethra longispicata* J. J. S.)
Treelet 5(-12)m. Secondary and mountain forest, 500-1525m.

CHLORANTHACEAE

Ascarina philippinensis **C.B.Rob.**

Tree 24m. Mountains 450-2850m.

COMBRETACEAE

***Lumnitzera littorea* (Jack) Voigt.**

Tree 25m. Mangrove forest

(*Lumnitzera racemosa* Willd.)

Shrub or small tree to 8m. Mangrove forest.

Terminalia bellirica (Gaertn.) Roxb.

A deciduous tree reaching 25-50m. **Lowlands, to 500 (1600)m.** Its fruits are provided with wings, subglobose to broadly ellipsoid in shape and measure 2-2.8 by 1.8-2.2cm when dried. The hard exocarp is 1-2.5mm thick when dried. The endocarp is densely sclerenchymatous. The fruit encloses a single seed. The fruit is used for the production of a commercial myrobalans used for tanning leather, as well as for the production of a black dye and ink. The unripe fruit is purgative, the ripe fruit is astringent (Exell, 1948).

***Terminalia calamansanay* (Blanco) Rolfe,**

Tree. Lowlands.

***Terminalia catappa* L.**

10-35m. Deciduous. Coasts.

Terminalia celebica Exell

Tree reaching up to 20m, endemic to Sulawesi and found in the primary forest (altitude: 250m). The fruits are oblong-ellipsoid in shape and measure about 4 by 2 by 1.5cm. In cross section they show a 3-4mm thick band of sclerenchymatous tissue. The fruit has one seed (Exell, 1948).

***Terminalia citrina* (Gaertn.) Roxb. ex Flem.**

20-30m. Forests at low and medium altitudes.

Terminalia copelandii Elmer

An up to 40m high tree found in the primary forest up to 500m altitude. The species is also present on the Sula islands. The edible fruits are ovoid or ellipsoid in shape, about 3.5-6.0 by 2-3cm large and show on cross section irregular sclerenchymatous tissue and a 2-3mm thick band of corky tissue around the outside. The fruit has one seed (Exell, 1948).

***Terminalia Kjellbergii* Exell**

Tree 15m. 300-400m. Endemic.

***Terminalia samoensis* Rech.**

Tree. Coral limestone.

Terminalia supitiana Koord.

Large tree (20-50m), endemic to Sulawesi, found in the primary forest between 0 and 500m altitude. The elliptical fruit measures 4.0-5.5 by

2.0-2.5cm, has two 7-10mm broad wings and contains one seed (Exell, 1948).

COMPOSITAE

Herbs, shrubs or trees, sometimes climbers, which produce fruits in the form of small dry nuts with a group of small hairs, making them airborne (Koster, 1935).

Eupatorium inulaefolium H.B.&K.
A large shrub.

Vernonia
11 species on Sulawesi (Whitten et al., 1989)
(*Veronia actaea* Koster)
Herb. 0-5m.
***Vernonia arborea* Han.**
Tree to 36m. Primary and secondary forest to 2000m.
(*Vernonia cinerea* (L.) Less.)
Herb.
(*Vernonia elmeri* Merr.)
Herb. 50-2000m.
(*Vernonia erigeroides* DC.)
Herb. 0-1800m.
***Vernonia kabaensis* Koster**
Tree? Dry soil 600-900m. Endemic.
(*Vernonia lanceolata* (Warbg.) Mattf.)
Herb. 30-1000m.
(*Vernonia moluccensis* (Bl.) Merr)
Herb.
(*Vernonia patula* (Dryand.) Merr.)
Shrub.
(*Vernonia reinwardtiana* de Vriese et Miq.)
Herb. 1100-1500m. Endemic.
(*Vernonia subtilis* Koster)
Herb. 300-850m. Endemic.

CONNARACEAE

Cnestis plathantha Griff.
A large liana, shrub or treelet growing in primary and secondary forests up to 500m altitude. It flowers from July to October and fruits from December to February. The pear shaped fruits measure about 4.5-7 by 1.5-2.5cm. They have a thick pericarp, which is probably fleshy when fresh, enclosing 1 large seed with aril. The seeds, and probably also the fruits are edible (Leenhouts, 1954).

Ellipanthus tomentosus Kurz

Shrub or small to medium tree to 25-30m. Forest, to 900m.

Ellipanthus tomemtosus Kurz. ssp. *tomentosus* var. *luzoniensis* (Vidal) Leenh.

A rain-forest shrub or tree growing up to 25m in height. **Mountains to 1100m.** The fruits have a woody pericarp and measure about 2.5-4 by 1cm. The seed is for 4-7mm covered with a 1 mm thick, hard, sarcotesta.

CONVOLVULACEAE

The plants in this family are herbs or shrubs which are sometimes parasitic. (Ooststroom, 1948)

Ipomoea aquatica Forsk.

A circumtropical herb with fruits in the form of 8-10mm large capsules. It is found both wild and in cultivation. It grows in wet, marshy areas from sea-level up to 1000m and can form very dense masses (e.g.. at the delta of the Djenemaedja river, south of Palopo in Sulawesi). The young shoots and leaves of the herb are used as vegetables and in the Malay peninsula, it is generally fed to pigs (Ooststroom, 1948). It is better known under the local name 'kangkong', and forms an important part of the diet of the babirusa in Jakarta and Surabaya Zoo, Java.

Ipomoea batatas (L.) Lamk.

A herb with subterranean edible tubers known as sweet potato. It is widely cultivated throughout the tropics and is occasionally found wild as a relic of cultivation. The young leaves and shoots are also eaten as vegetables (Ooststroom, 1948).

CORNACEAE

Mastixia trichomata Bl. var. *rhynchocarpa*

A 40m tall tree found in primary lowland forest as well as mossy forest up to 1800m. Its dark purple to blue fruit is an ovoid to elongate drupe (about 3 by 2cm) with a woody endocarp. (Matthew, 1974)

Mastixia pentandra Bl. ssp. *scortechinii* (King) Matthew

An up to 37 m high tree found in primary forest up to altitudes of 2400m. Its dark purple to blue drupe is oblong in outline, measures about 2.5 by 2cm and has a woody endocarp. (Matthew, 1974)

CRASSULACEAE

Kalanchoe pinnata Pers.

Robust unbranched herb from African origin, 0.3-2.0m high and in its basal part often somewhat woody. It has succulent leaves and red-and-green flowers. Seeds are often not developed in Malesian species. (Backer, 1948b)

CRYPTERONIACEAE

Crypteronia cumingii **(Planch.) Planch. ex Endl.**
Tree 40m. Lowlands to 1200m.

CUNONIACEAE

Caldcluvia celebica **(Bl.) Hoogland**
Tree.

Weinmannia blumei **Planch.**
Tree to 20m. 1200m.
Weinmannia borneensis **(Engl.)**
Tree to 16m. 1200-1800m.
Weinmannia celebica **Koord.**
Tree. 1000-1800m.
(*Weinmannia descombesiana* Bernardi)
Small tree. 1000-1500m. Endemic.
Weinmannia urdanatensis **Elmer**
Tree. Mountains 1800m.

DAPHNIPHYLLACEAE

Daphniphyllum gracile **Gage var.** *gracile*
Shrub or tree 4-20m. 200-3000m, rare.
(*Daphniphyllum glaucescens* Bl.)
(ssp. *celebense* (Rosenth.) Huang)
Shrub or small tree.

DATISCACEAE

Octomeles sumatrana Miquel
Big rain forest tree reaching up to 62(-80?) m in height, found especially along rivers up to an altitude of 800 m. The fruits are in the form of 12 mm long capsules with membranous pericarp, containing very small seeds (van Steenis, 1948a).

Tetrameles nudiflora R. Brown
Large tree (25-45 m), restricted to areas with a more or less well pronounced dry season. Flowers and fruits are present from September to December. The fruits are in the form of more or less globular, 4-5 mm high capsules with membranous pericarp, containing 1mm small seeds (van Steenis, 1948a).

DILLENIACEAE

Dillenia celebica **Hoogl.**
Tree 30m. Lowlands. Endemic.
Dillenia ochreata **(Miq.) Teijsm. & Binn.**
Tree 15m. From lowlands to 800m. Endemic.
Dillenia pentagyna **Roxb.**
Tree 25m. To 1000m.
Dillenia serrata **Thunb.**
Tree 30m. Lowlands. Endemic.
(*Dillenia talaudensis* Hoogl.)
Small tree 8m. Secondary forest.

DIPTEROCARPACEAE

Dipterocarp fruits are usually winged nuts, but a few are wingless. All fruits still have the remains of the outer layer of the flower bud (=calyx) attached. This calyx is divided into a number of lobes of variable length. It are the longer calyx lobes that form the wings of the fruit (Symington, 1943-1974).

Anisoptera costata Korth.
The only specimen collected from Sulawesi was a sterile specimen which was indistinguishable from *A. thurifera*. Until further collections with flowers are made, Ashton (1978) preferred not to record *A. costata* as present on Sulawesi. **Medium tree. Lowlands, on undulating land and hills to 600m, especially on sedimentary rocks and along ridges; regenerates profusely in secondary forest.**
Anisoptera thurifera (Blanco) Bl. ssp. *polyandra* (Bl.) Ashton
Tall or medium sized trees producing nuts almost completely surrounded by a calyx tube with a diameter of 17mm. Even the longer lobes of the calyx are still quite short. (Symington, 1943-1974; Ashton, 1978)

Hopea celebica Burck
Medium tree. Locally common in semi-evergreen forest below 500m. Endemic. Fruits in the form of long-winged nuts (Symington, 1943-1974).
Hopea gregaria van Slooten
Medium to large tree. Fruits in the form of long-winged nuts (Symington, 1943-1974).

Shorea assamica Dyer ssp. *koordersii* (Brandis) Sym.
Big tree. Primary semi-evergreen forest, lowlands. Its ovate-globose nuts measure about 1 cm in diameter and possess 5 long narrow wings (Symington, 1943-1974).

Shorea montigena van Slooten

Big tree. Hills. Fruits in the form of winged nuts (Symington, 1943-1974). **Doubtfully in Sulawesi.**

Vatica flavovirens Sloot.

Medium tree. Locally common on hill slopes below 400m. Endemic.

Vatica rassak (Korth.) Bl.

Large tree. Locally abundant on hills to 400m. Produces a fairly large (5 by 3.5cm) oblong to ovoid nut with a thick and corky pericarp. The calyx lobes are relatively short (12 by 7mm) (Ashton, 1978).

EBENACEAE

Diospyros

The fruits are berries with fleshy pericarp enclosing 1-16 seeds with thick endosperm. Fruits of some species are edible whereas those of others are used as fish poison. (Ng, 1978b) It may be that certain ebony species are similar to the ironwood (*Eusideroxylon zwageri*) of Sumatra and Kalimantan in producing large, nutritious but toxic seeds more or less continuously through the year (Whitten et al., 1987). The seeds of *Eusideroxylon zwageri* on Sumatra are eaten by porcupines (Whitten et al., 1984).

***Diospyros beccarii* Hiern**

Tree 10-20m. Lowlands.

***Diospyros buxifolia* (Bl.) Hiern**

Tree 15-37m. Lowlands to 600m.

(*Diospyros cauliflora* Bl.)

Small tree to 15m. Lowland forests.

Diospyros celebica Bakh.

Tree 15-35m. Lowlands. The berries measure about 4x2cm (Whitten et al., 1987). **Endemic. Major source of ebony timber.**

Diospyros discolor Willd.

A tree up to **25-32m** high producing fleshy berries globose in shape and measuring 5-12 by 7-10 cm. They enclose 8 to 10 seeds with endosperm. The tree is **widely grown** for its edible fruit. (Ng, 1978b)

***Diospyros ebenum* Koen.**

Tree to 25m. Lowlands. Produces commercial ebony timber.

***Diospyros eburnea* Bakh.**

Tree 15-20m. Endemic.

***Diospyros ellipticifolia* (Stokes) Bakh.**

Tree to 25m. Lowlands.

***Diospyros ferrea* (Willd.) Bakh.**

Tree to 35m. Lowland forests. Produces commercial ebony timber.

***Diospyros frutescens* Bl.**

Tree to 25m. Lowland forests.

Diospyros greshoffiana Kds. ex Bakh.
Tree 15-32m. 500-700m. Endemic.
Diospyros hebecarpa Cunn. ex Benth.
Tree 6-30m. Lowlands.
Diospyros korthalsiana Hiern
Tree 10-30m. Lowlands.
Diospyros macrophylla Bl.
Tree 10-45m. Produces commercial ebony timber.
Diospyros malabarica (Desr.) Kostel (Eben.)
Tree to 35m. Lowlands to 250(-650)m.
Diospyros maritima Bl.
Tree to 25m.
Diospyros minahasae Bakh.
Tree 10-25m. Lowlands to 700m.
(*Diospyros montana* Roxb.)
Small tree 12m. Lowlands to 700m.
Diospyros multiflora Blanco
Tree 25m. Lowlands to 500m.
Diospyros philippinensis A. DC.
Tree 30m. Lowlands.
Diospyros pilosanthera Blanco var. *pilosanthera*
var. *pilosanthera*
Tree to 20m.
Diospyros polita Bakh.
Tree 15-25m. Lowlands to mountains. Endemic.
Diospyros rumphii Bakh.
Tree 15-30(-40)m. Lowlands to 300m. Produces commercial ebony timber.
Diospyros sundaica Bakh.
Tree 25-35m. Lowlands (400m).
Diospyros ulo Merr.
Tree to 30m. Lowlands to 700m.
Diospyros venenosa Bakh.
Small or medium tree. Lowlands. Endemic.

ELAEOCARPACEAE

Elaeocarpus
With yellow-green fruit and white flowers (Whitten et al., 1987)
Elaeocarpus acronodia Bl.
Elaeocarpus angustifolius Bl.
Big tree. Secondary forest, lowlands.
Elaeocarpus argenteus Merr.
High mountains.
Elaeocarpus celebicus Weibel.
Endemic.

Elaeocarpus culminicola Warb.
Tree to 25m. Lowlands to 2750m, sometimes secondary, sometimes seasonal climates.
Elaeocarpus cumingii Turcz.
Tree 20m.
Elaeocarpus dolichodactylus Schltr.
Tree 10-22m. Lowlands to 1600m.
Elaeocarpus dolichostylus Schltr.
Tree 13-25(-40)m.
750-2050m.
Elaeocarpus fairchildii Merr.
Elaeocarpus kraengensis Knuth.
1250m.
Elaeocarpus lanipae Weibel
Endemic.
Elaeocarpus littoralis Teysm. & Binn.
Elaeocarpus macrocerus (Turcz.) Merr.
Tree 30m.
Elaeocarpus macropus Warb.
Tree.
Elaeocarpus mastersii King = *E. acronodia]*
(*Elaeocarpus merrittii* Merr.)
Treelet 5m. Lowlands.
Elaeocarpus minahassensis Knuth
Tree 20m. 1000m. Endemic.
Elaeocarpus multinervosus Knuth
Elaeocarpus pedunculatus Wall.
Elaeocarpus petiolatus Wall.
Big tree. 300-450m.
Elaeocarpus polystachyus Wall.
Elaeocarpus rubustus Roxb.
Tree 20m. Lowlands.
(*Elaeocarpus rumphii* Merr.)
Tree to 8m. To 1500m.
Elaeocarpus sphaericus (Gaertn.)K.Schum. = *E. angustifolius*
Elaeocarpus sphaeroblastus Stapf ex Ridley
(*Elaeocarpus teijsmannii* Koord. & Val.)
Small tree to 15m. To 450m, including ultrabasics.
Elaeocarpus sp. nov.
Tree. 2000m.

Sloanea celebica Boerl. & Koord. ex Koord.
Tree. 1100m.
Sloanea javanica (Miq.) Szys. ex K. Schum.
Tree (10-)20-30m. Lowland forest.

EPACRIDACEAE

Styphelia suaveolens Koord.
Small shrub with small pink berries.

ERICACEAE

Diplycosia
Seventeen species all of which are endemic some of which also smell slightly of wintergreen. Smaller berries than *Gaultheria.* The fleshy fruits are eaten by birds and mammals.

Gaultheria
small shrubs

Gaultheria celebica J.J. Smith
White, pink or red flowers. The leaves, flowers and large black berries taste strongly of wintergreen oil (methyl-salicylate) a substance which is often used to alleviate the symptoms of rheumatism. The fleshy fruits are eaten by birds and mammals.

Gaultheria viridiflora Sleum.
Greenish-white, red-based flowers. The leaves, flowers and large black berries taste strongly of wintergreen oil (methyl-salicylate) a substance which is often used to alleviate the symptoms of rheumatism. The fleshy fruits are eaten by birds and mammals.

Rhododendron
Twenty four species known from Sulawesi, 19 endemic. e.g.. *Rhododendron vanvuurenii* . Rhododendron has very small seeds with wings adapted for seed dispersal.

Vaccinium
The fleshy fruits are eaten by birds and mammals.

ERYTHROXYLACEAE

Erythroxylum cuneatum (Miq.) Kurz
A very tolerant small tree or shrub (8-40m) found in a variety of habitats including **lowlands**. Its red drupes are oblong-ovoid in shape, measure 7-12 by 3-6mm and enclose 5-10 small seeds (Payens, 1954).

Eythroxylum ecarinatum Burck
A 7-37m tall tree found in primary rain forest from the lowlands up to 2000m. Its red drupes are broadly ovoid measuring 8-12 by 5-7 by 4-5mm. It is also present on Buru and the Sula islands (Payens, 1954).

Erythroxylum novogranatense (Morris) Hieron.
A 1-3 m high bush or shrub which was native to South America but is now widely cultivated throughout the tropics, including Sulawesi

(Minahassa). The fruit is a red, elliptic-oblong, 9-11 by 4-5mm drupe containing a 8-10 by 3-4mm stone which in itself covers the seed provided with abundant endosperm (Payens, 1954).

EUPHORBIACEAE

Aleurites moluccana Willd.

The 'candlenut tree' is an evergreen tree **(8-20m)** producing 6cm wide fruits which grow in bunches of 3-6. It is widely cultivated throughout Malesia for its hard seeds which contain a lot of oil used for making candles, soap and paint (Airy Shaw, 1982; Corner, 1988). **15-753m.**

Antidesma

Shrubs or small trees with small roundish, juicy drupes ripening from red to black in colour which are positioned on drooping spikes like red currants. The fruits are probably all edible but sour (Whitmore, 1973c; Corner, 1988).

Aporusa

Small to medium trees or shrubs with fruits in the form of small (about 1 cm) yellow to reddish capsules with fleshy thin to very thick walls. The capsule splits from base to apex into 2-4 segments exposing the 1-6 seeds covered with bright yellow, orange or red arils. The seeds are probably dispersed by birds or small mammals attracted by the brightly coloured fleshy fruit walls or seed arils. (Whitmore, 1973c; Corner, 1988)

(*Aporusa dioica* (Roxb.)Muell. Arg.)

Tree 12m.

(*Aporusa frutescens* Bl.)

Tree to 8m.

***Aporusa grandistipulata* Merr.**

***Austrobuxus nitidus* Miq.**

Tree to 27m. Mostly lowlands.

Baccaurea

Small to medium trees. The fruit is a reasonably large berry with a firm fleshy wall enclosing 1-6 large seeds, each with a brightly coloured pulpy, juicy, sour aril in a enveloped in a transparent skin. The brightly coloured seed arils are contrasting with the fruit wall and probably attract animal dispersers in this way. The seed arils are edible to man but taste generally very sour. (Whitmore, 1973c; Corner, 1988)

***Baccaurea celebica* Pax & Hoffm.**

Endemic.

(*Baccaurea javanica* (Bl.) Muell. Arg.)

Bischofia
Large tree
Bischofia* see *Staphyleacease

Blumeadendron
Small to big trees with a large (2.5cm diam.) woody capsule enclosing 1-2 big edible seeds. (Whitmore, 1973c)

Blumeodendron tokbrai (Bl.) Kurtz
An 18m tall tree found in swampy places including peat swamps. Its round orange fruits measure about 3.2cm in diameter and contain 1 to 2 edible seeds with a creamy aril. (Whitmore, 1973c)

***Cleidion javanicum* Bl.**
Tree to 10m. Lowlands.
***Cleidion minahassae* Pax & Hoffm.**
Endemic.

(*Cleistanthus brideliifolius* C.B.Rob)
***Cleistanthus celebicus* Jabl.**
***Cleistanthus myrianthus* (Hassk.) Kurz**
Tree to 3-21m.
(*Cleistanthus sumatranus* (Miq.) Muell. Arg.)
Small tree.

***Drypetes celebica* (Boerl. & Koord.) Pax and Hoffm.**
***Drypetes cf littoralis* (C. B. Rob.) Merr.**
***Drypetes longifolia* (Bl.) Pax & Hoffm.**
Tree to 20m. Lowlands
***Drypetes* cf *maquilingensis* (Merr.) Pax & Hoffm.**
***Drypetes neglecta* (Koord.) Pax & Hoffm.**
***Drypetes ovalis* (J.J.Sm.) Pax & Hoffm.**
Tree of 10m.

***Endospernum moluccanum* (Teijsm. & Binn.) Kurz**
***Endospernum peltatum* Merr.**

Euphorbia
"Herbs or shrubs with copious white latex in all parts, sometimes thorny, sometimes with rather fleshy stems and branches." (Whitmore, 1973c) They fruit in the form of small capsules containing 3 seeds (Corner, 1988).

(*Excoecaria agallocha* L.)
Bush tree. Rocky coasts and mangrove swamps.

(*Excoecaria borneensis* Pax & Hoffm.)
Shrub 0.5m.
***Excoecaria indica* (Willd.) Muell. Arg.**
Small tree to 18m. Lowlands.

***Galearia celebica* Koord.**

Homalanthus populneus (Geisel.) Pax
A small (9m) tree with about 1cm large, round grey-green fruits (Whitmore, 1973c).

Macaranga

Small to medium trees found in sunny places in secondary forest. Its fruit is a leathery capsule containing black seeds with a thin covering of pink, orange, red or purple pulp (Whitmore, 1973c; Corner, 1988).

***Macaranga crassistipulosa* Pax & Hoffm.**
endemic.
Macaranga gigantea Meull. Arg.
Tree 15m.
Macaranga gigantifolia Merr.
Macaranga cf. *hispida* (Bl.) Muell. Arg.
***Macaranga* cf *inermis* Pax & Hoffm.**
***Macaranga magnifolia* Perry**
Macaranga cf. *mappa* (L.) Muell. Arg.
***Macaranga cf recurvata* Gage**
Macaranga tanarius Muell. Arg.
(*Macaranga* cf *triloba* (Bl.) Muell. Arg.)
Small tree

Mallotus phillippensis (Lam.) Muell. Arg. (corr. Merr.)
A small bushy tree (9m) of open places with fruit in the form of a 1cm wide thinly woody capsule (Whitmore, 1973c; Corner, 1988).

(*Neoscortechinia forbesii* (Hk. f.) Pax ex S. Moore)
Small tree or large shrub.
***Neoscortechinia nicobarica* (Hk. f.) Pax & Hoffm.**
Tree to 25m. 200-400m.

***Phyllanthus* cf *calycinus* Labill.**
***Phyllanthus celebics* Koord.**
(?) Endemic
Phyllanthus emblica L.
An up to 36m high tree of mostly open places in primary and secondary forest. Its greyish-yellow, round (1.7cm diam.), fleshy and juicy fruits are edible and have a sour taste (Whitmore, 1973c).
***Phyllanthus lamprophyllus* Muell. Arg.**

***Phyllanthus minahassae* Koord.**
? Endemic.
***Phyllanthus mindorensis* C.B.Rob.**
(*Phyllanthus reticulatus* Poir.)
Small tree.
***Phyllanthus tenuirhachis* J.J.Sm.**
***Phyllanthus trichosporus* Adelb.**
(*Phyllanthus urinaria* L.)
Herb.
(*Phyllanthus virgatus* Forst.f.)
Herb to 30cm.

***Pimelodendron amboinicum* Hassk.**
Medium tree.

Sapium* in part = *Excoecaria

FAGACEAE

The fruits of the *Fagaceae* are indehiscent nuts rich in starch and/or oil and are therefore readily eaten by animals. The fruits of some species are widely consumed by the local people after cooking or roasting (Soepadmo, 1972).

Castanopsis acuminatissima (Bl.) A. DC.
A primary- or relict-forest tree (10-36m), which occurs scattered in the mountains of Sulawesi **to 1700(-2500)m**. It is often found on loamy sandy soil and is fertile almost throughout the year. Like the European chestnuts, the fruits are enclosed in a kind of husk (=cupule). The dehiscent cupule of *C. acuminatissima* is provided on the outside with small, sharp, flat-triangular spines up to 2mm long. It measures about 1.5 by 1cm and has a 0.5-1.0mm thick wall. It is more or less globose and the fruit is partly emerging. The solitary fruit is ovoid conical in shape and measures 1.0-1.5 by 0.75-1cm (Soepadmo, 1972).

Castanopsis buruana Miq.
A tree of primary or secondary forest reaching a height of 20m and found at altitudes up to 1000m. It is also found on Buru and the Sula islands. The tree flowers from August to January and fruits from January to July. The cupule has a diameter of 1cm, is ovoid-conical, dehiscent, thin-walled and completely encloses the body of the fruit. It has 3-5mm sharp spines on the outside. The fruit within the cupule is also ovoid-conical and reaches 1-1.5cm. (Soepadmo, 1972).

Lithocarpus celebicus (Miq.) Rehd.
A 10-33m tall tree occurring on clayey soils in forest at 20-1200m. It flowers from September to May and fruits from June to April. The cupule has a thin woody wall, is cup-shaped, measures about 2-3cm in

diameter and covers 1/4 of the fruit. The ripe fruit is chocolate-brown in colour, has a 2mm thick woody wall and measures about 2.5cm in length and 1.5cm in diameter (Soepadmo, 1972).

Lithocarpus elegans (Bl.) Hatus. ex Soepadmo

A 5-30m tall tree found in forests from sea level up to 2400m, but more common at 1000-2400m. In areas south of the equator it is fertile throughout the year. The cupule has a woody wall, is cup to saucer-shaped and about 2-3cm in diameter. It covers 1/4-1/3 of the fruit. The ripe fruit is chocolate-brown in colour. It has an ovoid conical shape, a woody wall, and measures about 1.5cm in length and 2.5cm in diameter (Soepadmo, 1972).

Lithocarpus glutinosus (Bl.) Soepadmo

A forest tree reaching 20 m in height, found at altitudes up to 900m. The tree is fertile mainly in the second half of the year. The cupule is deeply cup-shaped, measures 2.5-3.0cm in diameter, has a woody wall and covers 1/3-1/2 of the fruit. The fruit itself is sub-hemispherical, has a woody wall and measures about 1.5cm in length and 2.5cm in diameter. (Soepadmo, 1972)

Lithocarpus havilandii (Stapf) Barnett

A tree or shrub (2-25m) of montane mossy forests at 1300-3000m. The fruits are ripe in June-July. Like the European oaks, the base of the acorns is encircled by a cup like structure (=cupule). The *L. havilandii* cupule has a thin, woody wall, about 2 cm in diameter and covers about 1/4 of the fruit. The ripe fruit is conical, dark chocolate-brown in colour, and measures 2.5-3cm in length and 1.5-2cm in diameter. Its wall is woody and 1-2 mm thick. (Soepadmo, 1972).

Trigobalanus verticillata Forman

This 10-36 m tall tree has been twice collected from Central Sulawesi. It occurs in forest at 850-1500m on blackish ultra-basic or loamy soil. It flowers from September to February and fruits from April to November. The cupule measures 4-6mm in length and 8-15 by 5-10mm in width, and encloses about 3-7 fruits. The ripe fruit is triangular in section, 5-7mm long and 3-5mm wide at its base. (Soepadmo, 1972).

FLACOURTIACEAE

In this family, the fruits can either be berries (fleshy or dry), capsules or (rarely) drupes. The seeds have a lot of endosperm and are sometimes provided with an aril. (Sleumer, 1954)

Casearia grewiaefolia Vent. var. *grewiaefolia*

The 2 to 24m tall tree or shrub is found in primary and secondary forest, especially in rather open and barren lowland sites. It is also present on the Sula islands. Its fruits are orange-yellow ellipsoid capsules containing several seeds provided with orange-red arils. The fruit apparently has a bitter burning taste. (Sleumer, 1954)

Casearia hosei Merr.

This tree or shrub reaches 3-5m in height and is found in primary forests at altitudes up to 1500m. The orange-red subglobose fruits measure about 8mm in diameter and contain a few seeds provided with red arils. (Sleumer, 1954)

Erythrospermum candidum (Becc.) Becc.

This is a shrub or slender tree **(25(-35)m)** bearing 1.25-1.75 by 1.5cm large, green or whitish, subglobose or subangular fruits, with woody pericarps. The tree is usually found in rather low, primary, non swampy, forest **and hill ridges to 540m**. (Sleumer, 1954)

Flacourtia zippelii Sloot.

A slender tree (5-10(-25)m, found in primary and secondary rain forest up to 1200m. Its fruits are globose, fleshy drupes, measuring 1.5-2cm in diameter and ripening from green to dark red. (Sleumer, 1954)

Flacourtia inermis Roxb. var. *inermis*

This 5-15m tall tree can be found cultivated as a fruit tree at altitudes up to 1200m high. It is also present on sandy soils near the sea. Flowering takes place from January to February and fruits are present from May to July. Its fruits are fleshy, globose drupes measuring about 2cm in diameter. The ripe fruits are cherry-red in colour and occur in sweet as well as sour, astringent varieties. Both varieties are edible but the sour variety is not eaten fresh but made into jams etc. (Sleumer, 1954)

Flacourtia indica (Burm. f.) Merr.

This 15m tall bush or tree is mostly found in rather open places with a seasonally dry climate. The fruits are in the form of fleshy drupes, globose to ellipsoid in shape measuring about 1cm in diameter. It is widely cultivated in tropical and subtropical countries and can often be found in villages as a fruit tree. Its fruits turn blackish-red when ripe and are rather astringent. (Sleumer, 1954)

Homalium

These trees produce fruits in the form of leathery, almost inferior capsules enclosing minute seeds. (Sleumer, 1954)

(*Homalium caryophyllaceum* (Z. & M.) Benth.)

Small tree 4-10(15)m. Forest up to 150m, usually by rivers.

***Homalium celebicum* Koord. (Flac.)**

Tree 20-50m. 30-550m, sometimes limestone.

Endemic.

***Homalium foetidum* (Roxb.) Benth.**

Tree 20-30(-50)m. Lowland forests, to 20-200(-350)m.

***Homalium minahassae* Koord.**

Tree 35m. Primary forest.

Hydnocarpus heterophylla Bl. ssp. *heterophylla*

A tree reaching 20(-36)m in height and growing in rain forests, often on calcareous or limestone soils. It flowers from January to June. The globose fruits (about 6.5cm diam.) are found from April to December. Their thick (about 5mm) pericarp encloses 15-20 seeds which contain a fatty substance used against skin-diseases. (Sleumer, 1954)

The ssp. *philippinensis* Sleum., with smaller flowers and fruits, is also present in Sulawesi according to Sleumer (1954).

***Hydnocarpus sumatrana* (Miq.) Koord.**

Tree (7-)15-25m. Lowland forest.

Itoa stapfii (Koord.) Sleum.

A 25-40m tall tree occurring in old mixed primary and secondary rain forest. It produces ovoid-elliptic fruits (7.5-10 by 3.5cm), enclosing flat, winged seeds. (Sleumer, 1954)

Osmelia philippina (Turcz.) Benth.

According to Sleumer (1954) this 5-8m tall tree or shrub of the primary forest is present in North and Central Sulawesi. It fruits in the form of 1-1.5cm oblong to subglobose capsules enclosing 1 to 2 seeds with a fleshy aril. (Sleumer, 1954)

Pangium edule Reinw.

An up to 40m tall tree with a dense crown and rather drooping branches. It is found in a wide variety of habitats both in primary and secondary rain forest, mainly below 300m but sometimes reaching altitudes of 1000m. The tree fruits mainly at the beginning of the rainy season

The pangi fruits are brown, roughly pear shaped and variable in size: 15-25(-30)cm by 7.5-12(-15)cm. They hang from a thick, brown stalk about 8-15cm long. The pericarp is 6-10mm thick and becomes soft and mushy in the ripe fruit. It encloses about 20 irregularly shaped, close-packed, ± 4-6 by 2-3 cm large seeds, themselves enclosed by a white fleshy aril. (Sleumer, 1954)

The fruit is frequently eaten by babirusa although it is not clear whether they eat just the mushy pericarp, or the seeds with their arils as well (Whitten et al., 1987). This is of relevance because the leaves, seeds and most other parts of the tree contain high concentrations of gynocardin, a glucoside yielding prussic acid (or hydrocyanic acid). For this reason, the local people will first wash, soak or roast the fruits or store them underground to eliminate the acid, before boiling and eating them (Sleumer, 1954). The fruits are also eaten by the macaques on Sulawesi (Anon, 1980; Bismark, 1982; Watanabe and Brotoisworo, 1982).

Scolopia luzonensis (Presl) Warb.

This 5m tall shrub or small tree can be found in secondary forests in dry thickets at altitudes up to 680m, or along sandy beaches and on limestone rocks. It flowers in September and March and fruits in April and June. Its fruits are in the form of ovate berries about 6mm in diameter (Sleumer, 1954).

***Scolopia spinosa* (Roxb.) Warb.**

Tree 10-15(-27)m. To 1100m.

Trichadenia philippinensis Merr.

This 20(-40)m tall tree grows in low, primary or old secondary, forest and produces subglobose green fruits (2cm diam.) with a leathery pericarp enclosing three seeds. (Sleumer, 1954)

Xylosma luzonense (Prel.) Clos

Found in S. Sulawesi according to Sleumer (1954). A 10m tall shrub or tree found in primary and secondary rain forest from 0 to 1200m altitude. Its rather dry berries are small and globose in shape (5-6mm diam.), with a thinly leathery pericarp enclosing 1-2 seeds (Sleumer, 1954).

GNETACEAE

(*Gnetum cuspidatum* Bl.)

Climber, stems flattered.

***Gnetum gnemon* L.**

Shrub or tree to 22m.

(*Gnetum gmenonoides* Brongn.)

Climber. To 300m.

(*Gnetum latifolium* Bl.)

Climber.

GOODENIACEAE

Scaevola oppositifolia Roxb.

A scrambling, rarely erect shrub or climber with a preference for open places at altitudes between sea-level and 2700m. Flowers and fruit are present from January to December. Its fruits are more or less fleshy drupes with a hard stone, obovoid to ellipsoid in shape and measuring 5-7 by 2.5-3mm. It is black in colour when ripe. It is expected that frugivorous birds are involved in the dispersal of the seeds (Leenhouts, 1957).

GRAMINAE

Grasses

Agrostis

Arundinella setosa Trin.

Axanopus

Axonopus compressus Beauv. = *Paspalum compressum* Rasp.

Cynodon dactylon Pers.

Imperata cylindrica Beauv.
Sword grass or alang-alang

Miscanthus sinensis Anderss.

Monostachya oreoboloides (F. Muell.) Hitchcock

Poa

Racemobambos
Climbing bamboo

Saccharum spontaneum L.
Wild sugarcane

Setaria sp.

Themeda triandra Forsk.

GUTTIFERAE

Calophyllum
Trees and sometimes shrubs found in lowland and montane forest. Its fruit is a small or medium sized drupe, usually green, but rarely yellow to orange in colour containing a woody stone with 1 large seed. Bats act as dispersers. (Whitmore, 1973d; Corner, 1988)
***Calophyllum aerarium* P.F. Stevens**
Tree 30m. Endemic.
(*Calophyllum calaba* L. var E)
Shrub 3m. 0-380m. Endemic.
***Calophyllum celebicum* P.F. Stevens)**
Tree 20-30m. 30-300m. Endemic.

Calophyllum echinatum **P.F. Stevens**

Tree to 26m. 20-300m. Endemic.

Calophyllum inophyllum **L.**

Tree 7-25(35)m. Rocky and sandy coast; widespread; often cultivated.

Calophyllum leleanii **P.F. Stevens**

Tree 8-25m. Locally common in primary slope and ridge forest. 45-914m.

Calophyllum neo-ebudicum **Guillaumin**

Tree 6-58m. Usually primary lowland to colline rainforests, to 825m.

Calophyllum soulattri Burm. f.

Tree 4, 5-26m. Lowlands to 1700m.

Calophyllum wallichianum **Planchon & Triana var.** *incrassatum*

Tree (3-)15-36m. Sometimes in swamp forest, 6-400(-1200)m.

Calophyllum **sp. 129.**

Tree to 31m. 30-200m.

Cratoxylum **see**

Hypericaceae

Garcinia

Evergreen trees, usually of small to medium size with fruits in the form of large fleshy to woody berries which contain one to many seeds, each embedded in pulp. They are important fruit trees, and some like the mangostene (*G. mangostana*) are cultivated for this purpose (Whitmore, 1973d; Corner, 1988). **Timber little value. Lowlands to mountains.**

Kayea = Mesua

Mesua

Mostly small trees. Lowlands. The fruits are in the form of a nut (Whitmore, 1973d).

Mesua ferruginea **(Pierre) Kost.**

Tree to 25m.

Mesua paniculata **(Blanco) Kost.**

Tree 30m.

(*Mesua pustulatum* **(Ridley) Whitmore comb. nov.)**

Small tree.

HERNANDIACEAE

Hernandia nymphaeifolia **(Presl) Kubitzi**

Tree to 18m. Sea coasts.

Hernandia ovigera **L.**

Hernandia peltata **Meissn.=** *H. nymphaeifolia*

HIMANTANDRACEAE

Galbulimima belgraveana **F.M. Bailey**

Tree. 800-1000m, Sopu valley, 400m Soroako.

HYPERICACEAE

Trees, shrubs or herbs (Robson, 1974).

Cratoxylum formosum (Jack) Dyer

Tree to 45m. Secondary and primary forest, to 600m. The fruit is a dehiscent lignous capsule filled with winged seeds (Robson, 1974).

Cratoxylum sumatranum (Jack) Bl.

Small tree to 12m. Lowland forest. The fruit is a dehiscent lignous capsule filled with winged seeds (Robson, 1974).

Hypericum leschenaultii Choisy

A 0.5-2.5m high shrub or treelet with fruit in the form of a dehiscent capsule (1-2cm) filled with winged seeds (Robson, 1974).

ICACINACEAE

Citronella suaveolens **(Bl.) Howard**

Tree (8-)15-36m. Lowlands to 1600m.

Gomphandra mappioides Valet.

Tree 25m. Lowland to mountain forests to 1600m.

(*Gomphandra velutina* Sleum.)

Tree 10m. To 1200m. Endemic.

Gonocaryum calleryanum **(Baill.) Becc.**

Tree 20m. Lowlands to 750m.

Gonocaryum littorale **(Bl.) Sleum.**

Slender tree 30m. Primary and secondary forest to 1200m.

Medusanthera laxiflora **(Miers) Howard**

Tree 27m. Primary and secondary forests 300-900m.

Merrilliodendron megacarpum **(Hemsl.) Sleum.**

Tree 25m. Lowland forest.

Platea excelsa **Bl.**

Tree to 24m. Lowlands, including peat swamps, to mountains 1800(2200)m.

Platea latifolia **Bl.**

Tree to 27m. Lowlands to 1500m.

Stemonurus celebicus Valet.

Tree 20-30m. Primary forest 20-1000m. Endemic.

JUGLANDACEAE

Engelhardtia rigida **Bl.**

Tree 30(-47)m. Mountain forests.

Engelhardtia serrata **Bl.**

Tree 20-25(-42)m. Dryland forest, to 2200m.

LABIATEAE

Erect herbs which are sometimes woody at their base (Keng, 1974).

Hyptis

Herbaceous or shrubby plants, often aromatic (Keng, 1974).

LAURACEAE

Small lower canopy trees as typical of undergrowth as the wild nutmegs, mangostenes or *Eugenia.* **Mostly timber trees, medium to large in size. Lowland and lower montane, mostly primary rain forest,** they usually become more abundant in the mountains (1200-1600m) where they reach the forest canopy and often form the so-called "oak-laurel forests". Their fruits are small to large one seeded berries with a pulpy pericarp. Many are eaten by a variety of animals including monkeys, squirrels, bats, civets and birds but some don't seem to be touched by the animals (Corner, 1988; Kochummen, 1989).

Actinodaphne

Beilschmiedia

Cinnamomum

Cryptocarya

Dehaasia

Dehaasia carocan **(Vidal) Allen**

Tree. Lowlands.

Dehaasia celebica **Kosterm.**

Tree to 28. Lowlands. Endemic.

Endiandra

Lindera

Litsea
Trees or shrubs with variably shaped berries containing one seed. Fruits of many species are said to be poisonous (Kochummen, 1989).

Machilus = Perseap

Neocinnamomum

Neolitsea

Nothaphoebe

Persea

Phoebe

LECYTHIDACEAE

Barringtonia
Usually small trees of the primary rain forest often found on riverbanks and in swampy places. The fruits are ovoid to ellipsoid, apple-like to banana-like and green, brown or reddish in colour. They are fleshy towards the outside, hard and fibrous towards the inside and contain a large stone with usually one large seed. Monkeys, squirrels, bears and civet cats eat the fleshy part but throw away the stone. Most species contain saponins in their seeds (Whitmore, 1973e; Corner, 1988).

***Barringtonia acutangula* (L.) Gaertn.**
Tree 2-13(-25)m. Swamp and fresh water mangroves.
***Barringtonia apiculata* Laut.**
Small to medium-sized tree, 8-25(-30)m. Lowlands to 1000m.
***Barringtonia asiatica* (L.) Kurz**
Tree 7-20(-30)m. Coastal forest.
***Barringtonia macrostachya* (Jack) Kurz**
Tree 30m. Primary and secondary forest.
Barringtonia racemosa (L.) Spreng. (Lecy.)
The green or red oblong or pear shaped fruits measure 6-9 by 4-5cm (Corner, 1988).
(*Barringtonia reticulata* (Bl.) Miq.)
Small tree 10m. Peat swamp forest.
***Barringtonia samoensis* A. Gray**
Shrub or tree to 20m. Swampy ground or along rivers, 10-1000m.

***Chydenanthus excelsus* (Bl.) Miers**
Tree 30m. Primary and secondary forest to 600m.

Planchonia valida (Bl.) Bl.

Small or large (up to 50m) tree **usually in the lowlands, to 660m,** with 3-4cm long ovoid fruits with a hard and fibrous endocarp. The fruits contain 1-15 seeds (Whitmore, 1973e).

LEGUMINOSAE

The characteristic fruits of this family are pods with one cavity and one row of seeds. They can be very variable in size, shape and substance. Some seeds such as those of *Acacia, Albizia* and *Parkia* have extremely hard coats which first need to decay in the soil for years before the seed can germinate. (Whitmore, 1972b; Corner, 1988)

Abarema sensu Kostermans = ***Archidendron***

Acacia farnesiana Willd.
Acacia tomentosa Willd.

Adenathera bicolor **Moon**
Tree to 30m.
Adenathera pavonina **L.**
Tree to 40m. Lowlands, coastal (?). Frequently planted.
Adenanthera tamarindifolia **Pierre**
Tree 28m.

Albizia acle **(Blanco.) Merr.**
Tree. Lowlands to 150m.
Albizia lebbekoides **(DC.) Benth.**
Tree. Monsoon forest.
Albizia procera (Roxb.) Benth.
Albizia retusa **Benth.**
Tree 2-30m. Lowlands, 50-990m.
Albizia saponaria **(Lour.) Bl. ex Miq.**
Tree 15 (24)m.

(*Archidendron clypearia* (Jack) Nielsen)
Small tree. Lowlands to 1700m.
Archidendron crateradenum **(Kosterm.) Nielsen**
Small tree to 15m. To 500m.
Archidendron minahassae **(Teysm. & Binn. ex Koord.) Nielsen**
Rain forest, 50-500m. Endemic.
Archidendron pauciflorum **(Benth.) Nielsen**
Tree to 20m. Rain forest, 0-1200m.
Archidendron tjendana **(Kosterm.) Nielsen**
Lowlands, secondary forest on limestone to 600m. Endemic.

Bauchinia

Cassia fistula L.
    Tree to 20m.
Cassia javanica L.
    Tree to 25.
Cassia siamea Lamk.
    Tree to 20m. Riverbanks. Introduced
(*Cassia timoriensis* DC.)
    Small tree to 12m. Lowlands.

Cylindrokelupha Kost.= *Archidendron*

(*Cynometra cauliflora* L.)
    Shrub or small tree, 5m. Fruit edible.
Cynometra ramiflora L.
    Tree to 26m. Back of mangrove forest, riverbanks, and swamps.

(*Dalbergia latifolia* Roxb.)
    Small tree.
Dalbergia mimosella (Blanco.) Prain
    Tree 18m.

Erythrina fusca Lour.
    Big tree to 27m. Lowland, often swamps.
Erythrina orientalis = *E. variegata*
Erythrina subumbrans (Hassk.) Merr.
    Tree to 27m. Lowlands including secondary forest.
Erythrina variegata L.
    Small to big tree. Lowlands, wild on sandy coasts. Widely cultivated.

Inocarpus fagifer (Parkinson) Fosberg
    Tree 30m. Seashores.

Intsia amboinensis DC.
Intsia bijuga (Colebr.) O.K.
    Tree to 27m. Coasts.
Intsia palembanica Miq.
    Big tree to 60m. Common in lowlands forest.

Kalappia celebica Kosterm.
    Tree to 40m. Coast to hills, scattered. Endemic to Malili area.

Maniltoa schefferi K. Sch.
    Tree 5-40m. Lowlands, near rivers or coastal.

Ormosia calavensis Azaola ex Blanco
Tree 13-25m. 100-870m.
Ormosia macrodisca Baker
Tree 30m.

Paralbizzia Kost. = *Archidendron*
Pararchidendron pruinosum (Benth.) Nielsen
Shrub or tree to 30m. Montane primary and secondary rain forest 400-2250m.

Peltophorum dasyrhachis Kunz ex Baker
Tree to 28m. Inland forests including secondary forest.
Peltophorum pterocarpum (DC.) Backer ex Heyne
Tree to 20m. Rocky and sandy coasts. Common ornamental.

Pericopsis mooniana (Thw.) Thw.
Tree 7.5-35m. Very handsome valuable timber. Dryland, near the coast and swamp forests including primary forest.

Pongamia pinnata (L.) Pierre
Small tree, occasionally 25m. Coastal forest.

Pterocarpus indicus Willd.
Big tree to 30m. Coastal forest. Commonly planted.

Samanea saman (Jacq.) Merr.
Tree 20m. Widely cultivated.

Saraca celebica De Wilde
Tree 20m. Lowlands. Endemic.
(*Saraca asoca* (Roxb.) De Wilde)
Small tree 4m.

Serialbizzia Kost.= *Archidendron*
Serianthes minahassae (Koord.) Merr. & Perry
Tree to 45m. Lowland primary forest.

Sindora galedupa Prain
Lowlands.

Tamarindus indica L.
Tamarind

Tephrosia

Wallaceodendron celebicum Koord.
Tree to 45m. To 800m.

LILIACEAE

Dracaena
Dragon tree

LINACEAE

Ixonanthes petiolaris **Bl.**
Tree to 30m. Primary and secondary forest to 800m.
Ixonanthes reticulata **Jack**

LOGANIACEAE

The fruits are in the form of either berries or capsules containing one to many seeds with plenty of endosperm. The seeds of capsular fruits are usually very light and adapted for wind dispersal whereas those of the fleshy berries are usually dispersed by birds and bats (Kochummen, 1973a; Corner, 1988).

Fragraea
Epiphytic or hemi-epiphytic shrubs, climbers or large trees of the forest edges and river banks. The fruits are sometimes largish, globular to ellipsoid berries with sticky white latex in their skin. The berries contain many small (1mm) seeds dispersed by bats, birds and sometimes ants (Kochummen, 1973a).

Fagraea auriculata **Jack**
Tree 20m, or shrub or climber. Forest and open vegetation to 1900m.
Fagraea blumei **G. Don**
Medium tree up to 26m, shrub, epiphyte or climber. Under 500m.
Fagraea ceilanica **Thunb.**
Shrub, climber or tree to 20m.
Fagraea elliptica **Roxb.**
Tree, 50m. Up to 1800m.
Fragraea fragrans Roxb.
An up to 30m tall tree **in humid, light forest, secondary forests and lalang fields (up to c. 900m)** producing 8mm wide berries ripening from orange to scarlet. The numerous minute seeds are mainly dispersed by fruit eating bats (Kochummen, 1973a).
(*Fagraea graciliflora* Leenh.)
Straggling shrub 3m. Mountains 2100m. Endemic, (G. Roroka Timbu).
(*Fagraea racemosa* Jack ex Wall.)
Tree 2-10(-16)m. Secondary forests, 0-2000m.
(*Fagraea tacapala* Leenh.)
Shrub. Primary and secondary forests 1000-2000m.

(Fagraea truncata Bl.)

Shrub 12m. Primary forests 700-1250m. Endemic.

Neuburgia celebica **(Koord.) Leenh.**

Tree 30m. Dryland and swampy forests.

Strychnos axillaris Blume.

Many species of Strychnos contain a high amount of alkaloids (such as strychnine and brucine) in their roots, bark, leaves and seeds (Kochummen, 1973a).

LYTHRACEAE

Lagerstroemia

Trees producing large woody capsules, splitting longitudinally in six parts thereby exposing the long-winged seeds (Everett and Whitmore, 1973; Corner, 1988).

Lagerstroemia ovalifolia **T. et B.**

Medium tree, 30m. Lowlands to 600m.

Lagerstroemia speciosa (L.) Pers.

A tree **(15m), along rivers** with masses of violet flowers often planted in cities (Whitten et al., 1987).

MAGNOLIACEAE

Aromadendron= Magnolia **sect.** ***Aromadendron***

Drimys piperita Hook. f.

Small magnolia (Whitten et al., 1987).

Elmerillia ovalis (Miq.) Danday

An up to 45 m tall tree **growing in lowlands to 1000m.** with ellipsoid fruits, the compartment walls of which disintegrate when the fruit is ripe, thereby exposing the seeds (Nooteboom, 1986).

Elmerrillia tsiampacca **(L.) Dandy ssp** ***tsiampacca*** **var.** ***tsiampacca***

Tree to 60m. Low to 1400m in primary forest. The most valuable timber in N. Sulawesi, already scarce by early this century.

Magnolia (section *Aromadendron*)

Fruit a fleshy composite fruit with one or two seeds in each compartments. The fruits do not fall down as a whole but the compartment walls fall off when the fruit is ripe thereby exposing the seeds which are still on the plant (Nooteboom, 1986).

Magnolia paulantha **Dandy ex Noot.**

Unpublished. Tree 30m. 1250-2200m. Endemic.

Subgenus *Talauma* (Juss.) Pierre

Sect. *Blumiana* Blume

Talauma celebica Koord.
    Tree to 35m. 500-1250m alt. Also on Buru.

Manglietia glauca Bl. var. *glauca*
    Tree to 35m. In forest 500-2400m.

Michelia x *alba* DC.
    Tree to 30m. Sterile and commonly cultivated as an ornamental.
Michelia champaca L.
    Tree to 50m.
var. *champaca*
    Commonly cultivated throughout the tropics.
Michelia pubinervia(Bl.)K.&V.= *M. champaca* var. *pubinervia*

MALVACEAE

(*Hibiscus acetosella* Welwitsch ex Hiern)
    Herb or undershrub.
Hibiscus decaspermus Koord. & Val.
    Tree 3-25m. Lowlands, along or near the sea-coast.
(*Hibiscus hirtus* L.)
    Undershrub, 1-1.5m. Lowlands.
(*Hibiscus indicus* (Burm. f.) Hochr.)
    Shrub. Sea-level up to c. 2000m.
(*Hibiscus lunariifolius* Wild.)
    Herb or undershrub, 1.5-2.5m. Lowlands.
(*Hibiscus panduriformis* Burm.f.)
    Herb or undershrub, 0.5-2.5m. Lowlands.
(*Hibiscus radiatus* Cav.)
    Herb or undershrub, 1m.
(*Hibiscus rosa-sinensis* L.)
    Herb. Cultivated throughout the tropics.
(*Hibiscus sabdariffa* L.)
    Cultivated in all tropical regions.
(*Hibiscus teijsmannii* Borss.)
    Shrub or small tree Endemic.
(*Hibiscus tiliaceus* L.)
    Low spreading tree. Common along rocky and sandy coasts. Often planted.
(*Hibiscus vitifolius* L.)
    Herb or undershrub, 0.5-2.5m. Lowlands to seasonal climate.

Thespesia populnea **(L.) Sol. ex Correa**
Tree to 20m. Mangrove swamps and rocky and sandy coasts.
(*Thespesia lampas* (Cav.) Dalz. Gibs.)
Shrub 0.5-2.5m. To 900m.

Sida sp.

MELASTOMATACEAE

Mainly herbs, shrubs and climbers with fruits either in the form of berries or of capsules (Corner, 1988).

***Astronia gracilis* Bakh.**
Tree Malili, endemic.
(*Astronia macrophylla* Bl.)
Tree 5-12m.
***Astronia spectabilis* Bl.**
Tree 10-20m.
(*Astronia stapfii* Kds.)
Tree to 18m. Endemic.

Melastoma polyanthum Benth. = *Anplectrum divaricatum* Triana,

Memecylon
The fruits are edible berries with a thin leathery or pulpy wall and a hard stone containing one seed (Corner, 1988).

(*Memecylon crassifolium* Bakh.f.)
Shrub. Endemic
***Memecylon lilacinum* Zoll. & Mor.**
Tree 5-25m.
***Memecylon paniculatum* Jack**
Tree to 30m.

Pternandra
The fruit is a green or bluish berry containing many small seeds (Corner, 1988).

***Pternandra coerulescens* Jack**
Tree to 26m.

MELIACEAE

This family produces generally quite large fruits which are either capsules filled with flat winged seeds or fleshy structures with large seeds often covered with pulp (Corner, 1988).

Aglaia
The fruits are up to 2.5cm wide, brightly coloured, fleshy and contain 1-3 large seeds covered by transparent white, yellow or orange pulp (Corner, 1988).

Aglaia argentea **Bl.**
Tree up to 30(50)m. Sometimes on limestone.
Aglaia barbatula **Koord. & Val.**
Tree to 25m.
Aglaia canariifolia **Koord.**
Tree to 20m. Endemic
(*Aglaia cauliflora* Koord.)
Tree to 15m.
Aglaia celebica **Koord.**
Tree to 25m. Endemic.
(*Aglaia cordata* Hiern)
Small tree to 10m.
Aglaia dyeri **Koord. = *A. cordata***
Aglaia dysoxylonoides **Koord = *A. cauliflora* Koord.**
(*Algaia elaeagnoidea* (A. Juss.) Benth.)
Small tree to 5(10)m. Often littoral.
Aglaia elliptica **Bl.**
Tree to 20(50)m. Sometimes on limestone.
Aglaia ganggo **Miq.**
Tree to 30(50)m. Sometimes on limestone.
(*Aglaia hemsleyi* Koord.)
Tree to 18m. Endemic ?
Aglaia Luzoniensis **(Vidal) Merr. & Rolfe**
Tree to 8 (20)m.
Aglaia menadonensis **Koord. = *A. sunlingi***
Aglaia minahassae **Koord.**
Tree to 50m.
Aglaia myristicifolia **C. DC.**
Tree to 20m.
(*Algaia oligocarpa* Miq.)
Tree to 15(25)m.
Aglaia reinwardtii **Miq. = *A. sunlingi***
Aglaia ridleyi **(King) Pannell**
Tree to 40m.
Aglaia roxburghiana **(Wight & Rn.) Miq. = *A. elaeagnoidea***
Aglaia sclerocarpa **C. DC. = *A. oligocarpa***
Aglaia smithii **Koord.**
Tree to 30m.
Aglaia stapfii **Koord. = *A. elliptica***
(*Aglaia stellipila* C. DC.)
Tree to 6m.

(*Aglaia sulingi* Bl.)
Tree to 8m.
Aglaia sp. 1
Aglaia sp. 2
Aglaia sp. 3
Aglaia sp. 4

Anthocarapa nitidula (Benth.) Penn. ex Mabb.
Tree to 30m. To 1400m.

Aohanamixis polystachya (Wall.) R. Parker
Tree or pachycaul treelet, to 20(-35m), polymorphic. To 1400m.

Azadirachta excelsa (Jack) Jacobs
Tree to 50m. To 350m.
Azadirachta indica A. Juss.
Tree to 16m. Exotic. Native in Burma (?), widely naturalised.

Carapa moluccensis Lam. = *Xylocarpus moluccensis*
Carapa obovata Bl. = *Xylocarpus granatum*

Chisocheton celebicus Koord.
Tree. To 700m. Endemic. NE Sulawesi - not collected this century.
Chisocheton ceramicus (Miq.) C. DC.
Tree to 30m. To 700m.
Chisocheton cumingianus (C. DC.) Harms
(Subspecies. *cumingianus*)
Tree to 37m. To 1300m.
Chisocheton divergens Bl. = *C. patens*
Chisocheton kingii Kooders = *C. koodersii*
Chisocheton koordersii Mabb.
Tree to 30m. To 600m.
Chisocheton patens Bl.
Tree to 35m, but usually much smaller. To 500m. Common and polymorphic.
(*Chisocheton pentandrus* (Blco) Merr.)
Treelet to 18m. To 1400m.
(*Chisocheton sarasinorum* Harms)
Pachycaul treelet to 15m. To 1150m.
(*Chisocheton warburgii* Harms)
Pachycaul treelet to 7m. Endemic

Dysoxylum
The large (2.5-13cm wide), brightly coloured, round or pear-shaped fleshy fruits contain large seeds covered by a waxy or pulpy, brightly coloured layer. The seeds are often dangling from the fruits on broad, mealy, white strands (Corner, 1988).

Dysoxylum acutangulum Miq.
Tree to 37m. To 800m.
Dysoxylum alliaceum (Bl.) Bl.
Tree to 38m, often of poor form. Polymorphic. To 1800m, common.
Dysoxylum amooroides Miq. = *D. gaudichaudianum*
Dysoxylum arborescens (Bl.) Miq.
Tree to 20 (-30)m, but usually a treelet. To 1500m. Very common even in relict hedgerows.
Dysoxylum caulostachyum Miq. = *D. parasiticum*
Dysoxylum cumingianum C. DC.
Treelet or tree to 25m. To 335m.
Dysoxylum densiflorum (Bl.) Miq.
Tree to 36(-45)m. To 1700m.
Dysoxylum excelsum Bl.
Tree to 35m. To 1800m.
Dysoxylum gaudichaudianum (A. Juss.) Miq.
('*D. amooroides*')
Tree to 30m. To 1800m. Common.
Dysoxylum hirsutum C.DC. = *D. nutans*
Dysoxylum molissimum Bl.
(Subsp. *mollissimum*).
Tree to 34(-58)m. To 1900m.
Dysoxyulum nutans (Bl.) Miq.
Treelet to 6m. To 1600m (incl. limestone and ultrabasics)
Dysoxylum parasiticum (Osb.) Kosterm.
Tree to 27(-36)m. To 2100m.
Dysoxylum paucijugum C. DC. = *D. nutans*
Dysoxylum sp. 1
Dysoxylum sp. 2
Dysocylum sp.

Lansium domesticum Correa
Tree to 30m. To 1100m.
Lansium humile Hassk. = *Reinwardtiodendron humile*

Melia azedarach L.
Tree to 40m. To 1200m. Wild in Indomalesia with ornamental cultavars naturalised throughout tropics and subtropics.
Melia azadirachta L. = *Azadirachta indica*

Reinwardtiodenron celebium koord.
Tree to 25m. To 600m.
Reinwardtiodendron humile (Hassk.) Mabb.
Tree to 27m. To 800m.
Reinwardtiodendron merrillii Perkins = *R. celebicum*

Sandoricum koetjape (Burm. f.) Merr.

An up to 50m tall tree **to 1200m, wild and naturalised** with 5-7.5cm wide fleshy brightly coloured fruits. **Wild in Malesia with selected cultivars naturalised throughout the archipelago.** The fruits are edible but not favoured by Europeans; the sweet variety is too sweet and the sour variety too sour (Corner, 1988).

Toona

Probably 3 species in Sulawesi and Malesia, all timber trees.

***Vavea amicorum* Benth.**

Tree to 30m, with Terminalia-branching. To 1250m, often on limestone.

Vitex bantamensis* Kooders & Valeton = *Vavea amicorum

Walsura

Probably 3 species in Sulawesi, one possibly a big tree.

***Xylocarpus granatum* Koenig**

Tree to 15(-20)m. Mangrove forests. Common

***Xylocarpus moluccensis* (Lam.) M.J. Roemer**

Tree to 18(-30)m. Mangrove forests. Common.

***Xylocarpus rumphii* (Kostel.) Mabb.**

Tree to 12(-18)m. Sea-cliffs and rocks (not mangrove)

MONIMIACEAE

In most Malesian genera the fruit clusters consist of fleshy, shiny black drupes (containing seeds with lots of oily endosperm) on top of fleshy, brightly coloured, enlarged receptacles (= the region at the top of the flower stalk carrying the floral parts) (Philipson, 1986) which give them the typical characteristics favouring dispersal by birds (Gautier Hion et al, 1985).

Levieria montana Becc.

Shrub or small tree growing up to 15m high mostly found in lower montain rainforest between 1200 and 1900m. The fruits are composed of numerous 8 by 5mm large drupes sitting on a leathery receptacle. The plant usually attracts a lot of birds and is sometimes preserved by the villagers for this purpose to make the bird hunting easier (Philipson, 1986).

Kibara coriaceae (Bl.) Tulasne

An up to 22m high tree, or rarely a shrub, found in forests from lowland up to lower montain areas (1600m), including swamp and limestone forests. Its 15mm large black drupes are positioned on a bright yellow-orange receptacle (Philipson, 1986).

Kibara obtusa Bl.

A primary rain forest shrub or tree (up to 20m) found from sea-level to 700m. The black, ovoid drupes (17-24 by 10-12mm) are positioned on a bright orange receptacle (Philipson, 1986).

Steganthera hirsuta (Warb.) Perkins

An up to 20m tall tree or occasionally a shrub or liane found in the understorey of the rain forest **in lowlands to 2450m, including seasonal swamps**. The black, ovoid drupes (about 13 by 10mm) are positioned on bright yellow or orange receptacles. The species is also found on the island of Buru (Philipson, 1986).

MORACEAE

Fruits of the 'Mulberry Family' are mostly large fleshy compound structure with many large or small seeds. Some species of Artocarpus and Ficus yield edible fruits (Kochummen, 1978a; Corner, 1988).

Artocarpus

Mostly evergreen trees with thick, white latex in all of their parts, including the unripe fruits. The fruits are small to gigantic fleshy heads which enclose large seeds enveloped by a waxy or pulpy succulent layer (Kochummen, 1978a).

***Artocarpus fretessii* Teysm. & Binn.**
Tree to 40m. To 700m.
***Artocarpus integer* (Thunb.) Merr.**
Tree 24m. To 500(-1400)m.
***Artocarpus reticularus* Miq.**
Tree 30m. To 700m.
***Artocarpus sericicarpus* Jarrett**
Tree 30)-40)m. Lowlands (-1000m).
Artocarpus teysmannii Miq. (Mora.)
Tree, 45m. Lowlands forests, swampy.
***Artocarpus vriesianus* Miq.**
Tree 28m. To 2000m.

Ficus

Fig trees occur in an enormous variety of habitats (all types of forest from the sea-shore to the mountains) and forms (trees, shrubs, epiphytic climbers and stranglers or woody creepers). The figs ripen from green to a variety of colours and will sometimes grow on the trunk or base of the trunk of the tree. Several species produce figs edible to man and figs are fed upon by many species of animals including the macaques of Sulawesi for which it is one of the main food sources (Kochummen, 1978a; Anon, 1980; Bismark, 1982; Watanabe and Brotoisworo, 1982).

Ficus adenosperma Miq.
(*Ficus allutacea* Bl.)
Shrub to 12m. Mountain.
(*Ficus altissima* Bl.)
Tree, epiphytic when young. Lowlands to mountains.
(*Ficus ampela* Burm. f.)
Shrub or small tree. Lowlands to mountains.
(*Ficus annulata* Bl.)
Strangler, to 24m. Lowlands to mountains.
(*Ficus aurantiacea* Griff.) var. *parvifolia* Corner
Climber.
Ficus aurita Bl.
Ficus benjamina L.
Medium sized to big strangler. Lowland to mountains.
(*Ficus binnendykii* Miq.) var. *cupulata* Corner
Strangler. 350-600m. Endemic.
Ficus botryocarpa Miq.
(*Ficus callophylla* Bl.)
Scrambler. Lowlands.
Ficus callosa Willd.
Tree, 23m. Lowland forests.
(*Ficus caulocarpa* Miq.)
Strangler
Ficus cauta Corner
Endemic
Ficus celebensis Corner
Endemic.
Ficus chrysolepis Miq.
Ficus congesta Roxb.
var. *manadena* (Miq.) Corner
Endemic.
Ficus copiosa Steud.
Tree. Lowlands to mountains.
Ficus cordatula Merr.
(*Ficus crassiramea* Miq.)
Talaud only, in Sulawesi.
Ficus decipiens Reinw. ex Bl.
Endemic.
(*Ficus deltoidea* Jack var. *motleyana* (Miq.) Corner)
Shrub, 2m. Seashore to mountains.
(*Ficus disticha* Bl.)
Strangler. Mountains.
Ficus drupacea Thunb.
Big tree. Lowlands to mountains.
Ficus elmeri Merr.
Ficus erythrosperma Miq.

Ficus falfax Miq.
Endemic.
Ficus forstenii Miq.
(*Ficus fulva* Reinw. ex Bl.)
Small tree, 18m. Lowland to mountains.
Ficus geocarpa Teysm. ex Miq.
Endemic.
Ficus glandifera Summerh.
Var. *brachysyce* Corner
(*Ficus glandulifera* (Wall. ex Miq.) King)
Small tree, 15m. Lowlands.
Ficus goniophylla Corner
Endemic.
Ficus gratiosa Corner
Endemic.
Ficus grossivenis Miq.
Ficus gul. Laut. et K. Schum.
(*Ficus heteropleura* Bl.)
Shrub. Lowlands to mountains.
Ficus heteropoda Miq.
(*Ficus hispida* L. f.)
Small tree, 12m. Lowlands to mountains.
Ficus irisana Elm.
Ficus kjellbergii Corner
Endemic.
Ficus lamponga Miq.
Tree, 24m. Lowlands and hills.
(*Ficus latimarginata* Corner)
Small tree 4m. Lowlands. Endemic.
(*Ficus lepicarpa* Bl.)
Small tree, 12m. Lowlands to mountains.
Ficus madhucifolia Corner
Endemic.
Ficus magnoliifolia Bl.
Tree, 33m.
(*Ficus melinocarpa* Bl.)
Tree. To 10-700m.
Ficus microcarpa L. f.
Large tree. Swamps and by the sea.
Ficus minahassae (Teysm. et Vr.) Miq.
Ficus miquelli King.
Ficus obliqua Forst. f.
(*Ficus obscura* Bl.)
Shrub or large strangler, 30m. Lowlands to mountains.
(var. *angustata* (Miq.) Corner)
(var. *borneensis* (Miq.) Corner)
Lowlands.

(var. *kunstleri* (King) Corner)
    Epiphyte or strangler. Mountains.
(var. *scaberrima* (Bl.) Miq.)
Ficus oleaefolia King var. *memcylifolia* Corner
(*Ficus parvibracteata* Corner)
    Tree 10m. Endemic.
Ficus pendunculosa Miq.
Ficus peninsula Elm.
Ficus polygramma Corner
(*Ficus pubinervis* Bl.)
    Tree. Lowlands to mountains.
(*Ficus punctata* Thunb.)
    Large woody creeper. Lowland to mountains.
Ficus racemosa L.
    Tree, 24m. Rivers.
var. *elongata* (king) Barrett
(*Ficus ribes* Reinw. ex. Bl.)
    Small tree 8m.
var. *cuneata* (Miq.) Corner
Ficus riedelii Miq.
Ficus ruficaulis Merr.
Ficus rumphii Bl.
    Large tree. Rocky coasts.
(*Ficus sagittata* Vahl.)
    Climber. To 400-1200m.
Ficus saxophila Bl.
(*Ficus schwarzii* Koord.)
    Small tree, 12m. Lowlands to 1200m.
(*Ficus spetica* Burm. f.)
    Shrub or small tree. Lowlands to 1200m.
Ficus stricta Miq.
    Tree, 18m. Lowlands.
(*Ficus subcordata* Bl.)
    Strangler. Lowlands.
Ficus subcuneata Miq.
(*Ficus subulata* Bl.)
    Climber, 24-30m.
(*Ficus sumatrana* Miq.)
    Tree, epiphytic when young. To 400-1200m.
Ficus superba Miq.
    Big tree. Rocky coasts.
Ficus tenuicuspidata Corner
    Endemic.
Ficus tinctoria Forst. f. ssp. *gibbosa* (Bl.)
    Big tree, 45m. From lowlands to 1200m.
Ficus tondayensis Elm.
Ficus tonsa Miq.

(*Ficus trichocarpa* Bl.)
Climber. Lowlands to 1000m.
(var. *obtusa* (Hassk.) Corner)
(*Ficus uniglandulosa* Wall. ex. Miq.)
Epiphyte or small tree.
***Ficus variegata* Bl.**
Tall tree, 33m. Open country, lowlands to 1500m.
(*Ficus virens* Ait.)
Tree. Lowlands to 1200m.
***Ficus virgata* Reinw. ex Bl.**
(*Ficus vrieseana* Miq. (var. *vrieseana*)
Shrub or tree. Lowlands to mountains.

***Parartocarpus venenosus* (Zoll. & Mor.) Becc.**
ssp. *forbesii* (King) Jarrett
Tree, 35m. Lowlands.

MUSACEAE

Banana family.

Musa
Edible bananas have originated from *M. acuminata* and *M. balbisiana* and numerous cultivars are present throughout the tropics (Stover and Simmonds, 1987).

MYRICACEAE

***Myrica javanica* Bl.**
Tree or erect shrub, 2-10(-20)m. Mountains 900-3300m.

MYRISTICACEAE

The nutmegs are typical trees of the lower storeys of the rain forest with roundish brightly coloured fruits. The fruit wall is thick and fleshy or thin and leathery and contains one large, hard, aromatic seed (the nutmeg) covered in a pink or red aril (=mace). The fruits are attractive objects on the tree as well as on the ground and are sought after by birds (especially pigeons) which act as dispersers (Whitmore, 1972c; Corner, 1988).

Endocomia macrocoma* (Miq.) de Wilde ssp. *macrocoma
Tree 5-209m Lowlands to 400m. Sulawesi (?)

Gymnacranthera
The fruits have a thick fleshy wall surrounding the aril-covered, oily seed (Whitmore, 1972c).

***Gymnacranthera farguhariana* (Hk.f. & Th.) Warb.**
var. *zippeliana* (Miq.) Schouten.
Gymnacranghera forbesii* (King) Warb. = *G. farguhariana
***Gymnacranthera maliliensis* Schouten**
Tree 20m. Ultrabasic soil. Endemic.

Horsfieldia
The fruits are roundish with a leathery (rarely fleshy) wall enclosing and aril-covered seed (Whitmore, 1972c). **Species solely numbered are from de Wilde's key in GBS 37(1984) 162-4, not yet described by him.**
***Horsfieldia coriacea* W.J.J.O. de Wilde**
***Horsfieldia costulata* Warb.**
Horsfieldia irya (Gaertn.) Warb.
Tree 30m. River, coasts, especially swampy places.
***Horsfieldia lancifolia* de Wilde (de Wilde 123)**
Tree to 10-30m. S & C Sulawesi, endemic.
***Horsfieldia parviflora* (Roxb.) Sinclair. (de Wilde 69)**
Tree to 10-20m. To 0-600m.
***Horsfieldia talaudensis* de Wilde (de Wilde 75)**
Tree to 15-35m. Lowlands, 70-200m. Endemic.

Knema
The fruits have a thick, fleshy wall enclosing the aril-covered, starch containing seed (Whitmore, 1972c).
Knema celebica de Wilde
Tree. Fruits hairy, ellipsoid-fusiform and measuring about 2 by 1cm (de Wilde, 1981). **Lowlands, ultrabasic soil. Endemic.**
(*Knema cinerea* (Poir.) Warb.)
Tree, 10-12m.
Knema matanensis de Wilde
A 6-25m tall tree with hairy fruits about 2 by 1cm (de Wilde, 1981).
Lowlands. Endemic.
Knema stellata Merr. subsp. minahassae (Warb.) de Wilde
Tree to 35m. Mountains. Endemic.
(*Knema tomentella* (Miq.) Warb.)
Tree 5-12m.

Myristica
The cultivated nutmeg = *M. fragrans* Houtt.
Usually large (2.5cm or more) seeds with a thick fleshy wall enclosing the aril-covered, oil and starch containing seed (Whitmore, 1972c).
***Myristica elliptica* Wall. var. *celebica* (Miq.) Sinclair**
Tree 20-26m.
***Myristica fatua* Hout. var. *affinis* (Warb.) Sinclair**
Tree 10-20m. Endemic variety.
(*Myristica impressinervia* Sinclair)
Small tree, 6m. Limestone at Tolala. Endemic.

***Myristica koordersii* Warb.**

Tree 17-25m.

***Myristica lancifolia* Poir. var. *bifurcata* Sinclair**

Tree 14-20m.

MYRTACEAE

Baeckea frutescens L.

A shrub or small tree up to 6 m with fruit in the form of a small minute capsule (Kochummen, 1978b; Corner, 1988).

Decaspermum

Fruit a globose berry with 8-10 seeds (Kochummen, 1978b).

Decaspermum paviflorum (Lam.) A.J. Scott.

A common shrub or treelet in clearings in eastern Sulawesi which produces small (5-8 mm across) blue-black fleshy fruits eaten by birds (Kevan, 1985).

Eucalyptus

The fruit is a woody capsule with numerous small seeds. (Kochummen, 1978b)

Eucalyptus deglupta Blume,

A dominating tree in almost all riverine forests **throughout Sulawesi** which are more or less undisturbed. The tree flowers at the height of the wet season and the fruit capsules open at the end of the wet season (Cossalter, 1980).

Eugenia

The fruits are roundish with a leathery, dry, pithy or pulpy wall surrounding 1-2 large seeds. Monkeys, squirrels and small fruit bats eat the fruit walls but throw away the seeds. Commercial clove-tree is *E. caryophyllus*. The cloves are made of the half grown dried flower buds (Kochummen, 1978b; Corner, 1988).

Eugenia sensu lato

Many species, probably over 100. Small, medium and a few big trees. All forest types, lowlands and mountains.

Kjellbergiodendron

"Large fruits (8x15 cm) were found belonging to a *Kjellbergiodendron* which is probably not the same as *K. celebicum* found in inland forests. The spongy flesh around the single seed is apparently eaten by bats" (Whitten et al., 1987).

***Kjellbergiodendron celebicum* (Koord.) Merr.**

Tree 40m. Mountains.

Kjellbergiodendron hylogeiton Burret

Big tree. Endemic.

Kjellbergiodendron limnogeiton Burret

Big tree. Endemic.

Leptospermum

Bushes or trees with fruits in the form of small woody capsule containing many tiny seeds (Corner, 1988).

Melaleuca

Paperbark. Bushes or trees with fruits in the form of small woody capsule containing many tiny seeds. (Corner, 1988)

Metrosideros

Local ironwood

Metrosideros petiolata Koord.

Tree 30m. 200-700m.

Metrosideros vera Lindl.

Tree 30m. Lowlands.

Planchonia valida Blume,

***Rhodamnia moluccana* Burret**

Shrub or tree to 21m. Lowlands to 850m.

Syzygium lineatum (DC.) Merr. & Perry

Syzygium lineatum (DC.) Merr. & Perry produced a mass of small (5 mm) flowers from mid-February to mid-March 1980. Its fruit are a whitish, fleshy drupes, 8-10 mm across with a single seed 5-7 mm across. The fruits are produced by the end of March and drop to the ground in large numbers around the adult trees. The fruits appear to be adapted for animal dispersal but no animal was observed eating the fruits either on the tree or on the ground. There were very few other fruiting trees and very few visitors were observed on any fruit. Competition from other fruiting trees was therefore an unlikely reason for the lack of animals feeding on the *Syzygium lineatum* fruits (Lack & Kevan, 1984).

***Syzgium* = *Eugenia* s.l.**

Tristania

Shrubs or trees with fruits in the form of splitting capsules filled with winged seeds (Kochummen, 1978b).

Tristania*: all Malesian spp. transferred to *Tristaniopsis

***Tristania celebica* Koord = *Kjellbergiodendron celebicum* (Koord.) Merr.**

Tristaniopsis decorticata (Merr.) Wilson & Waterhouse
Tree 15.

Xanthomyrtus angustifolia A.J. Scott
Tree to 20m. Mossy forest, 820-2000m.
(*Xanthomyrtus flavida* (Stapf) Diels)
Shrub or small tree to 2-3m. Forest or serpentine ridge forest, 1200-4100m.

Xanthostemon confertiflorum Merr.

NYCTAGINACEAE

(*Pisonia aculeata* L.)
Overhanging climber to 20m. Lowland to 500m.
(*Pisonia grandis* R. Br.)
Tree 30m. Dry or slightly dry coasts, sea level to 1200m.
Pisonia umbellifera (Forst.) Seem.
Tree to 28m. Usually coastal.

OCHNACEAE

Brackenridgea palustria Bartell.
Tree to 30m. To 1100m.

Gomphia serrata (Gaertn.) Kanis
Shrub or tree, to 25m. Up to 1200m.

Schuurmansia elegans Bl.
Treelet or tree to 15 (-30?)m. Sea level to 2000m.
Schuurmansia henningsii K. Sch
Treelet or tree, to 15(20?)m. From sea level to 3000m. Talaud only.

OLACACEAE

Anacolosa frutescens (Bl.) Bl.
Tree 5-25(-30)m). To 1400m.
Anacolosa heptandra Maing. ex Mast. = *A. frutescens*

OLEACEAE

Chionanthus celebicus Kds.
Tree. Endemic.
Chionanthus cordulatus KDs.
Tree
Chionanthus laxiflorus Bl.
Tree.

Chionanthus ramiflorus Roxb.

Tree.

Chionanthus rupicolus (Linglsh.) Kiew (ined.)

Tree.

Chionanthus stenarus (Merr.) Kiew (ined.)

Tree. Endemic.

Fraxinus griffithii (C.B.Cl.

Tree. 400-1500m.

Linociera = Chionanthus

ONAGRACEAE

Herb, sometimes aquatic or woody at their base (Raven, 1974).

Epilobium prostratum Warb.

Perennial herb (Raven, 1974).

OXALIDACEAE

***Averrhoa bilimbi* L.**

Shrub or tree to 15m. Lowlands, along rivers. Native of monsoon regions of Malesia.

Averrhoa carambola L.

A 14m high tree found along rivers in primary and secondary forest up to 1000m, often as a relic of cultivation. The ovoid-ellipsoid fruits can grow up to 12.5 by 6 cm large and contain up to ten 12 by 5mm large seeds enclosed by a fleshy aril. The fruits are eaten and dispersed by bats, mice and reptiles (e.g. *Calotes* sp., Agamidae). The fruits are also edible for humans and the tree is cultivated for its fruits which can either be eaten fresh or pickled (Veldkamp, 1972).

Averrhoa bilimbi L.

A shrub or tree (up to 14 m) found along rivers in primary and secondary forest, often as a relic of cultivation. The fruits measure up to 10 by 5 cm and hold up to fourteen ± 7 by 5 mm large seeds without aril. The fruits and flowers are edible but taste more acid than those of *A. carambola*. (Veldkamp, 1972).

Connaropsis = Sarcotheca

Sarcotheca celebica Veldkamp

A shrub or tree (up to 35m) endemic to Sulawesi and the nearby Kabaena Island. It occurs mainly as a coloniser in open places and by rivers at low altitudes. The indehiscent fruits are ellipsoid in shape, measuring 8-13 by 6-9mm. They ripen from red to black and have a sour taste. They appear to be adapted for bird dispersal, but so far no birds have been observed taking them. (Veldkamp, 1972; Lack & Kevan, 1987).

PALMACEAE

Actinorhytis
Tall tree palms found in lowland tropical rain forest to about 1000m altitude. The very large ovoid fruits have a smooth exocarp, a thin and fleshy mesocarp and a thin and bony endocarp enclosing the single globose seed. The fruits ripen from green to red (Uhl and Dransfield, 1987).

Areca
Small to moderate palms typical for the undergrowth of tropical rain forest. The brightly coloured roundish fruits have a smooth exocarp, a fleshy or fibrous, thin or moderately thick mesocarp and a fibrous endocarp. The fruits are a source of tanning (Uhl and Dransfield, 1987).
Areca vestiaria Giseke

Arenga
The wild sugar palms are of variable size, from dwarf- to tree palms. The fruits have a smooth and tough exocarp and a fleshy mesocarp. The endocarp is not differentiated. The fruits measure about 3 by 3cm and contain 1-3 large seeds. (Uhl and Dransfield, 1987)
The Sulawesi civet *Macrogalidia musschenbroekii* eats the pulp-covered seeds of the wild sugar palm but only when the fruit is ripe (Wemmer and Watling, 1986). Arenga fruits were also consumed by Kloss gibbons *(Hylobates klossii)* on Siberut, an island off the coast of Sumatra (Whitten, 1980). Consumption of arenga fruits by animals is remarkable because the pulpy mesocarp contains considerable amounts of oxalic acid (Whitten, 1980; Uhl and Dransfield, 1987) in its water-insoluble form, calcium oxalate, which forms needle-like crystals (Uhl and Dransfield, 1987). Even the presence in a fruit of the water-soluble form of oxalic acid (sodium oxalate) would create problems at consumption because sodium oxalate will absorb calcium from the mouth or other mucous covered tissue to form the sharp calcium oxalate crystals (Whitten, 1980). However, during the ripening process the oxalic acid in the arenga fruit is broken down and the ripe fruit can be eaten safely (Wemmer and Watling, 1986).
Arenga pinnata (Wurmb) Merr. (= *Arenga saccharifera* Labillardiere)

The palm is widely cultivated as a source of sugar, wine, fibre, thatch, sago and others (Uhl and Dransfield, 1987).

Borassus
Tall robust tree palms producing large fruits with a smooth exocarp, a thick, fibrous and often fragrant mesocarp and a hard endocarp (Uhl and Dransfield, 1987).
Borassus flabellifer L.

Large fan palm. Produces massive 18 cm fruits (Whitten et al., 1987).

Caryota

Moderate to large palms with globose, 1-2 seeded fruits. Their exocarp is smooth and either dark or brightly coloured, the mesocarp is fleshy and contains needle like crystals and the endocarp is not differentiated (Uhl and Dransfield, 1987).

Caryota mitis Loureiro

Corypha

Massive solitary tree palms found in rather open places and not in the climax forest. The globose one-seeded fruits have a smooth epicarp, a fleshy mesocarp and a thin endocarp (Uhl and Dransfield, 1987).

Corypha elata Roxburg

The flower spikes of this large fan palm project nearly 4.5 m above the top of the palm and set hundreds of thousands of fruits up to 5cm diameter (Whitten et al., 1987).

Gronophyllum

Tall, moderate or small palms found from the lowland forest at sea-level to the mossy mountain forests. The fruits are variable in shape and bright red to purplish black in colour. The pericarp is reasonably smooth, the mesocarp contains abundant tannin cells and fibre bundles and the endocarp is thin (Uhl and Dransfield, 1987).

Gronophyllum selebicum Beccari

Treepalm.

Licuala

Very small to moderate palms of the forest undergrowth. The fruits are variable in shape and usually have a brightly coloured exocarp, a thin to thick, fleshy mesocarp and a thin endocarp (Uhl and Dransfield, 1987).

Licuala celebica Miquel

Livistona

Shrub or tree palms often forming groves. The small to medium fruits are variably coloured and have a smooth exocarp, a thin or thick, fleshy or dry mesocarp and a bony to woody endocarp (Uhl and Dransfield, 1987).

Livistona rotundifolia (Lam.) Mart.

Metroxylon

Robust to massive tree palms of lowland swamps. The rounded, one-seeded fruits have a scale covered exocarp and a rather thick, corky or spongy mesocarp. The endocarp is not differentiated. The seeds are covered in a thin to thick aril (Uhl and Dransfield, 1987).

Metroxylon sagu Rottboel

Sago palm.

Nypa
Large, creeping palms confined to mangrove areas. The fruits have a smooth exocarp, a fibrous mesocarp and a thick endocarp (Uhl and Dransfield, 1987)

Oncosperma
Tall palms with spherical, dark blue-black fruits. Their exocarp is reasonably smooth, the mesocarp thinly fleshy and the endocarp thin. (Uhl and Dransfield, 1987)
Oncosperma horridum Scheffer
Found on hilly sites inland (Uhl and Dransfield, 1987).

Pholidocarpus
Robust treepalms with very large globose fruits. Their exocarp is smooth or warty, the mesocarp thin and somewhat fleshy and the endocarp brittle (Uhl and Dransfield, 1987).

Pigafetta
Massive tree palms and typical pioneer plants. The relatively small fruits have a scale-covered exocarp and a thin mesocarp. The endocarp is not differentiated and the seeds are covered in a thick, sweet aril. (Uhl and Dransfield, 1987)
Pigafetta filaris (Giseke) Beccari
Pigafetta filaris or "wanga" is a Malesian rain forest palm which favours altitudes between 300 and 1000 meters and is very abundant in North Sulawesi. In open forest seedlings can sometimes be found in small clusters suggesting dispersal by birds, squirrels, monkeys or other animals, but they appear not to progress beyond the one leaf stage. It appears that the seedlings are not tolerant of shade which is typical for pioneer plants (Dransfield, 1976; Whitten, 1987).

Pinanga
Very small to robust palms of the forest undergrowth. The fruits are variable in shape and colour and usually have a smooth exocarp, a thin, fleshy, sweet mesocarp and a fibrous endocarp (Uhl and Dransfield, 1987).

Salacca
Minute to rather robust palms of the primary rain forest undergrowth. The fruits are variable in shape with a scaly exocarp and a thin mesocarp. The endocarp is not differentiated. the 1-3 seeds are covered in very thick, sour or sweet tasting arils. The species *S. zalacca* is cultivated for its fruit; the fruits of some other species are also edible but can be very sour (Uhl and Dransfield, 1987).

Rattan palms:

"Rattans are spiny climbing palms belonging to the lepidocaryoid Major Group of the Palm family" (Dransfield, 1979). Most rattans fruits are covered with a scaly exocarp with just a thin dry layer underneath. One of the exceptions is the genus *Korthalsia* where this inner layer develops as a sweet fleshy layer. The fruits do not split open and the exocarp has to be actively removed to uncover the seeds. The seeds of nearly all rattans have a fleshy aril, the thickness of which varies according to the species. It is often sour and astringent but can be sweet and tasty. The arils are usually closely attached to the seeds and can only be eaten by taking the seeds in the mouth, sucking the aril and spitting out the seeds with the remains of the pulp. The fruits are very much sought after by animals (e.g.. monkeys, hornbills etc.) (Dransfield, 1979).

Calamus
Solitary or clustering, short stemmed to high climbing rattans. The fruits are variously shaped and usually contain a single seed covered with a thin to thick aril (Dransfield, 1979).

Daemonorops
Solitary or clustering, short stemmed to high climbing rattans. The fruits are variously shaped and usually contain a single seed covered with a thin to thick, sweet or sour aril (Dransfield, 1979).

Korthalsia
High climbing rattans, frequently branching in the canopy. The fruits have a fleshy wall (Dransfield, 1979).

PANDANACEAE

Freycinetia micrura B.C. Stone

Pandanus
    Giant pandans
Pandanus sarasinorum Warb.
    Climbing pandan (Stone, 1983).

PASSIFLORACEAE

Some members of this family are widely introduced for their fruits but many others are toxic and contain substances like prussic acid, gynocardin and bacterioside (de Wilde, 1972).

Passiflora foetida L.
    An introduced common weed found from sea-level to 1500m. It has yellow to orange coloured subglobose fruits measuring about 2cm in diameter (de Wilde, 1972).

PHYLLOCLADACEAE

Phyllocladus hypophyllus Hort. ex Carr.
Conifer

PIPERACEAE

Piper
Wild pepper
Piper aduncum L.

Piper aduncum is a wide-ranging tree of open sites and forest edges, native to South America but widely naturalised in Malesia and occurring as pure stands of secondary forest in the Dumoga valley. It grows very quickly and mature specimens flower and fruit continuously (Whitmore and Sidiyasa, 1986; Whitten et al., 1987). The fruit is a minute to moderate sized one-seeded berry. (Corner, 1988)As has been found in Central America, almost all the ripe fruits are taken by bats (Whitten et al., 1987).

PITTOSPORACEAE

Pittosporum ferrugineum (Pitt.)

A shrub or small tree of about 9m tall. It produces 1cm wide orange-ochre capsules growing in clusters of 4-12. The seeds are embedded in a red pulp and become detached en masse as the capsule splits in two (Corner, 1988).

PODOCARPACEAE

In this family of conifers, seeds are produced in cones composed of fertile scales positioned in the axils of so-called cone bracts which can either be small scales themselves or be leafy structures. In some instances, the fertile scales or the cone bracts (or both) are fleshy and only a few fertile units are fully developed, thus creating a plum-like fruit, or in other cases a fruit structure resembling the cashew (*Anacardium occidentale* L.). The fleshy fruits are eaten by birds and fruit bats which act as dispersers. In some species the fruits are edible (de Laubenfels, 1986b).

Dacrycarpus
According to Whitmore et al. (1989) *Dacrycarpus =Podocarpus* s.l. However, the revision work on which their Podocarpus list is based (de Laubenfels, 1969) are of an earlier date than the one used for this work (de Laubenfels, 1986b). For this reason, the classification proposed by the latter author (in which *Dacrycarpus* and *Podocarpus* are still kept separate) will be followed here. The seed bearing structures in this genus are built up of a greatly enlarging receptacle which is fleshy and ripens from orange over red to purple and finally brown (de Laubenfels, 1986b).

Dacrycarpus steupi (Wasscher) de laub.
A 4-36m tall conifer tree common in secondary forest and poorly drained areas between mostly 1500-2000m. The mature seeds are 5-6 mm long and 4.5-5.5 cm in diameter (de Laubenfels, 1986b).

Dacrydium
In most species the entire seed bearing structure becomes red in colour, fleshy and greatly enlarged when mature (de Laubenfels, 1986b).

***Dacrydium falciforme* (Parl.) Pilg.**
Shrub or tree 10-15(25)m. Mountain forests.
Dacrydium nidulum de Laub.
A 10-30m tall conifer canopy tree of primary and secondary rainforest mostly found from sea-level to 600m, but going up to 1200m. Small seed bearing structures enclose 4mm long seeds (de Laubenfels, 1986b).
Dacrydium nidulum* de Laubenfels var. *nidulum
Tree 30m. To 1000-1800m.
Dacrydium novo-guineense Gibbs
A 1.5-29m high conifer tree found mostly in open areas between 1500-2200m. Its small seed-bearing structures enclose 5mm long seeds (de Laubenfels, 1986b).

Phyllocladus hypophyllus Hook.f.
Large (up to at least 30m) short-trunked trees found in moist mountain forest from 900m up to the tree line (3200-4000m); with bright red seed cones about 1 cm long (de Laubenfels, 1986b).

Podocarpus
The 7-12 mm long receptacle becomes fleshy and greatly enlarged in most species (de Laubenfels, 1986b).

***Podocarpus amarus* Bl.**
To 60m. Mostly mountains (300)800-2000(3600)m.
Podocarpul blumei* Endl. = *P. wallichianus
***Podocarpus celebicus* Hemsl. = *Taxus celebica* (Warb.) Li,**
***Podocarpus cinctus* Pilger**
Shrub or tree to 30m. Mountains (900)2200-3200(3600)m.
Podocarpus dacrydiifolius* Wasscher = *P. cinctus
***Podocarpus imbricatus* Bl.**
Tree to 30m or more. To 2500m, particularly from 700-1700.
(*Podocarpus koordersii* Pig. ex Koord.)
Tree 14m. To 30m.
***Podocarpus laevis* de Laub.**
Tree to 25m. Lowlands.

Podocarpus neriifolius D. Don

A 5-40 m tall primary rain forest conifer tree found at altitudes up to 2100 with a bright red receptacle (de Laubenfels, 1986b).

(*Podocarpus pilgeri* Foxw.)

Tree to 15m. Mountains 1400-3000m.

***Podocarpus rumphii* Bl.**

Small or medium tree, 30m. Lowlands.

***Podocarpus steupii* Wasscher**

Tree 36m. From 1000 to 3420m.

***Podocarpus wallichianus* Presl**

Tree up to 48m. To 1600m.

POLYGALACEAE

(*Xanthophyllum celebicum* Meijden)

Tree 25m. Malili, endemic.

***Xanthophyllum papuanum* Whitmore ex Meijden**

Tree 43m.

***Xanthophyllum tenuipetalum* Meijden**

Tree to 26m.

PROTEACEAE

Those seeds which are edible are usually covered by a hard endocarp or testa and are therefore not easily accessible. Nevertheless fruits with holes hawed in the hard seed covers have been found and point to predation or dispersal by mammals and/or birds (Sleumer, 1956).

Grevillea elbertii Sleum.

A 10-17m tall tree occurring in dry bush formation from the sea-shore up to 900m. Flowers and fruits can be found in October and June. It fruits in the form of coracious to nearly woody follicles of an obliquely ellipsoid shape. They measure about 3 by 2cm and contain one or two seeds. The fruit is said to have a bitter taste.

Helicia

Mostly trees but occasionally shrubs. Their fruits are nut- or drupe-like with a rather hard and thin pericarp, containing one or two seeds.

Helicia celebica Sleum.

A tree reaching 24m in height, found in rain forests on sandy soil between 450 and 1600m altitude. Flowering and fruiting takes place in April. The fruits are ovoid-ellipsoid, ripening from dirty green to black in colour and measuring about 1.5 by 1.2cm. Its pericarp is thinner than 1 mm. Endemic.

***Helicia kjellbergii* Sleum.**

Tree 20m. Secondary forests. Endemic.

(*Helicia teysmanniana* Sleum.)
Small tree 1700-2600m. Endemic.

Macadamia hildebrandii van Steenis
A primary rain forest tree reaching 3-33m in height and found at altitudes from sea-level to 1700m. It flowers mainly between September and October and fruits from March to April. It has 1-2 fruits per raceme. The green brown fruits are globular with a diameter of 3.5cm. The pericarp is hard, only 2mm thick and encloses a globular, purple brown seed measuring 3 cm across. A common name for the fruit is the "Celebes nut". The seeds of the Celebes nut are probably just as tasty as those of the commercial Queensland nut (Sleumer, 1956). **Endemic.**

The above species is typical for Sulawesi, but the two Australian species *Macadamia ternifolia* F.M. and *Macademia tetraphylla* Johnson are widely cultivated in Australia, Malaysia and other tropical regions as a fruit tree or ornamental tree (Sleumer, 1956). It is therefore possible that these species also occur on Sulawesi in cultivated and/or naturalised conditions.
Macadamia ternifolia F.M.
Tree reaching 5-15(-20)m in height which flowers from May to October and fruits from January to February. Its fruits are green, globose (2.5cm diameter) and have a 2-3mm thick pericarp. They usually contain one hard, globular seed, with thick (2-4(-5)mm) testa. The nuts contain 70% oil and are similar shaped to hazelnuts but have a very hard shell. The flavour of the nut is said to have a finer aroma then the hazelnut (Sleumer, 1956).
Macademia tetraphylla Johnson
High shrub to medium sized tree reaching 5-15m in height. Flowers are present from September to October and fruits from January to February. The fruits are brownish in colour and globose (1.5-2cm diameter) in shape (Sleumer, 1956).

RHAMNACEAE

***Alphitonia incana* (Roxb.) Hatusima**
Shrub or tree to 30m. Secondary forest.
(*Alphitonia zizyphoidea* (Spreng.) Gray)
Small tree.

Colubrina
Trees or shrubs producing subglobose capsules with membranous pericarp (Latiff, 1989).

(*Columbrina asiatica* Brongn.)
Scrambler or small tree.

(Colubrina javanica **Miq.)**
Shrub.
***Colubrina peduculata* Baker**
Tree to 30m.

Zizyphus
Treelets, shrubs or lianas with fleshy drupes (Latiff, 1989).

Zizyphus angustifolia (Miq.) Hatusima ex Steen
Lowland tree (33m) with red, 1.4-2.2 cm long one-seeded berries (Latiff, 1989).
***Zizyphus celtidifolia* DC.**
Climber or tree to 21m.
(*Zizyphus crebivenosa* C.B. Rob.)
Shrub.
(*Zizyphus jujuba* Lamk.)
Small tree. Malesia. Often cultivated.
Zizyphus mauritiana Lam.
Called Z. *jujuba* in other publications but that name should be reserved for the Chinese Jujube. A small (to 12m) evergreen tree with about 2.5cm long single-seeded apple shaped fruits. It is cultivated world wide for its edible fruit, the jujube, which tastes like a sour-sweet apple (Latiff, 1989; Corner, 1988).
Zizyphus oenoplia Mill.
A 1-5m high thorn bush with 1cm wide black berries (Corner, 1988).

RHIZOPHORACEAE

Mostly mangrove species with fruits in the form of berries, drupes or (rarely) capsules

Bruguiera cylindrica (L.) Bl.
An up to 23m mangrove tree not occurring at altitudes more than 20m above sea-level. Not much information could be found on the fruits but the hypocotyls reach 8-15cm in length and 5mm in diameter before falling (Ding Hou, 1954). *Bruguiera* has a similar germination system than *Rhizophora* but the seedling disconnects from the parent tree at the height of the fruit stalk. It is therefore the seedling with the remains of the fruit that fall onto the surface (Whitten et al., 1987).
Bruguiera gymnorhiza (L.) Savingny
A tall mangrove tree reaching up to 36m in height and often dominating as a tall forest. Its fruits are about 2cm long and the hypocotyls grow up to 15-25cm in length and 2cm in diameter before the seedling falls to the ground. People in the Moluccas are said to eat the leaves and pealed hypocotyls after soaking them in water and boiling them (Ding Hou, 1954).

Bruguiera parviflora (Roxb.) W. & A. ex Griff.

An up to 24m high tree which occasionally occurs in pure stands and is mostly found on the inner side of mangroves. The tube formed by the fruit and the remains of the outer layer of the flower bud measures about 1.5-2cm long. The hypocotyl reaches 7.5-13cm in length, 0.5cm in diameter before the seedling falls from the tree (Ding Hou, 1954)

Bruguiera sexangula (Lour.) Poir.

A tall mangrove tree reaching up to 33m in height and often dominating as a tall forest. The hypocotyls grow up to 6-8cm in length and 1.5cm in diameter before the seedlings fall from the tree. The fruits are eaten by the people of Sulawesi after soaking them in water and boiling them. (Ding Hou, 1954).

Carallia brachiata (Lour.) Merr.

A large tree up to 50m tall, found in rain forests and edges of fresh water swamps up to 1800m altitude. It has pulpy globose fruits with a diameter of about 7mm (Ding Hou, 1954).

Ceriops decandra (Griff.) Ding Hou

This small tree (15m) can be found at edges of the mangrove swamps. It produces ovoid-conical fruits measuring about 1.5cm in length with hypocotyls growing up to 15-20cm long before the seedling falls down (Ding Hou, 1954).

Ceriops tagal (Perr.) C.B. Rob.

A small shrub growing up to 15(-25)m and found on well drained soils in inner mangrove forests. Its fruits are ovoid in shape, measuring 1.5-2.5cm long and have hypocotyls growing as long as 15-25cm before the seedling falls (Ding Hou, 1954).

Gynotroches axillaris Bl.

A 1-2m high shrub or a tree sometimes reaching heights of up to 15-30m. It frequents swampy places in rather open parts of primary and secondary forest at altitudes up to 2250m. It fruits in the form of small globose berries of about 3mm in diameter ripening from red to shiny black (Ding Hou, 1954).

Pellacalyx pustulatus Merr.

A primary forest tree reaching up to 18m in height and growing at altitudes up to 900m. Its berries are globose and measure 12-15mm in diameter (Ding Hou, 1954).

Rhizophora apiculata Bl.

An estuary tree reaching over 30m in height. Its fruits have an inversed pear shape and are 2-2.5cm long. In Rhizophora, the seed germinates within the ripe fruit while this is still hanging on the tree. The cotyledons (the first leaves of the embryo) remain within the seed while the root (hypocotyl) that is produced grows down from the fruit. The hypocotyl in *R. apiculata* can grow up to 38cm long and 12mm in diameter before the seedling (composed of the root and a leaf bud) falls down by disconnecting itself from the remainder of the fruit which is still hanging on the tree (Ding Hou, 1954; Whitten, et al., 1987; Sugden, 1992).

Rhizophora mucronata Poir.

A 27 m tall estuary tree producing 5-7 by 2.5-3.5cm large fruits with hypocotyls growing up to 36-64cm long and 1.75cm in diameter before the seedlings fall (Ding Hou, 1954).

Rhyzophora stylosa Griff.

This small (10m) tree is found exclusively along sandy shores and corral terraces. The mature fruits measure up to 2.5-4 by 1.5-2.5cm and the hypocotyls can grow up to 54cm long and 16mm in diameter before the seedlings fall (Ding Hou, 1954).

ROSACEAE

Acioa = Kostermanthus

Kostermanthus heteropetala (Scort. ex King) Prance

A big tree (36m) **from low undulating country** with hard drupes splitting at germination (Prance and Whitmore, 1973).

Maranthes corymbosa Bl.

A large tree (39m) of mainly coastal areas **(occasionally to 500m)** producing large (3 cm long) oblong-ellipsoid, black, fleshy, drupes with a hard endocarp (Prance and Whitmore, 1973).

Parinari laurinum A. Gray

Lowland tree to 25m, the fruits of which are large fleshy drupes with a thick and hard endocarp which are eaten by a number of vertebrates including pigs and monkeys (Prance and Whitmore, 1973).

Potentilla leuconota D. Don

Herb

Potentilla parva Frivald. ex Hampe, = *P. hirta* Haenke,

Herb

Prunus

Trees or shrubs with fruits in the form of drupes. The pulpy mesocarp is usually quite thin in wild species and encloses a woody or bony stone with one seed (Prance and Whitmore, 1973; Corner, 1988; Kalkman, 1993).

Prunus arborea (Bl.) Kalkman

An up to 35m tall tree, **rarely a shrub. Mostly lowlands; to 1300m.** The thinly pulpy fruits measure 5-11.5 by 7-17mm and are red, purple or black when ripe. (Prance and Whitmore, 1973; Corner, 1988; Kalkman, 1993).

Prunus clementis **(Merr.) Kalkman**

Tree to 30m. Primary and secondary forest to 1050m.

(*Prunus grisea* (Blume ex C. Muell.) Kalkman)

Shrub or small tree. Lowlands and mountains.

Prunus javanica **(T. & B.) Miq.**

Tree to 35m. Primary and secondary forest, 0-1200m.

Pygeum* = *Prunus
Pygeum latifolium **Miq. =** ***Prunus grisea***
Pygeum parviflorum **T. & B. =** ***Prunus arborea*** **(Blume) Kalkm.**

Rubus

Shrubs, containing tannins and therefore used to cure diarrhoea and soar throats. The fruits of all species are edible but not all as tasty as those of the familiar European blackberry *Rubus fruticosus*. (Kalkman, 1993).

Sanguisorba minor Scop.

A 0.5m tall herb found in Europe, northern Africa, western Asia and introduced and naturalised in North America. It is sometimes cultivated as potherbs in the mountains of Java. In Europe the leaves are used as vegetables in soups or salads. (Kalkman, 1993)

RUBIACEAE

This is the 5th biggest family of flowering plants after the Orchidaceae, Compositae, Leguminosae and Gramineae and show an enormous variation in its appearance and its fruits and flowers. Many of its members produce products of economical importance e.g. coffee and quinine (Corner, 1988; Wong, 1989). Mostly shrubs and small trees, a few herbs. Only a very few timber-size, spp., mostly in Tribe Naucleae which has been revised by Ridsdale, Blumea 24(1978)307-66. All forest types, lowlands and mountains.

Adinauclea fagifolia (Teys. & Binn.) Ridsd.

(= *Adina fagifolia*) A large tree with fruits in the form of individual fruitlets with a hard endocarp. (Ridsdale, 1978)

Anthocephalus chinensis **(Lamk.) A. Rich. ex Walp.**

Medium tree Locally common in lowland secondary forest, especially on alluvium. Perhumid climates.

Anthocephalus macrophyllus **(Roxb.) Havil.**

Medium tree Secondary forest, often gregarious. Grows faster than *A. chinensis*.

Canthium

Possibly has some big tree species.

Hedyotis sp.
Small tree

***Hymenodictyon* (Roxb.) Mabberley**
Tree to 35m.

Lasianthus spp.
Lasianthus capitatus Blume,
Lasianthus stercorarius Blume,

Morinda
Small trees or climbers with fruits fused together in fleshy heads (=composite fruits or syncarps). Although the fruits are edible, some have a very unpleasant smell when ripe (Corner, 1988; Wong, 1989).

Morinda tinctoria Noroha,

Mussaendopsis beccariana Baill.
An up to 35m tall tree with fruit in the form of obovoid, splitting capsules filled with small (2-4mm) seeds. It is found in fairly wet areas of the lowland forest (Wong, 1989).

Myrmecodia
(Epiphytic on trees. van Balgooy and Tantra, 1986).

Nauclea
Medium to large trees with fruits in the form of composite heads that become woody in character and are indehiscent. They contain non-winged seeds (Corner, 1988; Wong, 1989).

***Nauclea digitata* Blanco = *Schefflera blancoi* Merr.**
***Nauclea orientalis* (L.) L.**
Medium tree. Lowlands, usually riverine.
Nauclea subdita (korth.) Steud.
A small or medium tree (to 25m) of swampy, **usually riverine** places in lowland to hill forest and in rice fields. The fruiting heads measure 8-20mm in diameter (Wong, 1989).

Neonauclea
Fruits in the form of individual dehiscent fruitlets with a hard endocarp containing seeds with short wings or with little tufts of hair (Ridsdale, 1978; Wong, 1989).

***Neonauclea* sp.**
Big tree 50 m. Locally common Toraut, Dumoga-Bone National Park. Swollen hollow ant-inhabited twigs. Apparently a new species. (Whitmore & Sidiyasa TCW 3502, BZF, BO, K, L).

Neonauclea bunnermeyeri **Ridsdale unpublished**

Tree 38m.

Neonauclea celebica **Koord. ex Ridsdale**

Tree 40m.

Neonauclea havilandii **Koord. ex Ridsdale**

Neonauclea rubaensis **Ridsdale**

Neonauclea unicphala **Ridsdale**

Tree 20m, rheophyte when young.

Randia

Green, yellow or brown indehiscent fruits measuring about 2.5cm with a sometimes pulpy wall. The thick, woody endocarp encloses numerous seeds (Corner, 1988).

Randia pulcherrima Merr.

Timonius

Shrubs, treelets or trees with fruits in the form of round to oblong berries with many small woody seeds (Corner, 1988).

Timonius sericeus Schum.

Wendlandia

Some species reach 20m.

RUTACEAE

The 'Citrus Family'. The fruits can be capsules, berries, drupes or composed of separate follicles but the most typical citrus fruits are very pulpy berries where to pulp is formed of large juice(=citric acids and/or sugary sap with some oil droplets)-containing vesicles. This family is a source of many edible fruits (Stone, 1972).

Acronychia laurifolia **Bl. =** ***A. pedunculata***

Acronychia pedunculata (L.) Miq.

Shrub or tree to 28m. Primary and secondary forest lowlands to mountains, 2200m. Fruits usually subglobose, yellowish or white in colour and 5-15 mm wide. Exocarp and mesocarp together are about 0.5-3 mm thick, the mesocarp is subwoody and the endocarp cartilagous (Hartley, 1974).

Acronychia porteri **HK. f. =** ***Maclurodendron porteri*** **(Hk.f.) T.G. Hartley**

Acronuchia trifoliolata Zoll. & Mor. var. *trifoliolata*

Tree to 25m. Lowlands to mountains. Fruits usually subglobose and 5-13 mm wide. Exocarp and mesocarp together are about 0.3-2 mm thick, the mesocarp is subwoody and the endocarp cartilagous (Hartley, 1974).

Citrus

Rather small widely cultivated trees with fruits like an orange or lemon: "outer wall glandular, aromatic, orange, yellow or green, inner wall white, pithy, containing segments themselves containing both seeds and stalked spindle shaped juice-filled pulp vesicles" (Stone, 1972).

Citrus aurantifolia (Christm.) Swingle

Tree. Fruits green, globose, 2.5 cm in diameter and very sour tasting. Cultivated and perhaps wild in Malaya (Stone, 1972).

(*Citrus celebica* Koord.)

Small tree to 5m. Lowland forest.

Citrus grandis (L.) Osbeck

Tree. Fruits large, up to 18 cm in diameter with bland tasting not very juicy pulp. Cultivated (Stone, 1972).

Citrus hystrix DC.

Shrub or tree to 12m. Fruits round, 4-6.5cm in diameter with sour, bitter slightly fragrant yellowish-green pulp. Cultivated but probably also wild (Stone, 1972; Corner, 1988).

Citrus medica L.

Fruits lemon shaped, 5-7.5cm wide with yellow-white fragrant, sour but not bitter pulp. Cultivated and doubtfully wild (Stone, 1972; Corner, 1988).

Euodia sp

Usually mis-spelled *Evodia*. Trees or shrubs with fruits in the form of small dehiscent capsules (Stone, 1972; Corner, 1988). **Most spp. now considered to belong to *Melicope*..**

Euodia aromatica Pers.

Glycosmis

Small trees or shrubs with small few-seeded dry or juicy berries (Stone, 1972; Corner, 1988).

***Glycosmis cyanocarpa* (Bl.) Sprengel**

Small to medium trees.

Melicope

About 14 spp., 5 reach timber size.

Micromelum

Fruits red to orange 1-2 seeded dryish berries (Stone, 1972; Corner, 1988).

***Micromelum minutum* (Forst. f.) W. & A.**

Tree.

Micromelum pubsecens* Bl. = *M. minutum

Tetractomia
Trees or shrubs with fruits in the form of follicles filled with winged seeds (Stone, 1972).

Tetractomia barringtonioides **Hartley**
Tree 30m. Lowlands. Malili, endemic.
Tetractomia tetrandrum **(Roxb.) Merr.**
Tree to 27m. Lowlands to mountains 3300m.

Zanthoxylum
Trees, shrubs or climbers with fruits in the form of single or lobed follicles containing one black seed (Stone, 1972; Corner, 1988).

Zanthoxylum celebicum **Koor.**
Tree to 35m. Lowlands.
Zanthoxylum limonella **(Dennst.) Alston**
Tree to 35m. Lowlands, dryish forests.
(*Zanthoxylum nitidum* (Roxb.) D.C.)
Shrub, generally climbing. Lowlands to mountains 1100m.
Zanthoxylum rhetsa (Roxb.) D.C. = *Z. limonella*

SABIACEAE

Meliosma pinnata (Roxb.) Walp.
Big tree 42m. Forests to 3000m.
Meliosma sumatrana (Jack) Walp.
Tree 15-20(25)m. Primary and secondary forest, to 2200m.

SANTALACEAE

Santalum album L.
Low branching tree occasionally reaching 15(20)m, root parasite. Lowland monsoon forests. Native to C. Sulawesi (Paboya).
Sandalwood; very fragrant wood. Fruits black-red, ellipsoid, 1cm long drupes. (Backer and Bakhuizen van den Brink, 1965)

SAPINDACEAE

The fruits are very variable but characteristic for each genus; they can either be capsules, drupes or nuts. The seeds they enclose are sometimes provided with a fleshy aril. Economically important fruits of the family are among others rambutan and litchi (Corner, 1988; Yap, 1989).

Aphania* = *Lepisanthes

Arythera littoralis Bl.

An up to 30m lowland forest tree. Fruits measuring about 1.5-1cm with a leathery pericarp enclosing a single seed 3/4 covered with a red aril. (Yap, 1989)

***Cublia cubili* (Blanco) Adelb.**

Tree to 25m. Primary and secondary forest, lowlands.

Dimocarpus longan Lour. ssp. *malesianus* Leenh. var. *malesianus*

A tree up to **40m** tall, **sometimes a shrub**, found in cultivation and in primary lowland forest. The fruits measure about 1.6cm in diameter and enclose seeds enveloped by fleshy white arils. The aril is eaten raw and is quite popular (Yap,1989).

Euphoria* = *Dimocarpus

Ganophyllum falcatum Bl.

A coastal tree, up to **40m** high **mainly in monsoon forest, also in rain forest**. The fruits are red, ovoid 10 by 8mm drupes with a single seed. (Yap,1989)

Harpulia arborea (Blanco) Radlk.

An up to **33** m high lowland forest tree **to 1200m**. Its fruits are leathery 2-lobed capsules spreading 2-4cm across and enclosing seeds with an aril covering their basal region (Yap,1989).

Harpulia cupanioides Roxb.

An up to **20(-40)**m high tree **sometimes a shrub** found at the forest- and river edges of lowland forest **up to 1200(-1800)m**. The large fruits are capsules which measure 18 by 20cm and envelope seeds almost entirely covered with arils (Yap,1989).

Lepisanthes

Small trees or shrubs, some with edible fruits (Yap,1989).

***Lepisanthes falcata* (Radlk.) Leenh.**

Tree to 22m. Forest up to 1500m.

Lepisanthes fructicosa (Roxb.) Leenh.

Shrub or treelet (6m) found on slopes at **forest edges and open vegetation,** 100-1000m. The red, 3-lobed fruits contain seeds with sweet, fleshy arils (Yap, 1989).

Lepisanthes rubiginosa (Roxb.) Leenh.

The up to 10 high tree produces edible fruits and is found cultivated on roads and in villages. It is also found wild in coastal forests just behind the beach and in secondary forest. The fruits ripen from yellow over orange, red, and purple to nearly black (Yap,1989).

Lepisanthes senegalensis (Poir.) Leenh.
Up to **24** m high shrubs and small trees in **light forest and forest edges, lowlands.** Fruits ripen from green to yellow (Yap,1989).

Lepisanthes tetraphylla **(Vahl) Radlk.**
Shrub or tree to 23m. Lowland, forest as well as more open vegetation.

Mischocarpus sundaicus Bl.
Shrub or treelet, up to 6m tall tree **rarely to 30m** of sandy coasts, islands, estuaries or coastal swamps, and **lowland forest to 2000m.** The fruits are pear-shaped and measure 1.5 by 0.7cm. The wall of the fruit splits into 3 parts thereby exposing the single shiny brown seed engulfed by a thin, red, waxy pulpy layer (Corner, 1988; Yap,1989).

Mischocodon = Mischocarpus

Nephelium lappaceum L. var. *pallens* (Hiern.) Leenh.
Tree to 44m found in lowland forest and seasonal swamps up to 400m, but is also cultivated throughout Malesia for its fruit better known as rambutan. The fruit pericarp is red or yellow in colour and covered with long appendages. The fruit measures 5 by 3.5cm and encloses a seed covered with a white sweet or sour tasting pulpy aril (Corner, 1988; Yap,1989).

Paranephelium
Small to medium sized trees which produce dehiscent fruits with a thick woody pericarp usually enclosing a single seed without aril. Some seeds are edible (Corner, 1988; Yap,1989).

Pometia pinnata Forst. f. Glabra (Bl.) Jacobs
An up to 50m tall tree found **mainly lowland** along rivers **but up to 1700m** in hill forest. It produces indehiscent, 2.8 by 2.2cm large, red fruits with a thin pericarp enclosing a black seed covered by a sweet fleshy aril (Corner, 1988; Yap,1989).

Tristiropsis acutangula **Radlk.**
Tree to 50m. Swamp forest, lowlands.

SAPOTACEAE

The trees of this family have a white latex in their bark and sometimes also in the leaves, flowers and young fruits. The fruits are fleshy indehiscent berries with large hard seeds. The fruits of a number of wild species are edible but they are small and of little value to man. They are sought after however by monkeys, squirrels, fruit bats and civets (Ng, 1972; Corner, 1988).

Chrysophyllum lanceolatum (Bl.) DC.
nonn *C. lanceolatum* Cesar = *C. roxburghii*
Chrysophyllum roxburghii G. Don
Tree 15-55m. Lowland forest to 200m. The round fleshy fruits measure 2.5-4cm in diameter and enclose up to 5 largish seeds (Ng, 1972; Corner, 1988).

Madhuca
Seeds have little or no endosperm but thick cotyledons (Ng, 1972; Corner, 1988).

***Madhuca betis* (Blanco) MacBridge**
Tree 43m.
***Madhuca burckiana* (Koord.) H.J. Lam**
Tree 35m. Lowlands to 1000m.

Manilkara
Ovoid fruits containing 1-6 endosperm-rich seeds (Ng, 1972; Corner, 1988).

Manilkara celebica H.J. Lam
Tree 27m. Lowland forests. Banggai, endemic.
***Manilkara fasciculata* (Warb.) H.J. Lam**
Tree 35m. Lowlands.
Manilkara kauki (L.) Dubard
Evergreen tree **25m** producing 3 by 2 cm large, reddish, edible fruits with 1-6 largish seeds (Ng, 1972; Corner, 1988).

Mimusops elengi L.
An up to 15m high evergreen tree producing 2.5 by 2cm large, reddish, ovoid fruits with 1-2 seeds embedded in a floury yellow flesh. The fruits are edible but astringent (Ng, 1972; Corner, 1988).

Palaquim
Medium to very large trees with oblong fruits containing 1-3 seeds (Ng, 1972; Corner, 1988).

***Palaquium amboinense* Burck Tree 40m.**
Lowlands.
(*Palaquium calophyllum* (Teys et Binn.) Pierre)
Tree 15m. Lowlands along rivers, to 200m.
***Palaquium leiocarpum* Boerlage**
Tree 25m. Lowlands.
***Palaquium maliliense* van Royen**
Tree 30m. Lowlands Endemic.
Palaquim obovatum (Griffith) Engler
Lowland- and secondary forest tree up to 36m tall producing 2.5 by 2cm large ovoid to ellipsoid fruits which are rather pulpy when ripe.

The fruits contain 1-2 seeds without endosperm but with thick cotyledons (Ng, 1972; Corner, 1988).

Palaquim obtusifolium (Sapo.)

Tree to 45m. Lowland forests. The fruits are eaten by macaques on Sulawesi (Watanabe and Brotoisworo, 1982).

***Palaquium quercifolium* (de Vriese) Burck**

Tree to 40m. Lowland forests.

***Palaquium ridleyi* K. & G.**

Tree 30m. Lowland swamp and peat swamp forests.

***Palaquium rostratum* (Miq.) Burck**

Tree to 60m, 120(200)cm. Swampy forests at low altitudes.

Planchonella

Seeds with abundant endosperm (Ng, 1972).

***Planchonella duclitan* (Blanco) Bakh. f.**

Tree to 50m.

Planchonella firma (Miq.) Dubard

An up to **35m** high tree found in mossy mountain forest at altitudes between **600-1500m**. The 2 by 0.7 cm large obovoid fruits usually contain one seed (Ng, 1972).

***Planchonella linggensis* (Burck) Pierre**

Tree to 33m.

***Planchonella moluccana* (Burck) H.J. Lam**

Tree 8-35m. Lowlands to mountains.

Planchonella nitida* (Bl.) Dubard = *P. duclitan

***Planchonella obovata* (R. Br.) Pierre**

Tree to 40m.

***Planchonella obovoidea* H.J. Lam**

Tree to 35m.

(*Pouteria ?celebica* Erlee)

Small tree, 8m. To 800m. Endemic.

***Pouteria macrantha* (Merr.) Baehni**

Tree, 40m. To 500m.

***Pouteria malaccensis* (Clarke) Baehni**

Tree to 40m. Lowlands to 360m.

SARCOSPERMATACEAE

***Sarcosperma paniculatum* (King) Stapf et King**

Medium to big tree, 12-27m. Lowlands.

SIMAROUBACEAE

Generally trees and shrubs of the lowland forest. The fruits are usually in the form of pulpy drupes but some species have samaras (Kochummen, 1973b; Corner, 1988).

Ailanthus

Fruits in the form of long winged nuts or samaras (Kochummen, 1973b; Corner, 1988).

Ailanthus integrifolia Lamk.

Tree 60m. Lowland to 900m.

Ailanthus triphysa (Denst.) Alston

Tree, 18m. Lowland forest

Picrasma javanica Bl.

An up to 24m large tree with fruits in the form of red or blue ovoid drupes measuring 9 by 7-10 by 12mm. (Kochummen, 1973b). **Scattered, (0-1500)m.**

Quassia indica (Gaertn.) Nooteboom

Shrubs or trees up to 20 m high with bunches of 1-4 flattened fruits. (Kochummen, 1973b). **Lowland forest.**

SONNERATIACEAE

Duabanga moluccana Bl.

A 25-35m tall tree found in evergreen forests at altitudes between 60 and 1200m. The fruits are in the form of pulpy, ovoid-oblong capsules, 2.5-3.0cm long, containing five 6 mm long seeds (van Steenis, 1948c).

Sonneratia alba J. Smith

This 3-15(-40)m high tree has a preference for salt water and frequents shallow parts of calm seas, seashores and tidal creeks. Its berries are about 3cm high and 4cm broad and rest on the calyx tube (van Steenis, 1948c).

Sonneratia caseolaris (L.) Engl.

A 5-20m high tree found in the less salty parts of mangrove forests on a deeply muddy soil. It also often grows along tidal creeks with slow moving water. The ripe berry is green, 3-4cm high and 5-7.5cm broad, and rests on the flattened calyx-tube. The young berries have a sour taste and are eaten by the local people. The species is also found on the island of Buru (van Steenis, 1948c).

Sonneratia ovata Backer

Small or medium sized tree, 2-5(-20)m high. It is found on muddy soil in the less salty parts of tidal forests and along tidal creeks. The ripe berries are 3.00-4.75cm broad and 2.5-3.5cm high (van Steenis, 1948c).

SPHENOSTEMONACEAE

***Sphenostomon papuanus* (Ltb.) Steenis & Erdtman**

Treelet or tree to 24m. Mountains, mainly 800-3000m.

STAPHYLEACEAE

Bischofia javanica **Bl.**
Big tree to 30m. Lowland to montaine forests, often riverine.
Turpinia laxiflora **Ridley =** ***T. sphaerocarpa***
Turpinia pomofera **(Roxb.) DC.**
Tree to 20m. 0-2100m.
Turpinia sphaerocarpa **Hassk.**
Tree to 24m. Lowlands to montaine forests to 2000m.

STERCULIACEAE

Heritiera
Medium to large trees with fruits in the form of samaras (Kochummen, 1973c; Corner, 1988).
Heritierra arufurensis **Kosterm.**
Tree 20-45m. Lowland forests.
Heritiera borneensis **(Merr.) Kosterm.**
Tree to 34m. Lowland forest.
Heritiera javanica **(Bl.) Kosterm.**
Tree to 45m. Lowlands.
Heritiera littoralis **Aiton**
Tree to 25m. Common on sandy and rocky coasts and behind mangrove swamps.
Heritiera silvatica **Vid.**
Tree. Lowlands
Heritiera trifoliolata **(F. v. M.) Kosterm.**
Tree 20-30m. Lowlands to 2000m.

Kleinhovia hospita L.
An up to 20 m tall tree found in reasonably open country such as river banks and secondary forest. The fruit is a bladder-like 5-chambered capsule measuring 2-2.5 cm across with 1-2 seeds in each capsule (Kochummen, 1973c).

Melochia umbellata (Houtt.) Stapf
An up to 10 m high tree with fruit in the form of 8 mm long 5-lobed capsules (Kochummen, 1973c).

Pterocymbium javanicum R. Br.
Fruits in the form of clumps of 4 to 6 winged follicles. (Kochummen, 1973c). **Medium tree. Lowlands to 550m.**
Pterocymbium tinctorium **(Blco) Merr. =** ***P. javanicum***

Pterospermum
Fruits in the form of woody capsules containing many winged seeds (Kochummen, 1973c).

Pterospermum celebicum Miq.

Tree 40m.

***Pterospermum subpeltatum* C.B. Rob.**

Tree 20m.

Pterygota

Fruits in the form of woody, dehiscent pods containing many winged seeds (Kochummen, 1973c; Corner, 1988).

***Pterygota horsfieldii* (R. Br.) Kost.**

Tree 40m.

Sterculia

Trees or shrubs with leathery fruits positioned in clusters of 1-5 on a common stalk. The pink or scarlet fruits split open to expose the black seeds hanging from the split edges. The seeds have a thin layer of pulp. The dark seeds contrasting with the brightly coloured fruits are likely to attract various animal dispersers (Kochummen, 1973c).

***Sterculia ceramica* R. Br.**

Tree 24m. Primary forests 0-100m.

***Sterculia comosa* Wall.**

Tree 40m. Primary forest

(*Sterculia coccinea* Jack)

Shrub or small tree to 10m. To 1500m.

Sterculia foetida L.

An up to 30 m tall tree found on rocky sandy coasts and to 1000m. The woody, red fruits are roundish in form, measure about 10cm long and grow in clusters of 2-5. The 2.5cm long dark seeds with a little yellow waxy lump on the end are eaten as nuts (Kochummen, 1973c).

***Sterculia insularis* R. Br.**

Tree to 30m. Primary forest, 0-1000m.

***Sterculia kostermansiana* Tantra**

Tree 25m. Primary forest, 0-300m. Endemic.

***Sterculia macrophylla* Vent.**

Tree to 40m. To 900m.

***Sterculia oblongata* R. Br.**

Tree to 50m. 0-1560m.

***Sterculia rubiginosa* Vent.**

Tree to 20m. To 1600m.

***Sterculia sangirensis* Warb.**

Tree.

***Sterculia stipulata* Korth.**

Tree to 20m. Lowland primary and secondary forest.

***Sterculia urceolata* J. Smith**

Tree to 30m. Primary or secondary forest, 0-200m.

Tarrietia = Heritier

STYRACACEAE

Bruinsmia styracoidea Boerl. & Koord.
Tree 15-37m. (400-)700-1600m.

SYMPLOCACEAE

(*Sympolocos adenophyllla* Wall. ex Don.)
Shrub or small tree 15m. Lowlands to mountains.
Symplocos celastrifolia Griff. ex Clarke
Small tree to 30m. Lowland forests.
Symplocos cochinchinensis (Lour.) S. Moore
Small shrub to large tree. Lowland to mountain forests.
ssp. *cochchinchinensis* var. *philippinensis* (Brand) Noot.
Tree 25m. To 2000m.
(ssp. *laurinum* (Retz.) Noot. var *laurinum*)
Shrub 3m, to tree 6-14m. To 2000m.
Symplocos laeteviridis Stapf
Tree to 10(-21)m. Hill and mountain forest.
Symplocos maliliensis Noot.
Tree to 25-30m. Lowlands. Endemic.
Symplocos odoratissima (Bl.) Choisy ex Zoll.
Tree to 30m. Lowland forest.
Symplocos ophirensis Clarke
Tree to 18m. Lowland and hill forests to 350m.
(*Symplocos pendula* Wight)
Shrub or small tree. Mountain forests.
Symplocos polyandra (Blanco) Brand.
Tree 30m. Lowland primary and secondary forest.

TAXACEAE

Taxus sumatrana (Miq.) de Laub.
A large (45m), slow growing tree found in moist subtropical and mossy tropical forests at altitudes between 1400-2300m. The 6 by 5 by 4mm large seed is cupped by a fleshy bright red aril. (de Laubenfels, 1986c)

THEACEAE

Adinandra brefeldii Koord.
Tree 43m. Lowlands. Endemic.
Adinandra celebica Koord.
Tree 25m. Endemic.
Gordonia amboinensis (Miq.) Merr.
Tree 20(25)m. Lowlands to mountains 50-2000m.

Gordonia integerrima (Miq.) Keng

Tree 18-30m. 1000-1850m

THYMELAEACEAE

Plants in this family are mostly trees with fruits either in the form of woody thick-walled dehiscent capsules or thin-walled, possibly indehiscent capsules. In both cases the capsules contain large seeds, usually provided with an aril.

Gonystylus macrophyllus (Miq.) Airy Shaw

This large tree with a height of up to 45m can be found in primary forests at low to medium **(1200m)** altitudes. It flowers in September and from December to April. Fruits are present from May to June. The fruit is a large, globose and dehiscent woody capsule with a diameter of up to 7cm. The seeds are large (4 by 2.5cm), semi-ellipsoid in shape and have large horny cotyledons and a thin dorsal aril arising from the fleshy seed stalk (Airy Shaw, 1948).

(*Gyrinops dicipiens* Ding Hou)

Small tree 4m. Lowlands forest to 100m. Endemic.

***Gyrinops vresteegi* (Gilg) Domke**

Tree 21m. Lowlands forest to 900m.

Phaleria capitata Jack,

TILIACEAE

Grewia

Trees, shrubs or climbers producing fleshy or pulpy drupes containing 1-4 stones each with 1-2 seeds. Some species have edible, juicy, but acid tasting fruits (Kochummen, 1973d).

(*Grewia acuminata* Juss.)

Scrambler, shrub or tree. Sometimes secondary, sometimes seasonal forest.

(*Grewia celtidifolia* Juss.)

Small tree 7m.

(*Grewia eriocarpa* Juss.)

Tree 14m.

***Grewia glabra* Bl.**

***Grewia multiflora* Juss.**

Tree to 20m, or shrub. Primary forest.

(*Grewia retusifolia* Kurz)

Shrub.

Microcos* see *Grewia

Pentace

Fruits in the form of samaras with multiple wings (Kochummen, 1973d).

Pentace adenophora **Kost.**

Tree 25-35m. Lowlands.

Pentace polyantha **Hassk.**

Tree to 40m. To 1000m.

Trichospermum

The fruits are roundish, flattened capsules containing many seeds provided with long hairs (Kochummen, 1973d).

(*Trichospermum pleiostigma* **(Fiv. M.) Kost.)**

Tree to 33m. Lowlands.

Trichospermum talaudensis **Kost.**

Tree(?) 250m. Talaud.

Trichospermum kjellbergii **Burret**

Tree. Endemic.

TRIMENIACEAE

Trimenia papuana **Ridl.**

Tree to 20m. Lowlands to mid-montane forest.

ULMACEAE

Aphananthe cuspidata (Bl.) Planch.

A 30m tall tree found in areas with a pronounced seasonal climate. **It grows on lowlands to sub-montaine forests (to 1300m).** Its fruit ripens from June to July and again from November to December. The deep red, ovoid-globose fleshy drupes with hard endocarp are almost certainly dispersed by birds (Soepadmo, 1973).

Celtis

The fruits of members of this genus are orange, red or bluish black fleshy drupes composed of a thick and firm exocarp, a thin and fleshy mesocarp which contains slimy substances and a hard endocarp (Soepadmo, 1973). These are the typical characteristics of fruits specialised in dispersal by birds (Gauthier Hion et al, 1985) and it is therefore possible that the Celtis fruits are dispersed in this way (Soepadmo, 1973).

Celtis philippensis Blanco

An up to 30m high understorey tree in primary and secondary forest at altitudes between 0 and 650m. The orange to red ovoid fruits measure about 8-15 by 7-12mm and have a thin (1mm) exocarp. Flowering and fruiting takes place from July to April (Soepadmo, 1973).

Celtis rigescens (Miq.) Planch.

A large tree (up to 45m) of primary and secondary forest between sea-level and 1800m. The deep red ellipsoid drupes (about 15 by 10mm large) have 2-3mm thick rather woody exocarp. The species is also present on Buru and the Sula islands (Soepadmo, 1973).

Gironniera

Understory shrubs in primary and secondary forest with bright yellow or orange drupes. The drupes are ovoid globose with their thin exocarp in close contact with the hard endocarp. They are likely to be dispersed by frugivorous birds (Soepadmo, 1973).

***Gironniera parvifolia* Planch.**

Tree to 15m. Primary lowland hill forest to 900m.

***Gironniera subaequalis* Planch.**

Tree 40m. Primary and secondary forest to 1300m.

Parasponia

Trees found in freshly opened up habitats. The fruits are ovoid drupes with fleshy and fibrous pericarp and a hard and bony endocarp (Soepadmo, 1973).

***Parasponia rugosa* Bl.**

Tree 20m. Lowland forests.

Trema

Trees found in newly opened up habitats. The orange, red or black drupes with fleshy exocarp and hard endocarp are dispersed by various species of bulbuls (Soepadmo, 1973). The genus used to be positioned with the Urticaceae (Ridley, 1924).

Trema tomentosa (Roxb.) Hara

(=*Trema amboinensis* Bt.)

***Trema angustifolia* (Planch.) Bl.**

Small tree to 7m. Secondary forest lowlands to 1200m.

Trema orientalis (L.) Bl.

Tree to 27m. Secondary forest, lowlands to montain.

***Trema tomentosa* (Roxb.) Hara**

Tree, 5-15(-24)m. Secondary forest, lowlands and hills to 1000m.

Ulmus lanceaefolia Roxb. ex Wall.

A small to large tree (up to 48 m) found in lowland (200m) to submontane (1450m) forest. The fruit is an ovoid elliptic samara (= a dry nutlet with a membranous wing) (Soepadmo, 1973).

UMBELLIFERAE

"Herbs, never woody shrubs in Malaysia." (Buwalda, 1948).

Trachymene

URTICACEAE

Mostly herbs or shrubs but sometimes trees or woody scramblers, often armed with stinging hairs (Saw, 1989).

Dendrocnide
Evergreen trees up to 15 m high with fruits in the form of a small one seeded nutlet (Saw, 1989; Corner, 1988).

Elatostema
Herbs without stinging hairs and with fruits in the form of minute nutlets. They can be found on rocks, in streams or under shrubs (Ridley, 1924).

Pipturus
Trees or erect shrubs without stinging hairs and with fruits in the form of little nutlets enclosed on a fleshy receptacle (Saw, 1989).

Villebrunea
Trees or erect shrubs without stinging hairs and with minute fruits (Saw, 1989).

VERBENACEAE

The 'teak' family.

Avicennia
Mangrove forest trees with fruits in the form of leathery, pod-like capsules containing one seed which germinates inside the fruit (Kochummen, 1978c; Corner, 1988).
***Avicennia alba* Bl.**
Tree to 21m. Mangrove forest, seaward face.
Gregarious.
***Avicennia marina* (Forsk.) Vierh.**
Small tree to 12m. Mangrove forest, form soil on seaward face. Gregarious.
***Avicennia officinalis* L.**
Tree to 18m. Mangrove forest, stream banks, rarely gregarious.

Callicarpa
Fruits in the form of small, round, purple, black or white drupes seated on the remains of the outer layer of the flower bud (= calyx) (Kochummen, 1978c; Corner, 1988).

(*Callicarpa erioclona* Schou.)
Shrub.
(*Callicarpa longifolia* Lamk.)
Shrub or small tree.
***Callicarpa pentandra* Roxb.**
Tree, 3-26m.

Geunsia
Trees or shrubs with fruits in the form of small, round drupes (Kochummen, 1978c).
Geunsia paloensis (Elm) H.J. Lam ex H.N. Moldenke

Lantana camara L.
Introduced

Peronema canescens Jack
An up to 18m tall tree found in relatively open places such as secondary forest, river banks or forest clearings. The fruits are 7mm wide dehiscent capsules. (Kochummen, 1978c; Corner, 1988)

Premna
Small trees, shrubs or climbers with fruits in the form of small, roundish drupes with one stone (Kochummen, 1978c; Corner, 1988).

Premna foetida Reinw. ex Blume,

Stachytarpheta jamaicensis Gard.

Tectona grandis L. f.
A large deciduous tree producing single-stoned fruits contained within the remains of the outside of the flower bud (=calyx) and measuring about 2.5cm long and 1.5cm wide (Corner, 1988).

Teijsmanniodendron
Trees producing one-seeded drupes of about 1 cm long (Kochummen, 1978c).
***Teijsmanniodendron ahernianum* (Merr.) Bakh.**
Tree rarely to 30cm. Lowlands.
***Teijsmanniodendron bogoriense* Koord.**
Tree to 18m. Lowlands.
***Teijsmanniodendron coriaceum* (C.B. Clarke) Kost.**
Tree to 27m. Lowlands.

(*Teijsmanniodendron hollrungii* (Warb.) Kost.)
Small tree. Lowlands.
Teijsmanniodendron pteropodum (Miq.) Bakh.
Tree to 24m. Lowland, swampy forest.
Teijsmanniodendron sarawakanum (Pearson) Kost.
Tree. Lowlands.
Teijsmanniodendron simpliciofolium Merr.
Tree to 18m. Lowlands.
Teijsmanniodendron subspicatum (Hallier f.) Kost.
Tree. Lowlands.

Vitex

Small to medium sized trees with dry or pulpy drupes seated on an enlarged calyx (Kochummen, 1978c; Corner, 1988).

Vitex celebica Koord.
Tree 20-45m.
Vitex cofassus Reinw. ex. Bl.
Big strongly fluted tree with excellent, pale, dense timber.
Lowlands.
Vitex erioclona H.J. Lam Tree.
Endemic.
Vitex glabra R. Br.
Tree.
Vitex heterophylla Roxb.
Tree.
(*Vitex hollrungii* Warb.)
Climber or small tree.
Vitex longifolia Merr.
Tree.
Vitex pubescens Vahl.
Big tree 10-30(50)m. Lowlands.
Vitex trifolia L.
Shrub.

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CTA ZOOLOGICA ET PATHOLOGICA ANTVERPIENSIA N° 82/1992, p.9-27

BEHAVIOUR OF THE BABIRUSA (*BABYROUSA BABYRUSSA*) WITH SUGGESTIONS FOR HUSBANDRY

by

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INTRODUCTION

The babirusa is a remarkable pig, endemic on the Indonesian islands of Sulawesi, Buru and the smaller Sula and Togian islands. The single species of the genus is divisible into three living subspecies: *Babyrousa babyrussa babyrussa* (Sula Islands and Buru), *B. b. togeanensis* (Togian islands) and *B. b. celebensis* (Sulawesi) (GROVES, 1980), of which only the latter is currently represented in captivity. The species is listed in the IUCN Red Data Book as vulnerable (International Union for the Conservation of Nature and Natural Resources, 1978) and can be considered a marker animal for the disturbance of the primary rainforest. The Indonesian Department of Forest Protection and Nature Conservation (Perlindungan Hutan dan Pelestarian Alam: PHPA) has given it the second most important priority after the Indonesian rhinos.

Very few observations have been made of babirusa in the wild. One behavioural study on five animals was performed on Pangempan, one of the Togian islands (SELMIER, 1983) and recently video recordings of wild babirusa were made on the northern mainland of Sulawesi (PATRY & CAPIOD, 1989; PATRY, 1990). A few other behavioural studies have been made on captive animals. These have been limited to social behaviour between very small numbers of captive animals or are preliminary accounts of observations on larger groups (BOWLES, 1986; MACDONALD et al., 1988).

The present paper reports the results of studies carried out on a large number of babirusa. Observations were made in Antwerp Zoo in Belgium and in the Zoos at Surabaya and Jakarta in Indonesia. These institutions represent 3 different ways in which the babirusa are currently kept in captivity.

In Antwerp Zoo, each animal has its own enclosure; Surabaya Zoo keeps the animals in large groups and Jakarta Zoo houses them in pairs. Each of these different housing techniques had its own implications on the behaviour shown by the animals and this allowed us to make suggestions for their future husbandry.

MATERIAL AND METHODS

Observations were made on 76 babirusa in three zoos, 19 animals in Antwerp Zoo during 1988-1991, 44 animals in Surabaya Zoo during the summers of 1987 and 1988 and 13 animals in Jakarta Zoo, also in July and August of 1987 and 1988. Behavioural differences were clearly related to the physical environment in which the animals were kept. It is important therefore to provide a short description of the pen layout and construction in each zoo.

Antwerp

The animals in Antwerp were usually kept in separate enclosures. The female was only put with the male when she was in oestrus. Mother and infants shared the same pen until the piglets were 6-7 months of age, at which age they were separated and each piglet provided with its own enclosure. Two separate buildings housed the babirusa. Adult breeding animals were kept in a building with six indoor enclosures each with a concrete floor area of 3.4 by 2.0 m, and an adjoining roofed outdoor enclosure measuring 3.4 by 5.1 m. The first 70 cm of the floor of the outside enclosure was brick and the remainder filled with loose white sand. The outside pens were separated from each other and from the public by a wire mesh fence, 2.4m high. The outside pens were connected with one another by means of 70 cm wide doors of the same wire mesh material. In addition a horizontal steel bar, 80 cm high and 70 cm in front of the cage was located between the public and the animals. The young animals were housed off exhibit in 8 newly built stables with outside enclosures. The concrete floor of each indoor pen measured 2.0 by 2.9 m and had an open outdoor enclosure of 2.0 by 3.7 m. The first meter of the floor of the outdoor enclosure was concrete, and the remainder was filled with the same loose white sand as was used in the adult pens. The outside pens were separated by 1.6m high concrete walls and connected to each other by a 1m wide steel gate with vertical bars 8 cm apart.

The animals were fed at 9.00 hrs and 16.00 hrs. Twice a week, the animals were provided with branches and tree trunks; grass was given during the summertime. The pens did not have a mud wallow or a bathing pool. Throughout the year, the babirusa were sponged down with lukewarm water and in hot weather they were hosed down. Fresh straw was provided for bedding daily. A half square meter of floorspace in the indoor enclosure had underfloor heating.

Surabaya

In Surabaya Zoo, the animals were usually held outdoors in one large group. Females were sometimes separated for mating or prior to parturition. Occasionally, gates were used to subdivide the animals in four adjacent pens. A small pool, several small concrete shelters and a raised concrete feeding platform was available to the group in each pen. At regular intervals, areas of the pen flooded naturally or by pool overflow and were used as wallows. A single feed was given at 8.00 hrs. No bedding was provided.

Jakarta

In Jakarta Zoo, the animals were generally kept in pairs but the males were rotated after each litter. The accomodation consisted of five outdoor pens situated adjacant to one another, with a sixth outdoor pen off exhibit. Solid walls about 1.8m in height separated four of the pens, the last being devided by a wire mesh fence about 1.2m high. The pens, which were grass covered in parts were higher at the back than at the front. This resulted in the front of the pen being 2m below ground level. Each enclosure was provided with a small pool (2m^2) and a concrete shelter. The trunks of trees in the pen were protected by wire mesh. A single feed was given at 8.00 hrs. No bedding was provided.

Behavioural observations

On most occasions, the animals were observed from the public foot path. Detailed observations of the external signs of oestrus, ingestive behaviour and maternal behaviour were made from within the enclosures. Oestrus was observed in 12 females on a total of 37 occasions with the 8 females in Antwerp being studied on at least 3 occasions each. The preparturition and neonatal periods were observed on 9 occasions. On one occasion, the birth of the piglets was recorded using infra red lighting and a time lapse video camera (15 seconds were recorded at 45 second intervals). The distribution of births over 24 hours was derived from records kept at Antwerp since 1974.

The daily activity pattern of 36 babirusa at Surabaya Zoo was observed during the dry season in August 1988. Two detailed studies were carried out; in the first the activities of each individual was noted at 30 minute intervals from 4.30 until 18.00 hrs throughout the day; in the second, the activities of 6 individual animals were recorded every minute from 7.00 to 17.00 hrs. The behaviour categories noted were the following (after BOWLES, 1986):

– Lying	awake or asleep
– Foraging/Walking	defined as the animal putting its nose to the ground in an attempt to find food. This is usually accompanied by low grunting noises.
– Wallowing	either in mud or water
– Mating	

We have structured this paper as a report of the observations from Antwerp Zoo, but where the results from either Surabaya or Jakarta Zoos do not concur with, or are additional to the Antwerp studies, we have specifically drawn attention to these.

RESULTS

REPRODUCTIVE BEHAVIOUR

Oestrus and mating behaviour

In the non oestrus female the two labiae of the vulva were thin (less than 5 mm), longitudinaly wrinkled and in intimate contact with one another. The vertical axis of the vulva was reduced in length causing the thin wrinkled labiae to pout slightly in the middle. In the oestrus female (Plate 1, left) the labiae were swollen to twice the non oestrus size, increasing in length and thickness. The skin surface was stretched, fleshy, more pink in colour and the labiae were slightly everted, exposing the mucus membranes. Fluid was discharged from the vulva. Often, some of this material moistened the ventral surface of the tail and was distributed by its movements in a semi-circular arc over the posterior of the animal.

In Surabaya, one of the first things the adult males did after they woke up in the morning was to check all the females by nosing their perineal region. The females responded to this by arching their back and defecating and/or urinating. The male put his nose into the stream of urine or nosed and mouthed the faeces.

When a female came into heat the male would follow her, keeping his nose close to the perineal region and making deep clucking noises at a frequency of 3-5 per second. If the male that initially started following the female was a subordinate male, the dominant male would immediately take over and follow the female himself. If the female was not in oestrus, the dominant male abandoned her almost immediately. If she was in oestrus or coming into oestrus the female would often run away pursued by the male and attempt to hide in a shed or behind other babirusa. If closely pursued by the male she would sometimes lie down in an apparent attempt to prevent mating. When the male was chasing the female, he would raise his head sharply towards other males and thereby seemed to keep them away.

In almost every instance, in Antwerp and Surabaya, the pursued female would at some stage turn to face the male. One or a combination of several behaviours were then observed; the female vocalised in a continuous stream of sound; she pushed her nose against the nose of the passive male; the female could place her snout under the chin of the male and press upwards with the male resisting this pressure but not pushing down enough to press her head lower; she nibbled at the upper forelimb of the male; she nuzzled and licked the skin of the boar's face and behind his ears. It was the female which terminated these behaviours by turning around and walking off, closely followed by the clucking male. On some occasions the male would lie on his side in front of the female and she would then nuzzle and lick the skin behind his ears, the skin of his belly, prepuce and inside legs. The male seemed to respond by adjusting his position to allow her easier access to his ventral surface.

These aspects of the behaviour appeared in different combinations and could repeat themselves several times.

At some stage, the male eventually approached the female from behind, nuzzled her perineal region and put his chin on her lumbar region. If the female was not in full oestrus, she responded by vocalising in a loud continuous stream of sound. She would not stand still but bent her legs, wriggled out from under him and ran away. Subsequently, the whole behaviour spectrum of pushing nose to nose, putting the snout under the chin of the male and nibbling his forelegs reappeared in a seemingly random order. If the female was in full oestrus, she would immediately stand still after feeling the weight of the male's chin on her back and she would allow the male to mount. During the actual mating, both male and female made short staccato clucking noises, but the male vocalised louder than the female. In Antwerp, one copulation session that was more closely observed took about 15 min. During this time, the boar mounted 4 times and each mounting lasted for 48-61 seconds. These sessions were repeated several times during the day. Two other intromissions that were timed lasted 3 minutes and 7 minutes respectively. One mating observed in Surabaya occured over about 5 minutes and the male appeared to have 4 ejaculations. Before each ejaculation, the male would thrust about 10 times at a rate of two thrusts per second. After copulation, the male dismounted and stood by her as she lay down. He threatened every babirusa, especially the males, that came near. After about 30 minutes he left the female. In Surabaya Zoo, oestrus females were then mounted by several other males. The female herself did not seem to show any particular choice of mating partner, but the dominant male ensured that he was the first to mate her, keeping all other males away until he had done so.

End of gestation, parturition and neonatal period

About 2-4 days before parturition, the females became more antagonistic towards the keepers. The udder started to increase in volume and the labiae were swollen, their skin surface stretched, fleshy, more pink in colour and slightly everted, exposing the mucus membranes (Plate 1, right). Fluid was discharged from the vulva.

About one to two days before delivery the female became restless and if nest material was available, she would spend a large proportion of her time building a nest (Fig. 1). One day before parturition, the udder became very prominent.

In Antwerp, of the 16 births for which time of delivery is recorded, 14 births

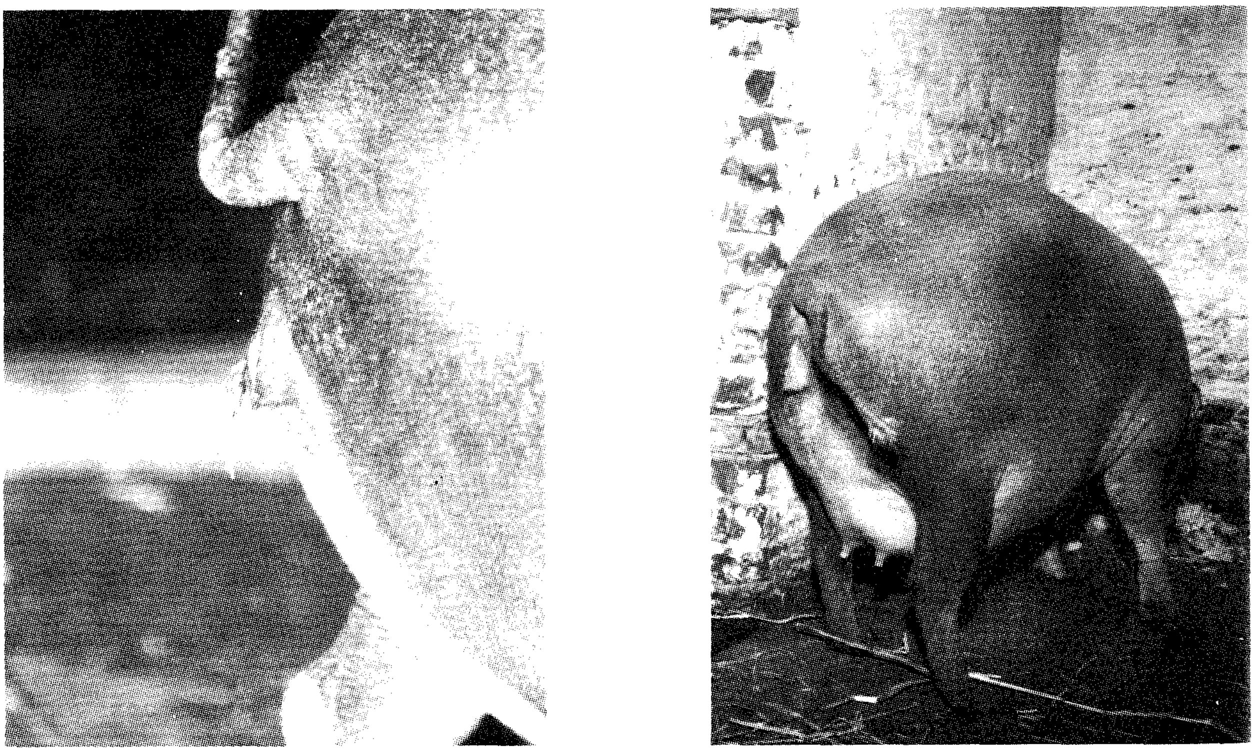

Plate 1 – Left: The vulva of an oestrus female demonstrating that the labiae are swollen, and slightly everted exposing the mucus membranes
Right: A female one day before parturition showing the swollen labiae of the vulva and the prominent udder

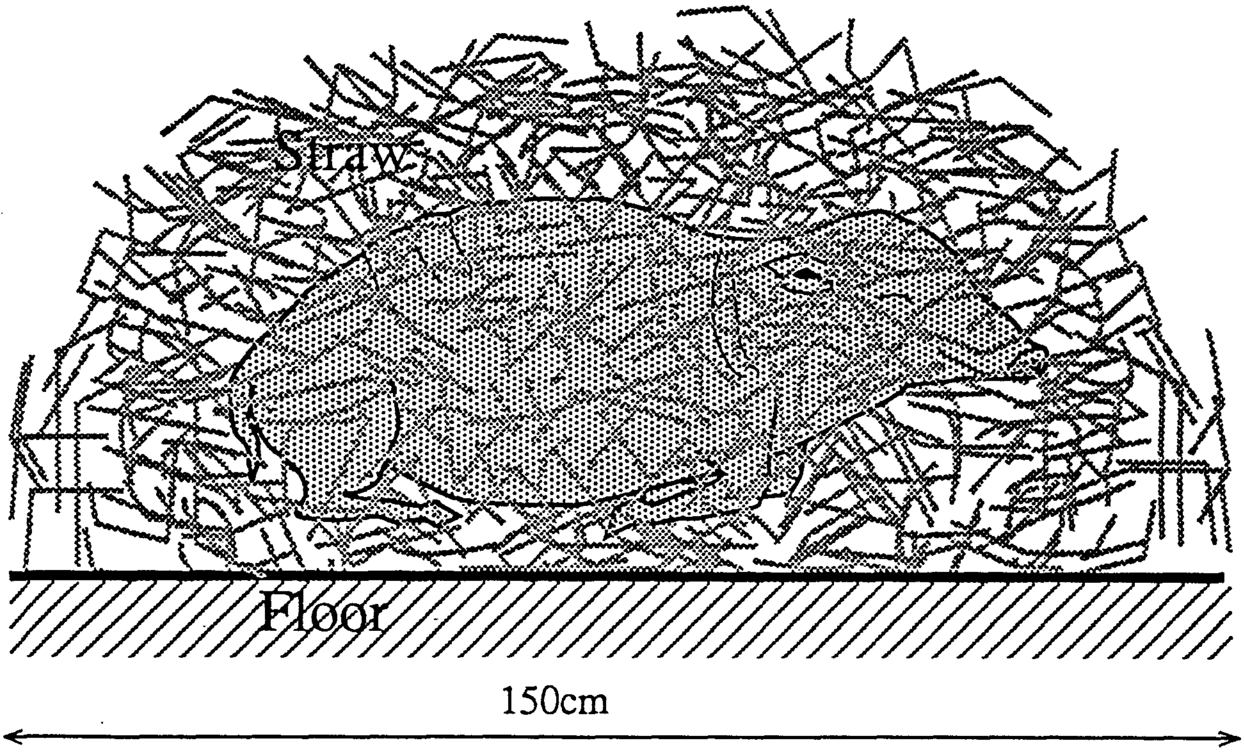

Fig. 1 –The parturition nest of a babirusa

took place between 18.00 and 8.00 hrs and 2 births happened between 8.00 and 18.00 hrs. One delivery of the first group was recorded on video. The female lay on her side when she delivered each of the three piglets. The second was born 4 minutes after the first and the third 23 minutes after the second. The first and third piglets were very active and tried to stand and walk around immediately. The second however hardly moved at all and 5 minutes after birth it showed convulsions and died. Between deliveries, the female stood up and walked around the inside enclosure without apparently paying particular attention to the piglets. She did not lick them dry or attempted to keep them close to her. She inspected the dead piglet once or twice with her nose but then seemed to ignore it and finally lay down on top of it. The initiative for suckling behaviour seemed to be taken by the piglets after the third piglet was born. In Jakarta and Surabaya the piglets were observed to initiate suckling by nuzzling either the female's snout or teats. She would then lie down on her side and expose her udder.

During the first 9 days after parturition, the females were very aggressive; they defended their piglets and attacked other animals and the keeper, when they came too close. In Antwerp, when the door to the inside enclosure was opened the mother usually positioned herself in front of the piglets so that the piglets stood either behind or underneath her. Whenever she felt threatened, she would point her ears forward and produce a low pitched continuous noise. In Surabaya, the female kept silent, even when she attacked the keepers. However both Antwerp and Surabaya females would vocalise with short clucking noises when the piglets wandered off too far away. About 9 days after parturition the intensity of the aggression began to decrease and after 14 days, the behaviour of the female towards the keepers returned to normal. No traces of dead piglets or the placenta were usually found in the pen.

In Surabaya and Jakarta the females gave birth in one of the shelters. The piglets would leave this when they were one week old. In all three Zoos, by the time the piglets were three weeks old, the female was moving around the pen with the piglets following her, sometimes up to 2m away.

The piglets started eating small amounts of solids after one week of age. They gradually increased the amount of solids in their diet as they grew older. However, five month old piglets were still seen to have occasional suckling periods.

GENERAL BEHAVIOUR

Daily activity

The general pattern of behaviour of a group of 36 babirusa in Surabaya was that animals slept at night and showed a greater range of activity during the day. Just before sunrise animals began to wake up and start walking around and foraging (Fig. 2). Only a very small proportion of the animals were seen lying down between 8.00 and 9.30 hrs because the food was given at this time and foraging was the main activity. There after, the foraging behaviour declined and animals rested or started to wallow. Wallowing behaviour was demonstrated mainly between 9.00 and 14.00 hrs, with an apparent peak from 11.30 until 13.00 hrs. After midday animals increasingly began to lie down until almost all were asleep by

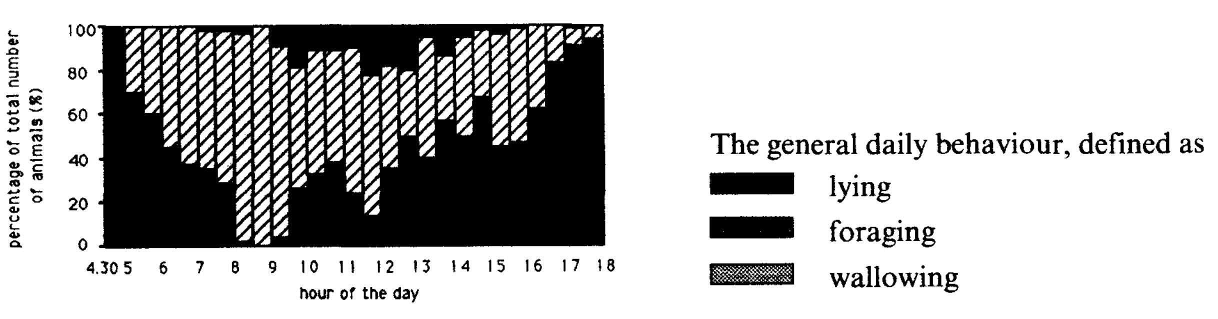

Fig. 2 – The general daily behaviour, defined as lying, foraging, wallowing of a group of 36 babirusa in Surabaya Zoo from 4.30 until 18.00 hrs

17.00 and 18.00 hrs, the time of sunset. Although animals were more difficult to count at night, photographs confirmed that most were asleep.

The pattern of daily activity shown by individual animals was variable, as illustrated in figure 3. The dominant male (Fig. 3A) mated with oestrus females only in the morning and late afternoon. Mating behaviour in the morning was interrupted when the food was offered at 8.00 hrs. Between 11.00 and 13.00 hrs, he spent all the time lying down or wallowing. Although the graph of group activity (Fig. 2) shows that from 14.00 hrs onwards more and more animals are lying down, the dominant male became more active and started mating again.

The now elderly formerly dominant male spent most of his time resting except in the early morning when dunging took place, females were checked for oestrus and food was available. He did not associate with the main group but preferred to remain solitary or together with another old male. An activity pattern similar to that of the dominant male was observed with an adult subordinate male, except that the latter lay down for the night earlier, at 16.00 hrs. The juvenile male and female spent most of their time alone while resting. The adult female (Fig. 3B) foraged in the early morning hours and lay down after the meal from 9.00 to 11.00 hrs. Between 11.00 hrs and midday, she spent more time wallowing than resting but thereafter lay down and slept for most of the rest of the day.

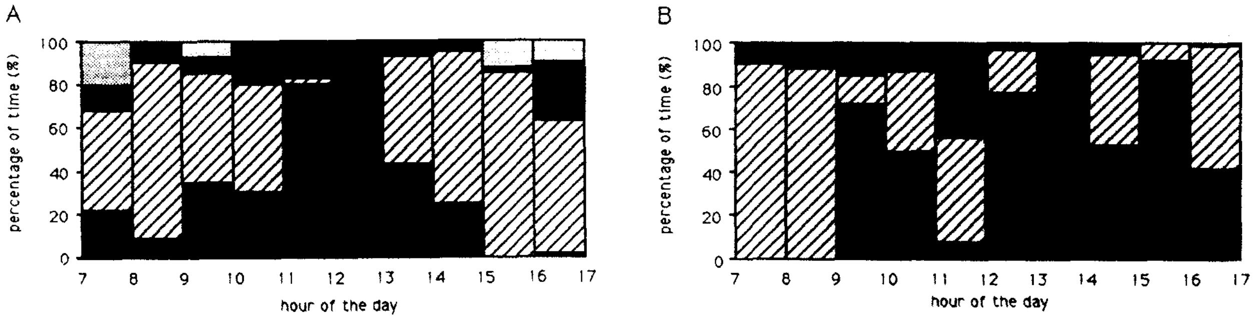

Fig. 3 –The pattern of activity, defined as lying ■ foraging ▨
wallowing ░ mating ■

of two individual animals in Surabaya Zoo from 7.00 until 17.00 hrs.
A: The dominant male
B: A non-oestrus female

Sleeping

In Antwerp, the animals always had free access to their outdoor enclosures by means of a flapping door. In the indoor enclosures, straw was provided for them to sleep in. For short resting periods in spring and summer, the animals usually chose to lie on top of the sand in a particular corner of the outdoor enclosure where they could lie in the sunlight. In Surabaya Zoo the babirusa usually slept through the heat of the afternoon (Fig. 2). It was always the males that initiated the resting periods. Thus they had the first choice of resting places and they preferred to sleep in the same areas of the pen in groups together. The Antwerp babirusa used the indoor enclosure for most of their night time sleeping, sometimes sleeping outside on hot summer days. Autumn and winter periods of daytime rest were spent in the indoor enclosures. Both males and females built sleeping nests with straw and branches. The nests were constructed by carrying packages of straw in the mouth to a corner of the enclosure. This continued until all the straw was piled up into one big heap. The animals then kneeled and crawled under the straw head-first thereby creating a tunnel through the straw. The dimensions of the nest varied with the amount of straw provided, but most sleeping nests were about 1.5m x 1m and 0.5m high. The farrowing nests built by pregnant females seemed to have the same general construction but were a bit larger: 1.5m x 1.5m and 0.75m high. The babirusa slept in 3 positions: lateral recumbency, ventral recumbency with the legs folded under their body and ventral recumbency with the front and hind legs stretched out.

When an oestrus female shares the pen of a male they always sleep in close contact with one another, often lying side by side and head to tail. In Surabaya, the babirusa slept together in groups, in shallow depressions made in the earth. They lay in all sorts of positions (on side, on belly, head to tail, head to head, tail to tail etc.) and as close together as possible. Sometimes they even piled on top of one another (Plate 2).

In Jakarta, the animals slept either in the open, or in the shelters provided. The infants always slept together, but separate from the boar.

In Antwerp, the babirusa slept from shortly after their evening meal (17.30 hrs) till about 7.00-7.30 hrs.

Foraging behaviour

Rooting behaviour on dry or compact ground has so far never been observed. Rooting did occur in the loose sand of the outdoor enclosures in Antwerp but whether this behaviour had a foraging function was not clear. In Jakarta, the animals were seen to turn over logs and stones with their snouts. The animals in

Plate 2. –A group of sleeping babirusa in Surabaya Zoo

Surabaya put their snouts deep in the mud of wallows to come up with a mouthful of this material that then seemed to be sieved: the material was handled within the mouth, while most of it trickled back out at the sides. Babirusa in captivity are offered a variety of roots (carrots, beets, cooked yams and potatoes etc.) but these are not the most favoured items: carrots and beets are usually eaten last or not eaten at all while potatoes and yams are not eaten unless they are cooked. The exact meaning of this food selection with regard to their natural foraging behaviour has yet to be discovered. The patches of grass in the pens of Jakarta were left untouched. There was no grass growing in the outdoor enclosures in Antwerp, but here the babirusa readily ate the fresh grass that was given to them twice a week in summertime.

While foraging, the babirusa walked around the pen, searching for potential food items with their nose very close to the ground while the rhinarium was continuously twitching. In captivity, this behaviour is displayed to search for left-over food items of their main meal that got scattered around in the enclosure, or to pick up potential food items (leaves, seeds, fruits etc.) that entered their enclosure from the surrounding environment (overhanging trees or shrubs) or were thrown in by the public (eg. peanuts in Surabaya and Jakarta). In Jakarta, the animals will try to pluck leaves from trees overhanging the enclosure by standing on their back legs and leaning against the fence with their front legs. In neither of the other zoos do the animals have access to shrubs or small trees in their enclosure. However, when branches are given to them by the keepers they will pluck off the leaves and buds or scrape off the bark.

Babirusa, like other pigs, are omnivorous and will hunt for small mammals and birds. Babirusa in Antwerp and Surabaya have caught mice and pigeons that accidentally entered their enclosures. They will also chase and eat baby babirusa if they gain access to their pen. Babirusa are relatively agile and have been seen to run rapidly and turn around very quickly if given enough space. In Surabaya, two young babirusa (6 months) regularly escaped from, and returned to, their pen overnight by climbing the 120 cm fence.

When there is competition for food in Surabaya (for instance when the visitors feed scraps) the most dominant male will take the food. A female will not touch the food if a male is too close.

Ingestive behaviour

The upper and lower incisors of the babirusa played an important role in the ingestive process. The upper incisors are curved backwards, and hold the food item. The tongue assisted keeping the item in place while the chisel-like lower incisors slid forwards and upwards into the material to chop off the piece that is in the mouth. The tongue then moved this piece to the back of the mouth for grinding. The use of the almost horizontally arranged lower incisors was evident and demonstrated when the animals ate bark from branches: the branch was caught and held tight with the upper incisors and the tongue, while the lower incisors scraped along the branch and peeled off the bark. If the strip of bark could not be bitten off, the animal held the branch down with one of its front legs and tore the strip of bark off with an abrupt swing of the head. The holding down of food items with one of the forelegs is a general technique that the animals used whenever they wanted to eat a large food item that couldn't be bitten to pieces easily (plucking leaves/buds of branches, eating lettuce etc.) or when a food item needed to be kept steady because precision was required (eating corn off the cob, peeling nuts, bananas etc.)

The babirusa jaw is strong and can crack very hard nuts. For instance, when eating dates they first ate the soft part and spat out the pit. However, if all the other favoured food items had disappeared, they very often came back to the pit, picked it up, ground it and ate it. For grinding, mostly straight up and down movements were used with very little lateral displacement on the lower jaw.

Dunging

The mornings in Surabaya started with all the animals moving to a fixed area near the centre of the pen where they almost always excreted urine and faeces. The males went around inspecting by both smell and taste the freshly voided material. The large adult males also inspected the vulva of every female when she moved to this area of the pen.

In Antwerp the babirusa usually went to the outside enclosure to defecate and/ or urinate. However, although there was no fixed dunging area in either the outside or inside enclosure, the animals seemed to prefer to defecate under branches and tree trunks. When defecating, both the males and females stood still, arched their back and bent their hind legs. Females urinated in the same position; Males sometimes stood still with all four legs straight when they urinated and sometimes kept walking around while urinating.

Wallowing

All animals with access to a pool or a mud wallow spent a proportion of their time getting wet. In Surabaya Zoo where both were available, and in Jakarta Zoo where generally there was only a pool, the males appeared to use the pool to the almost complete exclusion of the females. In Surabaya Zoo males bathed singly or in groups of up to four in number. Individual males in Jakarta would sometimes spend periods of 1-2 hours in the water.

Mud wallowing tended to be a group activity with several animals apparently following the lead of an individual. Up to ten animals would lie down and slide into the mud at about the same time. It seemed that the result of the wallow was a layer of wet mud over the whole body. This rapidly dried in the heat, cracked and came off the animal as a grey dust.

Dominance

Dominant and subordinate behaviour was observed in all three zoos. It was examined closely at Surabaya Zoo and the detailed results will be the subject of a separate communication. In general terms babirusa exhibited the signs of being a social animal. The males were ranked in order according to factors including weight and size. Females were subordinate to adult males and expressed that lower status variously by retreating, lowering the head or shrieking almost constantly when threatened.

Subadult animals formed the third rank in the social order, and although subordinate to both males and females would also play with both. The dominant male in Jakarta Zoo, when penned with two juvenile males would also romp and dash about the pen chasing, and being chased by them.

When adult males were placed on each side of a separating fence in Jakarta Zoo, they displayed and rushed at the fence with heads raised. They also rubbed the side of their head against the wire. Previous experience of this behaviour led Antwerp Zoo to organise the animal accommodation such that males were not housed in adjacent pens.

DISCUSSION AND RECOMMENDATIONS:

One of the most interesting and puzzling aspects of babirusa behaviour centred on the female's response to the boar when he detected oestrus. We found that the external signs of full oestrus are easily detected in most but not all females; some females do not seem to show any visual signs and this phenomenon of silent heat or silent oestrus has been reported in a number of species, including the domestic sow (FRASER, 1968). Recent studies have also shown that, as in other species, oestrus in the babirusa can be detected by measuring the urinary oestrogen excretion (CHAUDHURI et al., 1990). It was our impression that when in full oestrus, females are less cautious of the keepers and seem to seek human contact such as stroking and tickling. This was in marked contrast to the noise and apparent efforts to escape attention of the male when he was present. It was possible that in Surabaya the females were pursued at the earliest signs of the onset of oestrus by the males; the dominant male's persistant attentions when the female was not yet in full heat may have been driven by the inter-male competition within the pen. However, that was not the case in Antwerp Zoo. Further studies are required to examine these patterns of behaviour and the physiology underlying them.

It is clear that the pre-copulatory behaviour of male and female is highly structured. The different elements can vary considerably in frequency, length and order. How they relate to successful mating is not clear, but it seems to be of critical importance. When animals at the Jersey Wildlife Preservation Trust were kept singly and the male was introduced to the female during oestrus, the normal complex behaviour was shown. After the zoo started keeping the animals as pairs the behavioural elements of oestrus became less noticeable, although the external physical changes in the female remained evident. (BOWLES, 1986) In domestic pigs, the duration of heat in the female is reduced by the continuous presence of the male; the most successful stimulus to elicit repeated ejaculation by the boar is the presence of a new sow in oestrus (HAFEZ, 1975). This suggests that it may be wise to keep babirusa separated from each other until the female comes into oestrus. The reason why the animals in Surabaya are not affected by all this is possibly because males and females are kept together in large numbers. The males compete with one another for the oestrus females. The guarding behaviour shown by the dominant male is a clear sign of this competition among males. In order to ensure that his sperm fertilises the female, it is important for the dominant male to guard the female before and for a short time after the copulation; he must also mate with her at the right time. It is interesting that in Antwerp, where there are no competing males around, guarding behaviour is absent however, the males do get more aggressive towards the keepers on those days that they are together with the female; They will deny the keepers access to the enclosure.

By way of contrast, during oestrus, the male will allow the female to eat beside him and sometimes she may even eat first. However, as soon as oestrus has passed, the male becomes more aggressive when food is offered, even though he may be very docile towards the female during the rest of the day. He will invariably chase the female away and eat her portion also. The consequence is a stressed and underfed female and an overfed male. One solution is to feed the male and female separately between oestrus periods.

Nest building seems to be an important behaviour in babirusa. When material is provided, elaborate nests are constructed prior to the end of gestation. Studies of other Suidae indicate that parturition nests are a common feature and provide a thermostable environment where the neonatal piglets can lie close together or where they are warmed by the female (FRÄDRICH, 1965 & 1967). In the zoos of Jersey (BOWLES, 1986) and Antwerp (VERCAMMEN, 1991), experience has shown that it is sometimes necessary to put a heat lamp or floor heating in the parturition enclosure.

Parturition takes place after 156-161 days, with most piglets being born on the 158-159th day (VERCAMMEN, 1991). The first few days after parturition, the female is very defensive of her piglets. In all three zoos, the keepers do not enter the enclosure for cleaning or to supply food. Suckling behaviour has been described elsewhere (SELMIER, 1978; BOWLES, 1986; MACDONALD, 1991 and VERCAMMEN, 1991). Most female babirusa have 4 nipples and some have 6 (MACDONALD, 1991). The sixth and most anterior pair is thought to be non-functional but piglets have been seen to suckle this pair (VERCAMMEN, pers. comm.). In the case of one piglet, only one pair of nipples is used (BOWLES, 1986). In the case of twins, each piglet seems to use a pair of nipples; they nurse from the upper nipple first and then move to the lower one (SELMIER, 1978). It is not yet known how the suckling is organised in the case of triplets. Milk flow appears to dry up about six months after parturition. Piglets that try to suckle and cause small nibble-wounds on the females flanks and legs are chased away. In Antwerp, this is taken as the signal to separate the piglets from the mother.

Rooting in the ground with the use of the rhinarium is a predominant feature in the foraging behaviour of peccaries and most pigs (FRÄDRICH, 1967). *Hylochoerus*, and in most parts of its range *Phacochoerus* also root very little (D'HUART, 1991; FRÄDRICH, 1965), but *Babyrousa* is the only pig species that doesn't root in a more compact substratum. Their foraging behaviour, walking around with the snout close to the ground, can be encouraged by scattering their food throughout the pen, so that the animals spend more time gathering it. Branches and trunks in the pen can function as scratching posts as well as alternative material to eat. The exact function of the apparent sieving of mud by the babirusa is not clear. It is possible that the animals are looking for small invertebrates to eat. The fact that the babirusa eat invertebrates and even actively catch and eat small mammals and birds is not unusual. All pigs are omnivorous to some extend (FRÄDRICH, 1967; HAFEZ, 1975).

The technique of holding down food items with one of the fore-feet while tearing off pieces by a brusque upward toss of the head is also used by other pigs (FRÄDRICH, 1967). The cutting into sections by the lower incisors of the babirusa requires a forward and upward movement of the lower jaw. A morphological study of the skull and teeth revealed an almost non-restricted craniomandibular joint in babirusa, which easily allows such a movement. The joint and complex cheek teeth also allow the use of transverse masticatory movements (HERRING, 1972) However, when eating sweet potatoes, almost no lateral movement of the lower jaw of the babirusa could be observed. According to Fradrich (1967), *Sus scrofa* and *Potamochoerus* also chew without recognisable lateral movements of the lower jaw, while *Phacochoerus* does show transverse masticatory movements. A possible reason for these differences may be the type of food eaten.

Wallowing is a behaviour typical of ungulates and it probably has a skin maintenance as well as a cooling function (FRÄDRICH, 1965). The latter seemed to be important to the animals in Surabaya (Fig. 2 & 3). When it is not possible to provide a pool or wallow it was found to be satisfactory in Antwerp to regularly sponge the animals down with lukewarm water, or even to hose them down with cold water during the summer. When no bathing is available, the skin of the animals often becomes dry and starts to crack. These symptoms can be cured by rubbing the skin with baby oil.

Finally, it is clear that in order to sponge the animal down or rub it with baby oil, a close relationship is necessary between the keepers and the animal. If started young, the babirusa easily gets accustomed to its keepers. The consequence is that the cleaning of the pens can be done without locking the animals out, oestrus signs in females can be checked from close by, samples for scientific studies can be obtained more easily and medical examinations and treatment can often be carried out without anaesthetising the animal. For instance, when the belly is rubbed, most babirusa will lie down on their side which gives the opportunity to inspect and treat small wounds or remove bandages after an operation. When the inside of a leg is rubbed, a lying babirusa will automatically lift up its leg so that hoof inspection is possible.

Close attention to babirusa behaviour will contribute to its breeding success, general well-being and further knowledge of its biology.

ACKNOWLEDGEMENTS

These studies could not have been possible without the help of Dr. André Dhondt of Universitaire Instelling Antwerpen and the cooperation of the staff at Antwerp, Surabaya and Jakarta Zoos; in particular Mr Bruno Van Puijenbroeck, Mr Paul Vercammen, Mr Patrick Immens and Miss Michele D'Aes at Antwerp; Pak Stany Subakir, Pak Vincent Harwano Gepak and Pak Bambang of Surabaya and Dr Linus Simanjuntak at Jakarta. We thank Colin Warwick, Peter Cuypers and Fiona Manson for the drawing of the parturition nest and the photographs and thanks to Swaletreks and the International Scientific Supports Trust Ltd for coordinating travel to Indonesia. We are grateful to the following organisations for their financial support: The British Council, the Belgian "Nationaal Fonds voor Wetenschappelijk Onderzoek", The Wellcome Trust, The Carnegie Trust for the Universities of Scotland, The University of Edinburgh, The Royal Zoological Society of Edinburgh, The Pig Improvement Company Ltd., the Cotswold Pig Development Company Ltd and the Balloch Trust.

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SUMMARY

Observations were made on 76 babirusa in the zoos of Antwerp, Surabaya and Jakarta. The behavioural differences observed were clearly related to the physical environment in which the animals were kept. In Surabaya, where the animals lived in a large group, males daily checked all the females for oestrus and competed for the oestrus females. Courtship was complex and the dominant male guarded the female both before and for about 30 minutes after mating. In Jakarta, the babirusa lived in pairs in adjacent pens. In Antwerp, where the animals are housed singly, oestrus was detected by the keepers and the female was then introduced to the male. When a female was in the same pen, the male would deny the keepers access to the enclosure.

The complex behaviour pattern seen prior to mating was not evident when animals were kept together as a couple all the time.

Babirusa are largely diurnal. Sleeping nests were built if nesting material was provided. When more than one babirusa was kept in a single pen, they usually slept in close contact with one another.

Babirusa did not root in compact ground. They foraged for food by walking around with their snout close to the ground. When there was competition for food, it was the dominant male which ate first. A female would not touch the food if a male was too close. The upper incisors were used to hold food and the lower incisors acted as chisels to cut through it. Almost no transverse masticatory movements could be observed.

The animals were very fond of water and mud and would bathe and wallow whenever given the opportunity.

Analysis of the patterns of behaviour enabled suggestions to be made with respect to the husbandry of the babirusa, its management and the role of the keeper.

Z. Säugetierkunde 58 (1993) 18–30

ISSN 0044-3468

Agonistic behaviour in captive Babirusa *(Babyrousa babyrussa)*

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Receipt of Ms. 24. 2. 1992
Acceptance of Ms. 13. 7. 1992

Abstract

The agonistic behaviour of captive babirusa *(Babyrousa babyrussa celebensis)* was studied at zoos in Indonesia, Belgium, and the Channel Islands. Observations were carried out on ninety-five babirusa of which 25 males and 21 females were kept in Surabaya Zoo, Indonesia. Male-male, male-female and female-female interactions were analysed with respect to body size, shape of upper canines, age and sex. The agonistic behaviour was described and could be categorised. "Threat at a distance", "surprise rush", and "the lying lunge" were used frequently by both males and females. The submissive babirusa generally lowered its head and vocalised its submission by means of a repeated, breath-long, rumbling squawk. The canine teeth were never seen to be used as weapons. "Boxing" was the ultimate form of agonistic behaviour exhibited between male babirusa. Body size was the most important factor determining the outcome of a "boxing" match. "Boxing" between females was never observed. Female agonistic behaviour was mainly aimed at biting the forelimb of the opponent. Adult females were submissive to adult males, but adult females were dominant over sub-adult males. Large females were dominant over smaller females.

Introduction

The babirusa is endemic to the Indonesian islands of Sulawesi, Buru and the smaller Sula and Togian islands. Very few observations have been made of babirusa in the wild. One study of the behaviour of five animals was performed on the Togian island of Pangempan (Selmier 1983) and recently video recordings of wild babirusa were made on the northern mainland of Sulawesi (Patry and Capiod 1989; Patry 1990). Several other behavioural studies have been made on captive animals. These either describe the social behaviour of very small numbers of captive animals, are preliminary accounts of observations on larger groups or are detailed accounts of reproductive behaviour (Geoffroy-St-Hillaire and Cuvier 1842; Selmier 1978, 1983; Bowles 1986; Macdonald et al. 1989; Leus et al. 1992).

The few studies of the babirusa in the wild and in captivity suggest that they are social animals, one or more adult females living together with young and juveniles, the adult males solitary or singly associated with family groups. They appear to employ a range of behaviours, to obtain or maintain dominance and position. This study reports on a variety of agonistic behaviour found between individual babirusa.

Material and methods

Observations were made largely at Surabaya Zoo, Indonesia with additional observations recorded on the Channel Islands at the Jersey Wildlife Preservation Trust, at the Royal Zoological Society of Antwerp, Belgium, and in Ragunan Zoo, Jakarta, Indonesia. In July and August 1987 and 1988 between 0500 h (one hour before sunrise) and 2200 h (four hours after sunset) observations were carried out on 25 male and 21 female babirusa in six adjacent and inter-connecting pens in Surabaya Zoo. The main enclosure housed up to 35 animals, and details of the layout and sizes of the pens were published earlier (Macdonald et al. 1989). Vocalisations were recorded on tape and subsequently analysed and described in relation to the behaviour with which they were associated.

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The results of 220 of the agonistic encounters observed in 1988 at Surabaya Zoo were grouped in the following way. A sample of 142 observations of the outcome of fighting behaviour (boxing) between male babirusa was analysed. Precise ages were unknown, but the males were classified into four subgroups, according to the following criteria:

juvenile:	(small sized body, upper canines are just appearing)
sub-adult:	(body smaller than the adult male, canines narrow and upper canines tightly curved)
adult:	(large body size, canines thick, the upper canines curved back towards the head or are broken and more straight, dewlap present)
old adult:	(large body size, skin is scarred, creased and folded, upper canines usually broken and more vertical).

A further sample of 32 observations listed the results of agonistic male-female behaviour which were analysed according to sex and 'age' subgroups. A third sample of 50 observations examined the outcome of confrontations between female babirusa which were classified into three subgroups; juveniles, small adults and large adults.

In 1991, Surabaya Zoo moved its remaining 13 males and 16 females to a single new pen 35 m × 15 m in area. The animals were observed in December 1991 and January 1992 between 0500 h and 1500 h. Particular attention was paid to the agonistic behaviour in its different component parts shown by the dominant male of the group. In additon, the agonistic behaviour shown by the females towards one another and to the males was examined. Additional observations, which were gathered from a further forty-nine babirusa are included in this report; these were collected during studies of behaviour at the Jersey Wildlife Preservation Trust from 1983–1987, at Ragunan Zoo, Indonesia during the months of July and August 1987 and at the Royal Zoological Society of Antwerp, Belgium from July 1989–91.

Results

The agonistic behaviour could be allocated to seven different categories by using the terms "threat at a distance", "surprise rush", "nose in the air", "head under jaw submission", "front half supported", "boxing", and "the lying lunge".

Male-male interactions

"Threat at a distance"

The dominant male needed only look, or make an upward thrust or toss of the head in order to threaten another male. The threatened animal moved cautiously in relation to the dominant male though not necessarily far from him and seemed to keep a close eye on his movements. When a threat was perceived the submissive animal lowered his head and uttered a breath-long rumbling squawk, which may be repeated.

"Surprise rush"

Males often made sudden, and apparently unprovoked charges at other males. This startled the attacked male into facing the onrushing animal, lowering his head and uttering the rumbling squawk sound of submission. Usually these attacks were not carried through to physical contact; the attacking male charged forward with his head held high for a short distance only. However, in those few instances when the charge was carried through, the mandibular canine of the attacker struck the upper and/or lower canines or the shoulder of the submissive animal. If the attacked male was not intimidated the attacker became the attacked. The dominant male ended a standing confrontation by walking away.

"Nose in the air"

Two or more animals approached each other with their heads raised and their noses held in the air. They manoeuvred with their heads held high and at 60 to 240 degrees to one another (Fig. 1). The animals backed off slowly and then suddenly rushed several steps forward, again with heads raised and noses elevated. This complex of circling and feinting manoeuvres could either develop further, or the animals wandered away from each other.

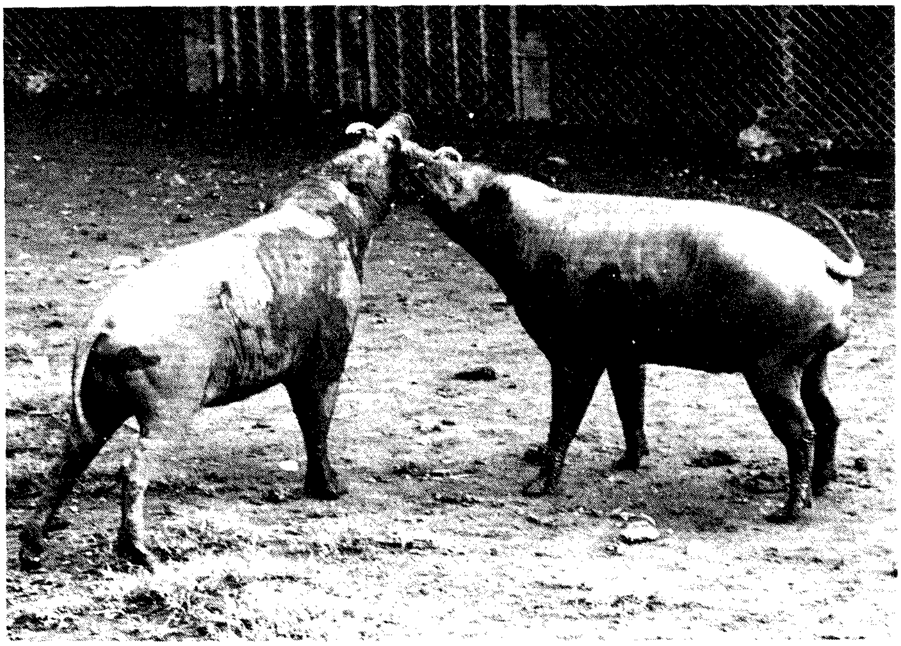

Fig. 1. Two adult male babirusa demonstrating the "nose in the air" agonistic behaviour

"Head under jaw submission"

When two males were in close proximity the submissive animal took up a position at an angle, often at about 90 degrees, to the head of the dominant animal, lowered its head such that its nose was positioned under the mandible of the superior male and uttered a very short squawk or a continuous rattling stream of sound, the pitch and intensity of which increased as the animal seemed to perceive increased threat. The dominant male made a sucking "tuh" sound apparently by lowering its mandible and then pulling its tongue off the upper palate. Both males circled one another with the subordinate animal usually in the middle. Even after being nipped in the nose or mouth, the subordinate male did not give up but remained where he was, often complaining noisily. In some instances the dominant male turned rapidly to face another male in close proximity and the behaviour was repeated. Usually the dominant male seemed to be the one to break off the confrontation by ignoring his opponent and wandering off.

"Front half supported"

Two males approached one another such that their heads were held side by side and pointing in the same direction. Their bodies were often held at 60 degrees to one another. The animals manoeuvred side by side until one male mouthed the tusks of the other and layed his head on the snout of the other. If this manoeuvre was successful, the male whose head was highest leant his head on the head of the other male (Fig. 2). The two animals could be at an angle or facing one another. Often the upper male seemed to be actively pushed upwards by the lower animal until his forefeet were off the ground. Sometimes he actively climbed until his chest was on the head of the inferior animal (Fig. 3). The upper male paddled with his front legs against the back and shoulders of the lower animal. The position of the canine teeth of the lower animal was such that they rubbed on the exposed neck and chin of the upper animal (Fig. 2), but without causing damage. This position was maintained for a variable length of time, the lower animal sometimes uttering the submissive squawk. It was the superior male which ended the behaviour by dismounting and walking away from the other male.

On one occasion, when two relatively young (2–3 years) males were squabbling in a narrow corridor, the hind legs of the upper male slipped and he lost the grip of his forefeet

Fig. 2. Two adult male babirusa engaging in an early stage of the "front half supported" behaviour. Note that the maxillary canines of the lower male are in contact with the neck of the superior animal

on the back and shoulders of the lower male. The two animals had manoeuvered into a 90 degree angle with each other and as the superior animal lost his balance the inferior animal tossed his head. The left lower canine of the lower male struck the neck of the falling male and penetrated about 3 cm. The upper male became locked on the tusk of the lower male and started a loud, continuous, high pitched scream. The lower male persisted in making upward movements with his head. He made no attempt to end the confrontation. The animals were eventually separated by the keepers. The animal with the pierced neck behaved in a very submissive fashion for weeks thereafter.

"Boxing"

Only about 5 % of interactions resulted in boxing behaviour. Boxing usually started from the "nose in the air" behaviour with both animals facing each other and each trying to place his head on top of that of the other animal. Each raised himself off the ground until both were standing on their hind legs facing one another. Once in this position they leant and paddled against the chest and shoulders of their opponent (Fig. 4). Their snouts were held as high as possible. The animals seemed able to remain on their hind legs for about one minute at a time. If one of the animals fell onto all four legs it reared up again and the boxing continued. The boxing match usually lasted for 2 to 5 minutes, but could extend for up to 20 minutes. The pushing and shoving could lead to large distances being covered within the pen. During the boxing the animals often fought with their mouths open but there was little or no vocalisation.

The superior animal often appeared to be the one that raised his head the highest; he also had his ears pointed forward. The dominant male usually broke off the confrontation by ignoring his opponent and wandering off. The submissive animal may or may not lower his head below that of the doimant animal when they both came back onto all fours but rarely did he vocalise his submission with the short squawk or continuous rattling stream

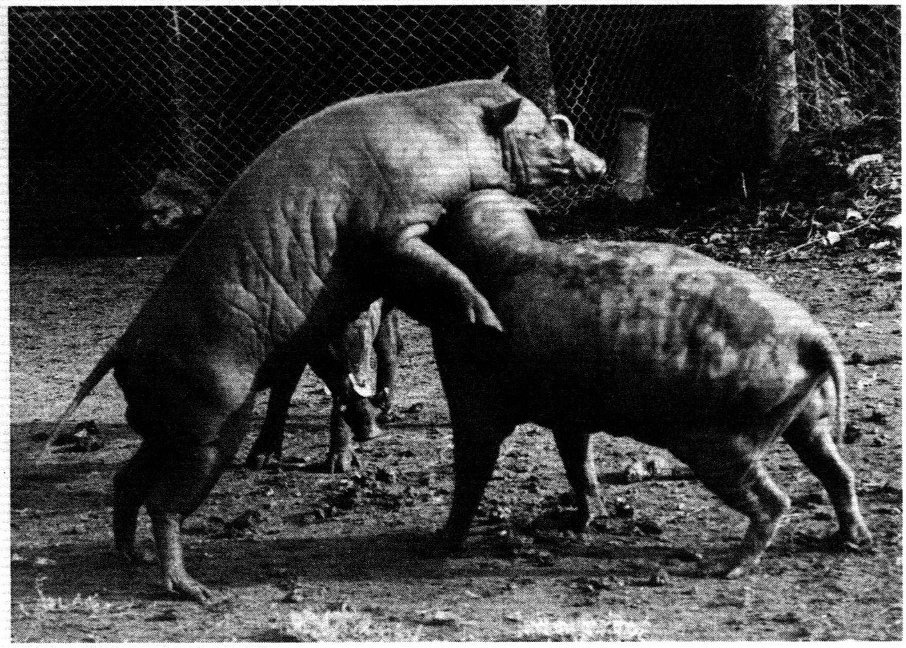

Fig. 3. The final stage of "front half supported" behaviour as exhibited by two male babirusa. The neck and chest of the upper male rest on the face and teeth of the lower male

of sound described above. Occasionally a third male intervened by raising his head between the competing animals and causing the boxing match to stop. In some instances, the intruder himself began boxing with one of the two combatants. It also happened that the intruding male would join forces with one of the two combatants and the third animal would then back off in the face of the two advancing males.

The deciding factor seemed to be the ability to stretch the highest and push your opponent off balance and onto all four legs. The tusks seemed to play little or no part in the contest (Fig. 4). The contests could become violent in which case the males made greater use of their strength and threw their weight at one another. In those instances the upper male uttered a rolling, deep-throated, low pitched growl and would often froth at the

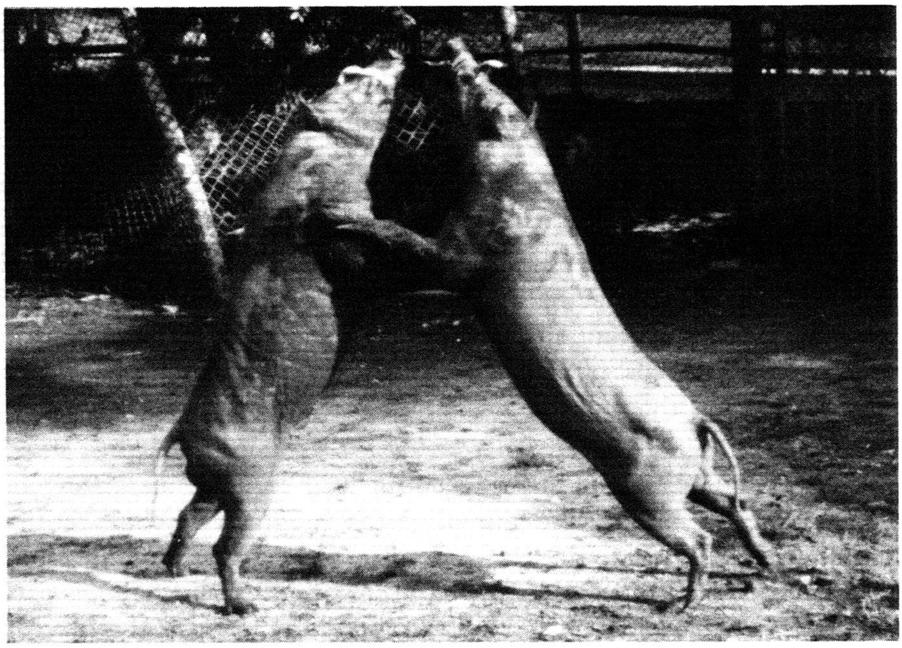

Fig. 4. "Boxing" behaviour being demonstrated by two adult male babirusa. Both animals have reared onto their hind legs, faced one another, and are leaning and paddling with their forefeet against the chest and shoulders of their opponent. Note that their noses are being stretched as high as possible

mouth. These battles attracted the attention of other males which often interfered in the fight and broke it up.

An analysis of 72 boxing encounters between males of different size showed that the larger male was dominant on 71 occasions. In 28 further encounters where the males were evenly matched for size, straight tusked animals were dominant 16 times and those with curved tusks were dominant 12 times. When age of the animal was examined during another 38 encounters, sub-adult or adult males were dominant over elderly males on 30 occasions. No clear outcome was apparent in the remaining eight interactions, and in four other boxing matches no distinguishing feature was apparent between the animals.

Boxing was most common among the young adult males. Old males were never seen boxing and often seemed to ignore conflict except for vocalisation and biting at animals when food was available. In the winter of 1991/92 the alpha male, which was not the largest male in the group, was rarely seen boxing. However, he patrolled the pen almost constantly and showed the other types of intimidatory behaviour on many occasions. Infants of only a few days of age were seen pushing each other and attempting to get on top of each other. Siblings of either sex and aged from about two months until weaning were seen to rear up on their hind legs and playfully paddle against one another's chests with their forelegs. More serious boxing between males was observed when the juveniles were about one year of age, when the tusks were emerging. Boxing could take place at any time of the day but usually did so more often when it was cooler, in the early morning and late in the afternoon.

"The lying lunge"

When lying in the pen a male was sometimes seen to swing his head up and round towards an approaching animal which appeared to be about to lie down beside him. A loud shriek of short duration (< 1 sec) was usually uttered by the submissive pig. The threat was sometimes followed by a nip at the nose, flank or leg of the threatened animal.

Male-female interactions

Intimidatory behaviour of the three types, "threat at a distance", "surprise rush" and "the lying lunge" were found between males and females in which either sex may be dominant. The "head under jaw submission" with squealing vocalisation was seen in association with both reproductive behaviour and perceived threat. The female tended to bite at the front legs during an attack and would do so also in defence. When the female nipped defensively at the feet of the male he uttered a low "gruff-gruff" sound. Only twice was an adult female seen to come to an adult male with her nose raised in the same way as was described between two adult males; when this happened they manoeuvered to face each other, and began boxing. Neither animal vocalised.

On one occasion the same female repeatedly climbed onto the front of the same male until her chest rested on his head. He terminated the interaction by moving away without a sound.

In 31 of 32 interactions between adult males and females, the male was dominant. When an adult female confronted either a sub-adult or juvenile male the adult female dominated in 11 out of 13 occasions. In five interactions between juvenile animals the males were dominant.

Female-female interactions

Examples of "distant threat", "surprise rush" and "the lying lunge" have been seen between females. Usually, when one female rushed at another, the attacked female ran off closely pursued for some distance by the attacking female. We often saw the dominant female chase the submissive female repeatedly over a period of about ten minutes.

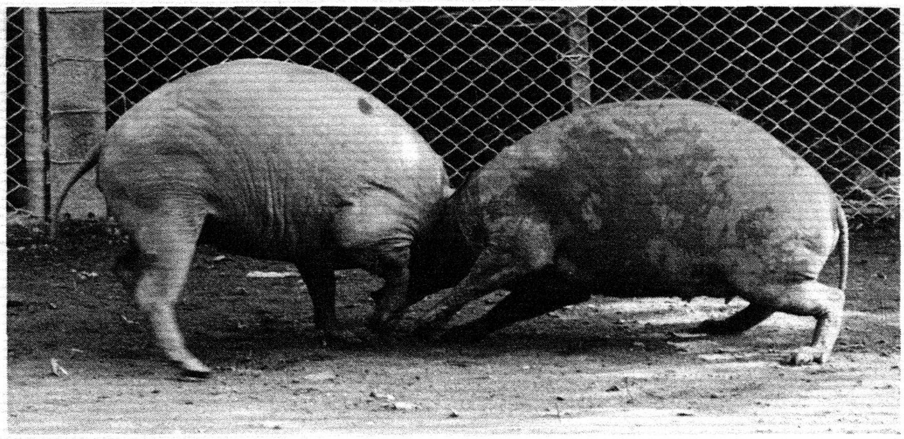

Fig. 5. Typical agonistic behaviour between two adult females in which the female on the right is attempting to reach below the head and neck of the female on the left in order to bite the latter's front leg. The female on the left has anticipated this move and has lifted her right front foot away to prevent it from being bitten

Of the other four behaviours, "nose in the air" and "head under jaw submission" were seen rarely between adult females and "front half supported" and "boxing" behaviours were never seen. When two females confronted one another it was often quite violent, fast moving and noisy. Clear attempts were made to reach below the head and neck of one another; the objective seemed to be to bite the leg or foot of the opponent (Fig. 5). The female which had her head highest and allowed her fore or hind limb to be bitten lost the contest and uttered a high pitched squeal of short duration. The superior female often expressed a deep-throated growl during the contest. Fifty female-female interactions were observed and in 41 of these the larger animal was dominant. In only four occasions was the smaller female superior. On five occasions the interacting females were of the same size.

When single females were put in adjacent wire-sided enclosures two different reactions were observed. Some females appeared indifferent of one another whereas others would repeatedly show aggression towards each other. The latter would run back and forth along the separating fence with their heads elevated and ears pointed forward, making sharp upward thrusts of the head towards their opponent. They also often pushed side to side through the fence and growled at one another, nipping with their lower incisors in the direction of the legs and flanks of their opponent.

Discussion

We have identified and described a series of agonistic behaviours of the babirusa. These results confirmed and extended the fragmentary observations reported for this species by Selmier (1978, 1983), Macdonald et al. (1989), and Leus et al. (1992). The repertoire of behaviours exhibited by the babirusa fell within the broad classifications of threatening, display and fighting behaviour which are used for assessment between individuals of a wide variety of species (Maynard Smith 1982). The babirusa seems to employ the behaviours "threat at a distance", "nose in the air" and "boxing" as the sequence of increasing level of threat.

The same classifications can be recognised in the range of agonistic behaviours described for a number of pig species including the wild boar *(Sus scrofa),* the bush pig *(Potamochoerus porcus),* the warthog *(Phacochoerus aethiopicus)* and the giant forest hog *(Hylochoerus meinertzhageni)* although it is clear from the published descriptions that the details of the behaviours exhibited vary between genera (Frädrich 1965, 1967; Beuerle 1975; Cumming 1975; Skinner et al. 1976; Kingdon 1989).

"Threat at a distance" as demonstrated by the babirusa with a slow or faint movement of the head upwards has also been reported for the wild boar, the warthog and the bushpig (FRÄDRICH 1965, 1967; CUMMING 1975; SEIDACK 1990). A more overt toss of the head into the air in the direction of the opponent is shown by all pigs (FRÄDRICH 1967).

Display is reported in the wild boar as the presentation of the body broadside to the opponent with the back arched, the front part of the body stretched out, the head elevated and the hair of the body erect (FRÄDRICH 1967; BEUERLE 1975). By way of contrast, bush pig opponents face one another, thereby presenting to one another their conspicuously marked head and erected dorsal main (SKINNER et al. 1976; SEYDACK 1990). The only behaviour exhibited by the babirusa which could be identified as the equivalent of display was stretching of the head and "nose in the air". The animals will sometimes do this at a distance, but more usually close to their opponent and, like the warthog, may exhibit a range of positions from parallel head to head to frontal nose to nose (FRÄDRICH 1965; CUMMING 1975).

The subspecies of babirusa from Sulawesi, unlike the other two subspecies of babirusa, lacks the hair coat of the wild boar. The species also lacks the conspicuous facial colouration of the bush pig and the facial warts of the warthog. However, the male babirusa has prominent maxillary canines which grow upwards in such a way that they pierce through the skin of the snout and curve over in front of the forehead (Figs. 1–4 and 7). The lower canines grow upwards alongside the snout and curve more gradually caudally. Whether the canines are important to display is not known. Moreover, whether those babirusa subspecies with longer hair coats use these in display also remains a matter for speculation.

"Boxing" was the ultimate form of agonistic behaviour exhibited by the babirusa under observation in the zoos. This form of agonistic behaviour has not been reported for any other species of pig with the exception of *Sus scrofa cristatus*, on the island of Sri Lanka (BARRETTE 1986). One of the main differences between these two sets of observations

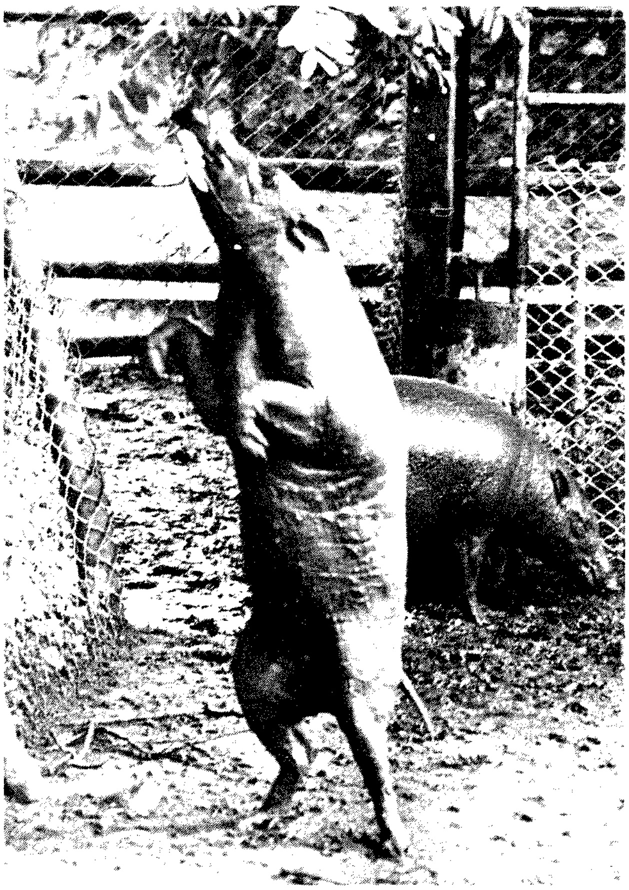

Fig. 6. An adult female balancing on her hind legs while browsing the leaves of a tree in the enclosure concerns the female animal; adult female babirusa were never seen to box with one another whereas this did occur between female wild boar. Female babirusa did have the ability to balance on their hind limbs, and were seen browsing in this position (Fig. 6). They were also occasionally seen to box with male babirusa whereas adult male and female wild boar were never observed boxing with one another (BARRETTE 1986). Another difference was that the babirusa would repeatedly rear up on their legs if they slipped or were toppled momentarily, whereas the first occasion that the wild boar was knocked off balance decided the competition (BARRETTE 1986). The third main difference between the two species was the lack of retreat shown by the babirusa when defeated; the superior animal, which was usually the largest and the one which stretched the tallest on its hind limbs, walked away from the loser. This is in marked contrast to the pursuit of the loser shown by the wild boar (FRÄDRICH 1967; BEUERLE 1975; BARRETTE 1986).

It is possible that "boxing" may not represent the most extreme form of fighting behaviour in babirusa. BARRETTE (1986) suggested that the behaviour shown by the wild boar in Sri Lanka was a mechanism allowing delay or avoidance of the relatively high risks inherent in a tusk fight between wild boar, as has been described for this species by BEUERLE (1975). Male babirusa have large canine teeth (Fig. 7) which are either absent or rudimentary in the female (MOHR 1960). It has been suggested that the upper canines may be used by one animal to hook one of the lower canines of his opponent; in this way the sharp maxillary canine of the opponent would be disarmed while he was free to inflict injury with his own lower canine to the opponent's eye, the side of his face or throat (GEIST 1966; MACKINNON 1981).

Our study of the anatomy of the maxillary canine showed that conflict of this sort is unlikely. The maxillary canine has a relatively shallow socket, whereas that of the lower canine occupies a large proportion of the length of the mandible (Fig. 7). This implied that large leverage forces would be placed on the root of the upper canine by the well anchored lower canine of the opponent during this suggested hooking manoeuvre (MACKINNON 1981; WHITTEN et al. 1987) which the socket of the upper tooth would not be competent to withstand. Moreover, the upper canine has been described as loose in its socket (MOHR 1960) and not very strong, being liable to split or break (HEINSIUS and VOGT 1916; MOHR 1960; SCHAFTENAAR 1991). On no occasion did we observe the interlocking of tusks in any of the zoos.

The use that the adult male babirusa makes of his canine teeth during agonistic behaviour remains incompletely known. GRAAFLAND (1898) suggested that the animals deliberately break their upper canines in order to make them better weapons. On the contrary, the evidence of the present study would indicate that the curved maxillary canine teeth are not used as weapons but as a shield preventing the lower tusks from reaching or deeply penetrating the opponent's body in most instances. With every upward thrust of the head towards the body of the opponent, it will be the curved upper tusks that first make contact with the opponent's body. The sole occasion that we witnessed one animal impaled on the lower canine of another was the result more of an accident than a deliberate attack. Indeed both animals seemed confused by the situation. The babirusa in Surabaya sometimes showed superficial scratch wounds on their shoulders, back and sides but we never saw how these were inflicted.

Ritualised fighting behaviours among other wild pigs have been divided into two categories; 1) frontal fighting involves head to head pushing and is shown by bush pig, warthog and giant forest hog and 2) lateral fighting which involves shoulder to shoulder pushing (either nose towards tail or head to head) is shown by wild boar (FRÄDRICH 1965). The presence of elaborate tusks, and the wear pattern on the upper tusks of *B. b. babyrussa* have been interpreted as evidence that frontal fighting might be used by this subspecies (FRÄDRICH 1965; MACKINNON 1981). Alternative explanations, such as the movement of stones and branches with the snout remain conceivable and may be preferable explanations

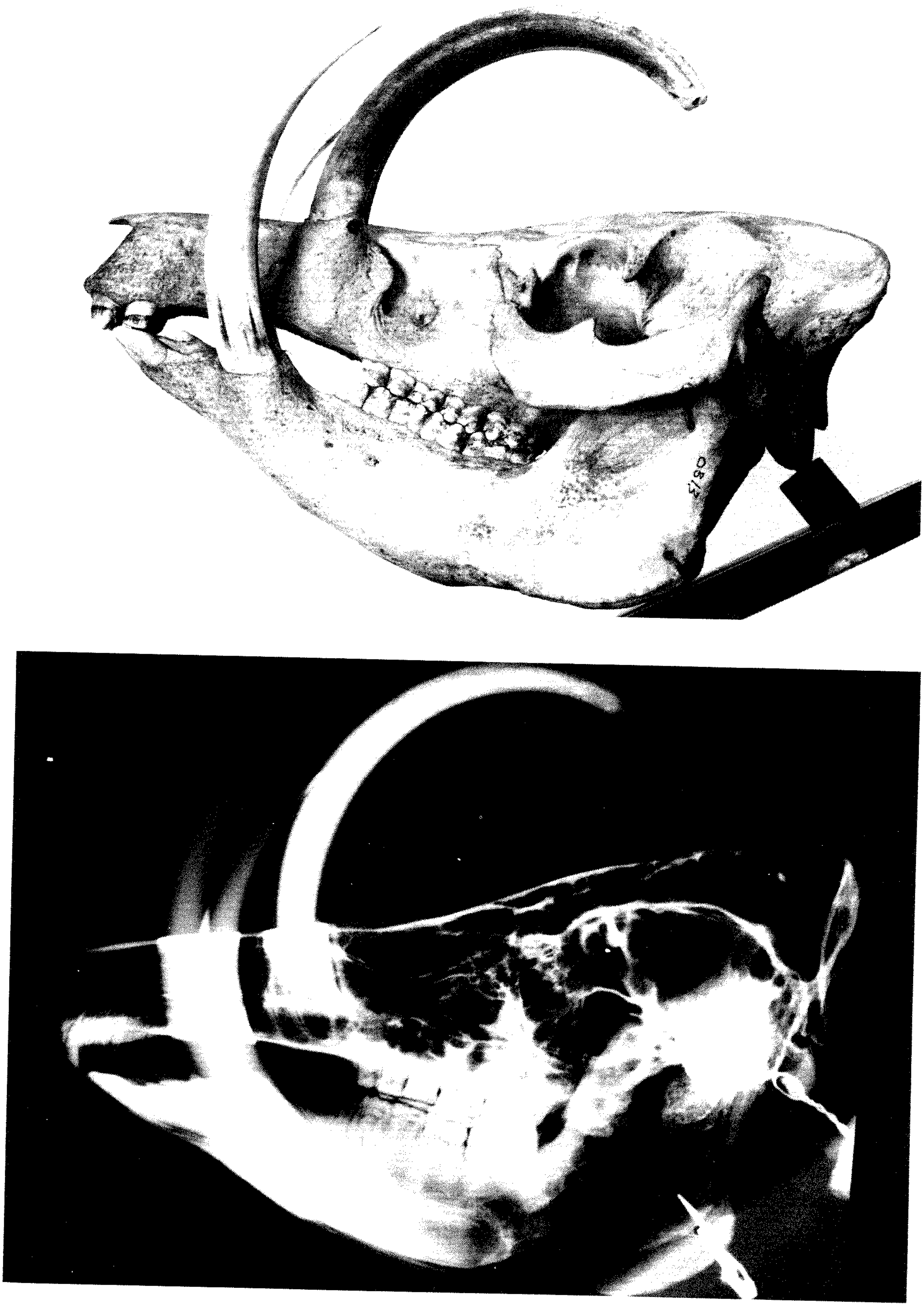

Fig. 7. The skull of an adult male babirusa (*Babyrousa babyrussa celebensis*) from Sulawesi (above) photographed and (below) X-rayed to demonstrate the shape, relative position and socket size of both the mandibular and maxillary canine teeth. Note that the socket of the maxillary canine tooth is significantly smaller than that of the mandibular canine

of wear when the relative fragility of the thinner canines in this subspecies is taken into account (MOHR 1960; GROVES 1980). We believe that "boxing" may correspond to an additional category of pre-ultimate fighting behaviour in pigs. The "wrestling" described for *Sus scrofa cristatus* on Sri Lanka seems to fall within this third category (BARRETTE 1986).

The outstretched head and neck with the head lowered is one of the submissive postures shown by a range of ruminant artiodactyla as well as by all the wild pigs (SIMPSON 1964; FRÄDRICH 1965; EWER 1968; CUMMING 1975; SEYDACK 1990). However, unlike wild boar, warthog, giant forest hog, and female babirusa, male babirusa do not run away in submission (FRÄDRICH 1965; CUMMING 1975; KINGDON 1989). Wild boar, warthog, bush pig, and babirusa all make a submissive noise when threatened or cornered (FRÄDRICH 1965; BEUERLE 1975; CUMMING 1975; SEYDACK 1990). The noise made by the babirusa is similar to that described in detail for the wild boar (KLINGHOLZ et al. 1979; BRIEDERMANN 1990).

Fights between female warthog, bush pig, and giant forest hog were carried out in the same manner as between male animals (FRÄDRICH 1965; CUMMING 1975). In contrast, the agonistic behaviour of the female babirusa differs from that of the male in a number of significant ways. Most noticeably, the female bites with her incissors more actively than does the male. A female submits by holding her head close to the ground; in this way she both indicates submission and protects her lower limbs from being bitten. In addition, the submissive scream is more prevalent than in the male. Thirdly, the alpha female babirusa tends to be very aggressive and persistent, like the alpha female bush pig (SKINNER et al. 1976; SEYDACK 1990); the inferior females seem to actively seek to avoid her attentions.

In the wild, agonistic behaviour of pigs is found in association with reproduction and with environmental resources such as food, water, nesting sites and hiding places. The amount, distribution and availability of these to the babirusa is presently unknown. It is therefore not yet possible, for example, to say whether this species exhibits a territorial claim on food, like the bush pig (SKINNER et al. 1976; SEYDACK 1990), or not as shown by the wild boar, warthog and giant forest hog (BEUERLE 1975; CUMMING 1975; D'HUART 1978). It is likewise not clear whether or not babirusa in the wild engage in agonistic encounters within the context of territorial claim for mating partners and/or any of the other environmental resources. Additional studies, of home range, social organisation and habitat exploitation in the wild are required in order to answer these questions.

Acknowledgements

The hospitality shown by PAK STANY SUBAKIR, PAK BAMBANG and PAK VINCENT HARWONO GEPAK and the help and cooperation of the staff of the Kebun Binatang Surabaya is gratefully acknowledged. The interest shown by Dr. LINUS SIMANJUNTAK and his staff at Kebun Binatang Ragunan, Jakarta, and the cooperation of the staff at Antwerp and at the Jersey Wildlife Preservation Trust was much valued. The hospitality of Freifrau ULLA VON MENGDEN and PAK DESIANTO was greatly appreciated. We acknowledge the help of Swaletreks for coordinating travel to Indonesia. Grateful thanks to the National Museums of Scotland for the loan of the babirusa skull (cat. no. 1989.073.061 – 0313) and COLIN WARWICK for photography. The financial support of the following organisations is gratefully acknowledged: Carnegie Trust for the Universities of Scotland; University of Edinburgh; Development Trust of the University of Edinburgh; Commission of the European Communities; Royal Zoological Society of Edinburgh; British Council; Wellcome Trust; James Rennie Bequest Fund; Weir Fund of the University of Edinburgh; Sir Stephen Watson Prize from the Edinburgh School of Agriculture; Duphar Veterinary Ltd.; Cotswold Pig Development Company Ltd.; Pig Improvement Company Ltd.; the Balloch Trust.

Zusammenfassung

Agonistisches Verhalten beim Hirscheber (Babyrousa babyrussa) in Gefangenschaft

An 95 Hirschebern aus Zoos von Indonesien, Belgien und den Kanalinseln wurden agonistische Verhaltenselemente in Abhängigkeit von Geschlecht, Körpergröße, Alter und Form der oberen Eckzähne untersucht. Insgesamt konnten 7 agonistische Verhaltensweisen erfaßt und beschrieben werden. Von diesen traten 3 regelmäßig in beiden Geschlechtern auf, 2 ausschließlich bei männlichen Individuen und 2 weitere hauptsächlich bei Männchen, gelegentlich aber auch bei Weibchen. Unterwerfung wurde stets durch gesenkten Kopf und besondere Lautäußerungen signalisiert. Die Eckzähne wurden nie als Waffen eingesetzt. Die Verhaltensweise "Boxen" ist typisch für Auseinandersetzungen zwischen männlichen Individuen, wohingegen weibliche Tiere stets versuchen, in die Vorderläufe der Gegnerin zu beißen. Adulte Weibchen waren gegenüber adulten Männchen unterwürfig, aber gegenüber sub-adulten Männchen dominant. Große Weibchen waren auch dominant gegenüber kleineren.

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Anim. Prod. 1993, **56**: 121-128
0003-3561/93/20680121$02·00

The effect of breed (Large White × Landrace *v.* purebred Meishan) on the diets selected by pigs given a choice between two foods that differ in their crude protein contents

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Abstract

Two pig breeds, one improved (Cotswold F1 hybrid Large White × Landrace pigs = LWX) and the other unimproved (Chinese Meishan pigs = CM) were used to test the proposition that the genotype of the pig has an effect on the selection of a diet from two foods that differ in their crude protein content. From 21 to 34 kg live weight, the pigs were given access to either one of three foods or a choice of two foods with similar digestible energy concentration (16 MJ digestible energy per kg) but a different crude protein (CP) concentration. This resulted in four dietary treatments: (i) free and continuous access to low (L) crude protein food alone (130 g CP per kg, no. = 4 of each breed); (ii) free and continous access to high (H) crude protein food alone (252 g CP per kg, no. = 4 of each breed); (iii) free and continuous access to moderate (M) crude protein food alone (206 g CP per kg, no. = 4 of each breed) and (iv) free and continuous access to both foods L and H as a choice (no. = 6 of each breed). On all treatments the LWX performed significantly better than the CM pigs in terms of live-weight gain and food conversion efficiency ($P < 0{\cdot}001$). The LWX and CM pigs given access to a single food contained the same amounts of protein in their bodies at 34 kg live weight, but the CM pigs had a considerably higher lipid ($P < 0{\cdot}001$) and a lower water content ($P < 0{\cdot}001$). When given a choice, the LWX pigs selected a significantly higher proportion of food H (521 v. *116 (s.e.d. 49) g food H per kg for LWX and CM respectively) and therefore, a higher CP content in their diet (194* v. *144 (s.e.d. 5·4) g CP per kg respectively) than the CM pigs. The performance of pigs given a choice between two foods, in terms of live weight and rate of protein gain, was comparable with the best performance achieved on a single food (M) for the LWX, and better than the best performance on a single food (L) for the CM pigs. Thus, when given a choice between an appropriate pair of foods that differ in their crude protein content, pigs are able to select a diet that meets their requirements and allows them to express the growth characteristics typical for their breed (genotype).*

Keywords: *breed, food preferences, growth, pigs, protein intake.*

Introduction

A theory of diet selection for pigs, based, in part, on recent experiments (Kyriazakis, Emmans and Whittemore, 1990 and 1991; Bradford and Gous, 1991a and b) has been developed. It suggests that pigs given a choice between a pair of appropriate foods that differ in their crude protein (CP) content, will select a diet that meets their requirements for maintenance, growth and fattening, and avoid, to some extent at least, excess protein intake. The theory has been tested, successfully, in a number of different ways. It has been shown, for example, that age does not influence the ability of pigs to select a diet that meets their protein requirement (Kyriazakis, Emmans and Taylor, 1993) and that both the sex of the pig and its state — defined as the level of fatness in the body — have a profound influence on its diet selection (Kyriazakis and Emmans, 1991), through differences in the animals' requirements for nutrients.

Another test of the theory of diet selection is to investigate the effect of the breed or genotype of the pig on its diet selection. The effect of genotype on diet selection has been the subject of a number of studies with a variety of other animals. Some of these have demonstrated an effect of genotype on diet selection (in chickens: Brody, Cherry and Siegel, 1984; Shariatmadari and Forbes, 1990; in rats: Anderson, Leprohon, Chambers and Coscina, 1979; Castonguay, Rowland and Stern, 1985), whereas others have been unable to do so (in chickens: Emmans, 1977; Rose, Burnett and Elmajeed, 1986). The reason for these latter failures was likely to have been the lack of sufficient differences between the different genotypes used.

The objective of this experiment was to test the proposition that the genotype of the pig, which influences the requirement for protein, has an effect on the selection of a diet from two foods that differ in their CP contents. In order to ensure a sufficient difference between the genotypes used, pigs from two very different breeds were used: a modern European breed (Cotswold F1 hybrid Large White × Landrace) and an unimproved breed (purebred Chinese Meishan). Apart from the differences in physical appearance between the two breeds (large, droopy ears, short snouts with wrinkles, a dropping belly and a large amount of skin organized in folds for the Chinese Meishan), the Chinese Meishan pig is also characterized by early sexual maturity, high prolificacy, slow growth, smaller mature size, and a higher fat content in the body, when compared with modern European breeds (Cheng, 1983 and 1984).

Material and methods

Animals and housing

Two pig breeds were used for this experiment, one improved (Cotswold F1 hybrid drawn from Large White × Landrace lines of pigs = LWX) and the other unimproved (Chinese Meishan pigs = CM). Twenty-two entire male LWX pigs from seven different litters out of the Edinburgh School of Agriculture pig herd and 22 entire male CM pigs from six different litters out of the Institute of Animal Physiology and Genetics Research herd were moved from the farrowing house immediately after weaning (at 4 and 6 weeks of age respectively) and housed individually in cages of the experimental unit described elsewhere (Kyriazakis *et al.*, 1990). When moved into the experimental unit, the LWX pigs had a mean live weight of 8·09 (s.d. 1·76) kg, and the CM pigs had a mean live weight of 11·95 (s.d. 2·61) kg.

According to the experimental procedure, each pen was provided with one or two metal food troughs with a tray underneath to collect spillage. The position of the pens with two food troughs was randomized within each room of the experimental unit. Free access to water was provided through a nipple drinker present in each pen.

Foods

Two basal foods (L and H) with similar calculated digestible energy (DE) contents, but different CP concentrations, were formulated and made into pellets (Table 1). Food L had a low CP concentration and was formulated to be inadequate to support potential growth when given alone and *ad libitum* (Agricultural Research Council (ARC), 1981). Food H had a high CP concentration and was intended to be above the requirements of the pigs. Both foods were intended to be non-limiting in minerals and vitamins but food H contained more macrominerals to maintain suitable ratios to protein. A mixture of food L and H was also made (food M = $^1/_4$ L + $^3/_4$ H) with a CP concentration of 206 g/kg, which was expected to be around the nutritional requirements of the LWX pigs (ARC, 1981). The chemical composition of food M is also shown in Table 1.

Table 1 *The composition and the chemical analyses (g/kg fresh weight) of the three foods*

	Foods		
	L	M ($^1/_4$L + $^3/_4$H)	H
Ingredients			
Oatflakes	822·75	481·99	368·40
Denatured skimmed milk	105	282·25	340
Herring meal		150	200
Soya oil		3	4
Threonine		0·45	0·60
Molasses	50	50	50
Vitamin and mineral supplement	5	5	5
Dibasic calcium phosphate	11	26·75	32
Limestone	6	1·50	
Salt	0·25	0·06	
Components			
Digestible energy (MJ/kg)†	15·3	15·5	15·6
Metabolizable energy (MJ/kg)‡	14·9	14·8	14·8
Dry matter	869	878	891
Crude protein	130	206	252
Ether extract	30	53	60
Ash	55	88	99
Crude fibre	33	25	23
Gross energy (MJ/kg)	15·9	16·4	16·5

† Values calculated from food tables.

‡ Calculated by the ARC (1981) equation ME/DE = 0·997 − 0·000189 CP (g/kg).

Design

Initially, all pigs were offered a high quality commercial food (Dalgety Agriculture, 300 Ultra Start pellets, with 190 g CP per kg) until they reached 17·5 kg live weight. At that stage, four pigs of each breed were slaughtered and their body compositions measured.

The remaining pigs were allocated to four treatments: (i) free and continuous access to food L alone (treatment L, no. = 4 of each breed); (ii) free and continuous access to food H alone (treatment H, no. = 4 of each breed); (iii) free and continuous access to food M alone (treatment M, no. = 4 of each breed) and (iv) free and continuous access to both foods L and H as a choice (treatment LH, no. = 6 of each breed). The allocation of pigs to the treatments was randomized and balanced as far as possible for litter origin. The position of the troughs for the choice-fed pigs was randomized across pigs and was not changed throughout the experiment, since pigs do not select their diet on the basis of the food position (Kyriazakis *et al.*, 1990).

The pigs were allowed to sample independently the two foods that subsequently were going to be offered as a choice (food L and H). These foods were offered alone and *ad libitum* on alternate days for a period of 6 days according to a method described by Kyriazakis (1989) which has been found to be an important part of a choice feeding training programme. The pigs that subsequently were going to be fed on the single foods were also submitted to this training period in order to make the results of the single- and choice-fed pigs comparable.

The experiment ended when each individual pig reached 34 kg live weight at which point they were all slaughtered and their bodies chemically analysed.

Management and slaughter procedures

The slaughter procedures, chemical analyses and management of the pigs were as described by Kyriazakis and Emmans (1991) with the exception that, after slaughter, in this case only the liver, bladder and gastrointestinal tract were removed and weighed separately. The empty bodies were analysed for dry matter (DM), and the nitrogen (N), ash and gross energy (GE) contents of the DM. The lipid contents of the DM were calculated from the GE (kJ/g DM) and N (g/g DM) values, using the equation:

$$\text{lipid (g/g DM)} = (\text{GE}) - (23{\cdot}8 \times 6{\cdot}25 \times \text{N})/39{\cdot}6 \quad (1).$$

The air temperature was set at 26°C when the pigs were first moved and was subsequently lowered by 1 to 1·5°C per day. The temperature aimed at was 16°C at 17·5 kg live weight in order to avoid limitation, as far as possible, of the food intake and therefore growth rate, by a too high an environmental temperature (Kyriazakis and Emmans, 1991).

Analysis of the results

The results were treated as a randomized design and were analysed by an analysis of variance with treatment and breed as variates. For the analyses of live-weight gain, food intake and food conversion efficiency the live weight at the end of the 6-day experience period was used as covariate. In all of the other analyses the covariate used was the live weight at the beginning of the experimental period. One CM pig on treatment M was excluded for health reasons, and its data were treated as missing values.

The path of diet selection was traced by plotting the cumulative difference between the intakes of the two foods $(X - Y)$ against the cumulative food intake $(X + Y)$ (Kyriazakis *et al.*, 1990).

Results

Diet selection of the pigs given a choice

There was a highly significant effect of breed ($P < 0{\cdot}001$) on the proportion of food H selected, with 521 and 116 (s.e.d. 53) g food H per kg total food intake selected by the LWX and CM pigs respectively (Figure 1a). This difference was reflected in the average CP contents of the diets selected over the entire experimental period which were 194 and 144 (s.e.d. 5·4) g CP per kg fresh food for the LWX and CM pigs respectively (Figure 1b).

The LWX pigs showed a preference for food H in the first part of the experimental period but this then declined and finally changed to a preference for food L. Thus, the content of CP in the diets selected by the LWX pigs declined very rapidly (from 215 to 170 g CP per kg) with increasing age, and therefore increasing live weight (Figure 2). The CM pigs did not select diets similarly. The plots of the individual paths of diet selection of the CM pigs (Figure 3) show that four pigs followed a similar path of diet selection and kept their preference for food L throughout the whole experimental period. Two other pigs showed a brief period of indifference between L and H, after which they also changed towards a preference for food L.

Growth and carcass composition for all pigs

The pigs had reached a live weight of 20·5 kg at the end of the experience period. The effect of treatment on the daily live-weight gain, food intake (FI) and the food conversion efficiency (FCE) for both breeds

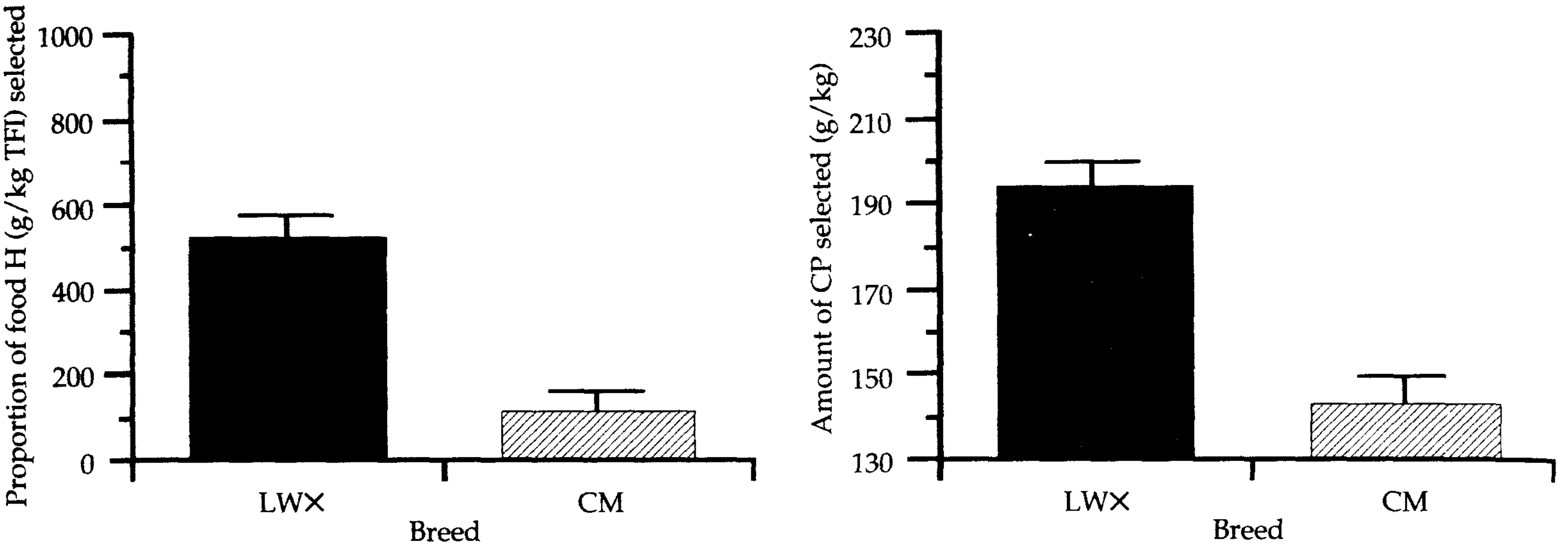

Figure 1 The diet selected by Large White × Landrace (LWX ■) and Meishan pigs (CM ▨) given access to two foods as a choice: the proportion of the high (H) protein food (kg/kg total food intake) and the crude protein (CP) (g/kg) of the selected diets.

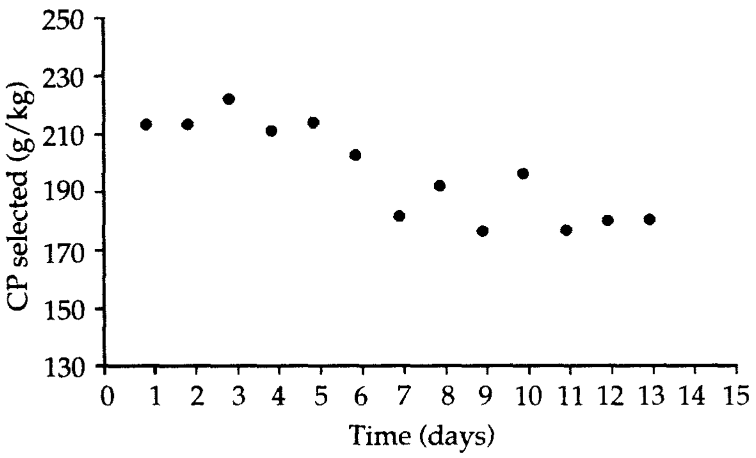

Figure 2 The crude protein content (g CP per kg fresh food) of the diets selected over time by six Large White × Landrace pigs given a choice between foods L and H.

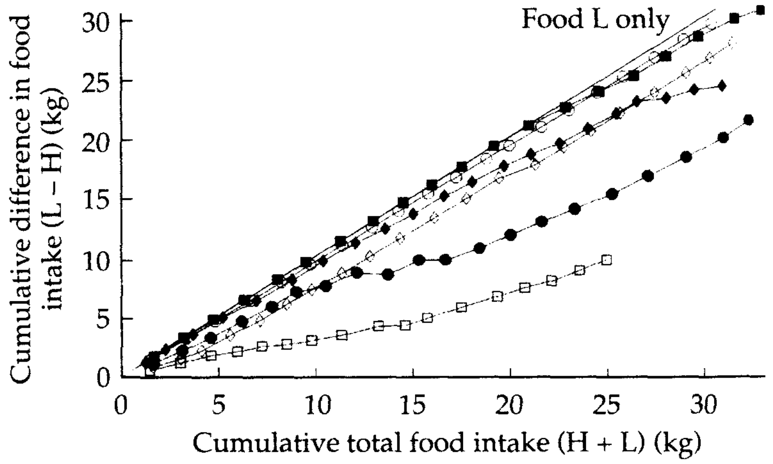

Figure 3 The paths of diet selection of six Meishan pigs given a choice between foods L and H. Each line refers to an individual pig.

Table 2 *Breed and treatment effects on food intake (FI), live-weight gain (LWG) and food conversion efficiency (FCE) of pigs from 20·5 to 34 kg live weight*

Breed	Treatment	FI (g/day)	LWG (g/day)	FCE (g gain per g intake)
Large White ×	L	1461	648	0·442
	M	1295	834	0·641
	H	1251	831	0·659
	LH	1328	842	0·635
Chinese	L	1533	552	0·367
Meishan	M	1359	532	0·391
	H	1207	509	0·422
	LH	1538	636	0·414
s.e.d.		91	51	0·034
Significance of† :				
Breed		*	***	***
Treatment		**	**	***
Breed × treatment			*	**

† There were no significant effects of the covariate.

from 20·5 to 34 kg live weight is shown in Table 2. On all feeding treatments, the LWX performed significantly better ($P < 0·001$) than the CM pigs in terms of live-weight gain and FCE. There was a significant interaction between treatment and breed ($P < 0·01$) for live-weight gain and FCE, which was the result of the poor performance of the LWX pigs on food L (648 *v.* 836 g (s.e.d. 51) g/day and 0·442 *v.* 0·645 (s.e.d. 0·034) g/g for live-weight gain and FCE respectively). The growth rate achieved by the choice-fed LWX pigs was not significantly different from the highest growth rate achieved on a single food, which was observed on food M. The highest growth rate of CM pigs given access to one food was achieved on food L. The choice-fed CM pigs, however, had a somewhat higher growth rate than that of the CM pigs on food L.

The LWX pigs had an overall lower FI than the CM pigs of 1334 *v.* 1409 g/day. For both breeds, the pigs on food L had the highest FI and the lowest FCE and

Table 3 *Breed and treatment effects on the chemical composition of the empty body of pigs at 34 kg live weight*

Breed	Treatment	Live-weight gain	Empty body	Component weights (kg) Protein	Ash	Lipid	Water	Gross energy (MJ)	Protein: ash ratio	Lipid: protein ratio	Water: protein ratio
Large White ×	L	34·40	32·65	4·825	0·958	4·646	21·582	29·88	5·06	0·97	4·47
	M	34·07	32·30	5·101	0·896	3·156	22·587	24·64	5·70	0·62	4·43
	H	33·53	32·17	5·229	0·986	2·940	22·527	24·09	5·30	0·56	4·31
	LH	34·32	32·93	5·275	0·935	3·383	22·792	25·95	5·66	0·65	4·32
Chinese	L	33·70	31·79	4·874	0·913	5·965	19·317	35·22	5·34	1·22	3·97
Meishan	M	34·36	32·11	4·995	1·044	4·904	20·507	31·31	4·78	0·99	4·11
	H	31·14	32·30	5·208	1·026	5·029	20·441	32·31	5·08	0·97	3·93
	LH	34·15	32·49	5·002	0·960	6·106	19·750	36·09	5·22	1·23	3·95
s.e.d.		0·39	0·47	0·160	0·043	0·555	0·570	2·02	0·18	0·13	0·09
Significance of†:											
Breed						***	***	***	***	***	***
Treatment						**	*	**		**	
Breed × treatment				*	*				***		

† There were no significant effects of the covariate.

FI decreased and FCE increased with rising protein content of the food.

The body compositions at 34 kg live weight are shown in Table 3. The CM pigs tended to have a lower empty body weight than the LWX pigs, which reflected their higher gut-fill, but this effect was not significant. Body protein weight at 34 kg live weight was not affected by breed and only slightly affected ($P < 0·05$) by treatment. The latter was mainly due to the lower protein weights of the LWX on food L (4·83 *v.* 5·20 (s.e.d. 0·16) kg). On all treatments CM pigs had a higher lipid weight ($P < 0·001$) and GE content ($P < 0·001$) in their empty bodies, than the LWX pigs. Treatment had a significant effect on both body lipid weight and GE content ($P < 0·01$), since pigs on food L had a higher lipid weight than pigs on M, H and, in the case of LWX pigs, LH. Water weight was affected mainly by breed, with LWX having a higher water weight than CM pigs (22·37 *v.* 20·00 (s.e.d. 0·57) kg respectively; $P < 0·001$) and treatment ($P < 0·05$); the LWX pigs on L, and CM pigs on L and LH, had the lowest water weights in their bodies. Ash weight at 34 kg live weight, was not significantly affected by breed or treatment.

LWX pigs had a significantly ($P < 0·001$) lower lipid : protein ratio, and higher protein : ash and water : protein ratios in their bodies, than CM pigs. The treatment effect on these ratios was significant only for the lipid : protein ratios ($P < 0·001$), due to the higher ratio in the bodies of pigs on L. There was a highly significant interaction ($P < 0·001$) between breed and treatment on the protein : ash ratio, since this ratio was significantly affected by treatment only for LWX pigs on L (5·06 *v.* 5·55; s.e.d. 0·18).

The rates of tissue deposition from 17·5 to 34 kg live weight are shown in Table 4. There was a significant interaction between breed and treatment on the rates

Table 4 *Breed and treatment effects on the daily deposition rates of protein, ash, lipid, water and gross energy (GE) in the empty body of pigs from 17·5 to 34 kg live weight*

Breed	Treatment	No.	Rates of tissue deposition (g/day) Protein	Ash	Lipid	Water	GE (MJ/day)
Large White ×	L	4	86	19	104	359	6·15
	M	4	134	24	70	546	5·98
	H	4	137	28	56	527	5·46
	LH	6	131	24	73	514	6·03
Chinese	L	4	85	17	108	323	6·29
Meishan	M	4	86	21	73	350	4·90
	H	4	91	20	74	341	5·10
	LH	6	100	21	127	381	7·42
s.e.d.			11	2	25	36	1·00
Significance of†:							
Breed			***	***		***	
Treatment			***	**	*	***	
Breed × treatment			*			*	

† There were no significant effects of the covariate.

of protein and water deposition ($P < 0{\cdot}05$). This was due to the slower rates of protein and water retention achieved by the LWX pigs given access only to food L. Both LWX and CM pigs on food L, and CM pigs on LH, grew lipid at a faster rate than pigs on the other treatments ($P < 0{\cdot}01$). On all treatments, LWX pigs grew protein, ash and water at significantly faster rates than CM pigs, but the rate of lipid deposition was similar between the two breeds. For both breeds, pigs given a choice between two foods (treatment LH) grew protein, ash and water at rates comparable with the highest rates obtained on a single food.

Discussion

The LWX and CM pigs given access to a single food contained the same amounts of protein in their bodies at 34 kg live weight, but the CM pigs had considerably higher lipid, and lower water, contents. These results are consistent with previous comparisons between these two breeds by Bonneau, Mourot, Noblet, Lefaucheur and Bidanel (1990), who reported that, at the same live weight, CM pigs, as representative of an unimproved breed, have a high lipid content in their bodies. The lower weights of water in the bodies of the CM pigs may have been partly due to the fact that these pigs, compared with the LWX, had a higher proportion of skin in their body and therefore contained a larger amount of skin protein that has less water associated with it. Bonneau *et al.* (1990) reported that the proportion of skin in the empty bodies of castrated male pigs at 30 kg live weight, was twice as great in the CM as in the pure Large White pigs (77 and 38 g/kg respectively). Because the CM pigs took a longer time to reach 34 kg live weight, they had slower rates of protein, ash and water deposition.

The two breeds also differed in their responses to the single-feeding treatments. The fastest live-weight gain of the LWX pigs was achieved by pigs given access to food M, and the slowest by pigs on food L. The latter reflected the inadequate protein content of food L for LWX pigs. By contrast, the highest growth rate of the CM pigs was achieved on food L and the poorest on food H. However, the difference between the two extremes was small, not significant ($P < 0{\cdot}05$), and mainly associated with faster lipid gain. Given that the protein growth of the CM pigs on the three foods was similar, it is likely that pigs on food L met their protein requirements, at least for a period, by increasing their rates of food intake. It is concluded from the performance of the single-fed pigs that food L was much more limiting in protein for the LWX pigs than it was for the CM pigs and that the protein requirements of the CM pigs were lower than those of the LWX pigs. There is no other information, to our knowledge, on the protein requirements of the CM pigs or on their responses to foods of different protein contents. The growth rates achieved by CM pigs on food L are higher than the ones reported in the literature for pigs of the same live-weight range (Bonneau *et al.*, 1990; Haley, d'Agaro and Ellis, 1992). In these experiments the CM pigs were given a food similar to that given to the LW pigs. They were therefore fed on a high protein diet which, as shown in this experiment, reduces their growth rate probably through a limitation imposed by the thermal environment. The differences in growth rate between experiments are also likely to reflect differences in the thermal environments. The pigs in this experiment were kept at 16°C, instead of a temperature of 22°C at which pigs are usually kept, because we did not want to impose any constraints on their growth through their abilities to dissipate heat (Kyriazakis and Emmans, 1991).

Given the performance of the pigs on a single food it would be expected that LWX pigs would need to choose a higher CP content in their diet than the CM pigs if they were to meet their protein requirements. In fact the LWX pigs selected diets with 194 g CP per kg food while the CM pigs selected diets with 144 g CP per kg ($P < 0{\cdot}01$). The CP concentration of the diet selected by the CM pigs reflected their clear preference for food L throughout the experiment. By contrast, the average proportion of food L or H selected by the LWX pigs was not different from random selection (i.e. equal intakes of both foods). However, the proportion of food H, and consequently the CP concentration of the diet selected by these pigs, declined rapidly with increasing live weight and age, and it was only fortuitous that the average proportion of food H selected was not different from random selection. It is therefore concluded that both breeds of pigs selected their diet in a systematic and non-random way when given foods L and H as a choice.

The performance of the pigs given a choice between two foods, in terms of live weight and protein gain, was comparable with the highest performance achieved on a single food for the LWX, and better than the highest performance on a single food for the CM pigs. The performance of the latter might reflect the fact that, for the early stages of the experiment, food L was somewhat limiting in protein. Since the choice-fed CM pigs had the opportunity to select a higher CP content than that of food L, they grew slightly better than the pigs fed on food L alone which did not have such a choice. However, as the protein requirements of the pigs declined with time and live weight, the choice-fed pigs had their requirements met by food L only. It is also possible that their protein requirements could be met by a food with a lower CP content than food L, at the heavier live weights reached in the later stages of the experiment, but the pigs did not have such an option. The fact that even in the last stages of the experiment, the CM pigs did consume some small amounts of food H is consistent with previous experiments (Kyriazakis *et al.*, 1990; Bradford and Gous, 1991a) and probably reflects the need of the animals to continue to sample their environment in order to keep informed about the foods on offer (Lea, 1979).

There were small, but consistent, differences in the diets selected by individual pigs within a breed. Since all pigs were kept in identical environmental conditions, these differences could be attributed to small differences in genotypes among pigs within a breed. However, the differences in the diets selected by pigs, of the different breeds clearly exceeded those expressed by pigs of the same breed. Thus, when given a choice between two appropriate foods that differed in their CP concentration, the pigs selected a diet that met their requirements and allowed them to express the growth characteristics typical for their breed. This complies with the previously stated theory of diet selection. The reason that some of the previous attempts to test the effect of the genotype of an animal on its diet selection have failed to demonstrate an effect (Emmans, 1977; Rose *et al.*, 1986), lies in the fact that the differences between the genotypes on test were not sufficiently large to overcome the variation in the diet selection within a breed or a strain. This was best demonstrated in the experiment of Rose *et al.* (1986), where the two strains of chickens used were so similar that they had to be identified by toe-clippings. By contrast, the effect of genotype on diet selection was clear in the experiment of Brody *et al.* (1984), who used chickens which had undergone selection for a high or low live-weight gain for 24 generations. The birds from the fast live-weight gain strain, with probably a greater requirement for protein, selected a higher amount of protein in their diet.

The results of the above experiment suggest that the method of diet selection can be used to determine the requirements of an animal when these are unknown. The animal is thereby allowed to express the growth characteristics and body composition determined by its genotype. Instances where the requirements of animals are unknown can include the introduction of new animal genotypes created by genetic manipulation and the keeping of wild animals in captivity.

Acknowledgements

This experiment was supported by an AFRC/BOCM Silcock cooperative research grant and KL was supported by a bursary of the Commission of the European Communities. We gratefully acknowledge the financial help of these organisations, as well as that of the Development Trust of the University of Edinburgh. We would also like to thank T. McHale, D. H. Anderson and J. Fraser for their technical support.

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(*Received* 22 *June* 1992—*Accepted* 1 *September* 1992)