DIET OF TREE HYRAXES *DENDROHYRAX ARBOREUS* (HYRACOIDEA: PROCAVIIDAE) IN THE EASTERN CAPE, SOUTH AFRICA

ANGELA GAYLARD AND GRAHAM I. H. KERLEY

Terrestrial Ecology Research Unit, Zoology Department, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, South Africa

This study identified the dietary composition of the arboreal tree hyrax *Dendrohyrax arboreus*, a rare, poorly known, forest mammal, in three eastern Cape forests. Fecal analysis showed *D. arboreus* to be a selective browser with an average of 7.2, 12.4, and 9.5 species of plants in the diet at the Pirie, Alexandria and Springmount forests, respectively. The economically important yellowwood *Podocarpus falcatus* was the principal dietary item at Pirie forest, whereas the principal dietary items at Alexandria forest were *Schotia latifolia*, *Cassine aethiopica*, and *Eugenia capensis zeyheri*. Principal food items at Springmount forest were *S. latifolia* and *Euclea natalensis*. Dietary preferences could not be explained by dietary abundance of plants, and appear to be related to the complex energetics of arboreal folivory. This delicate energy balance, together with the fact that the tree hyrax is a selective feeder, has implications for the selective removal of plant species from forests of the eastern Cape.

Key words: *Dendrohyrax arboreus*, arboreal folivore, diet, fecal analysis, South Africa

Mammals in the mass range of arboreal folivores (<15–20 kg) are predicted to face severe problems meeting energy requirements from fibrous diets (Cork and Foley, 1991), because retention time of the gastrointestinal tract varies as a fractional power of body mass ($W^{0.28}$) and smaller animals have lower digestive efficiencies (McNaughton and Georgiadis, 1986). Folivores must be able to use fiber as their main source of digestible energy or maintain a sufficiently high intake of foliage from digestion of contents of the cells. Because many arboreal folivores live close to the limit of their energy budgets, they have certain characteristics in common (Eisenberg, 1978). These include decreased speed of locomotion, small size of home ranges and litters, a relatively dense pelage, and heat-conserving mechanisms. Herbivores feeding primarily on woody foliage of plants also have significantly lower metabolic rates (Mattson, 1980). Folivores often have antipredator strategies that depend on crypticity and they seldom live in large groups and frequently are nocturnal. They also have well-developed communication systems for localizing their positions relative to one another (Eisenberg, 1978).

The tree hyrax *Dendrohyrax arboreus arboreus* is a small (1.5–3.35 kg—Kingdon, 1971) forest mammal residing in the indigenous forests of the eastern Cape and Kwazulu-Natal, South Africa. Elsewhere in Africa the species occurs along the eastern side of the continent in Uganda, Kenya, Tanzania, Zaire, Zambia, Malawi, and Mozambique (Skinner and Smithers, 1990). It belongs to the only genus of hyracoid that typically is arboreal and folivorous (Cork and Foley, 1991; Eisenberg, 1978). This species is classified as rare in South Africa, apparently due to loss of habitat (Smithers, 1986). A recent study, however, failed to demonstrate loss of indigenous forests in the eastern Cape over the past 50 years (Castley and Kerley, 1993), and we hypothesize that this species may be limited by the loss of specific resources within its habitat. This study addresses the issue of the dietary resources of *D. a. arboreus* in the eastern Cape, South Africa.

The high-quality food items needed by arboreal folivores are rare in the environment and small species like *D. arboreus* are expected to have feeding apparati that allow for a greater degree of selectivity. This has led to considerable morphological change in dentition, musculature of jaws, and morphology of the gastrointestinal tract (Eisenberg, 1978). The relatively narrower muzzle of *D. arboreus* has been related to a selective, browsing diet, and the central incisors are broader than the lateral ones, allowing for the selective picking of individual leaves from twigs (Janis, 1988). Furthermore, the enlarged surface of the molars permits more effective mastication of plant material and increases the ease of direct digestion of starch or indirect digestion of cellulose by microbial symbionts (Eisenberg, 1978). Brachydont premolars and molars are an additional indication of browsing (Walker et al., 1978).

As a small, arboreal folivore, *D. arboreus* is expected to select foliage low in fiber and high in available energy or nitrogen (Cork and Foley, 1991; Cork and Sanson, 1990). It has been assumed that the diet of the eastern Cape tree hyrax consists largely of browse in the form of leaves, as well as fruit, the young shoots of trees, and possibly grass, as in the other subspecies of *D. arboreus*. The East African subspecies also is purported to eat insects (Skinner and Smithers, 1990). However, because of the difficulties of studying this secretive, nocturnal species, composition of its diet remains anecdotal. The objectives of our study were to determine the use of species of plant by *D. a. arboreus* in the eastern Cape, and to ascertain the dietary preferences of *D. a. arboreus* by comparing plants eaten to their natural abundances.

Materials and Methods

The study was conducted at three forest sites in the eastern Cape, South Africa (Fig. 1), representing a range of elevations and forest types. One study site was situated in the montane forests of the Amatola Mountains at the Pirie Forest Reserve (32°43′S, 27°16′E), whereas lowland forest was represented at both wetter inland (henceforth referred to as Alexandria; 33°48′S, 26°42′E) and drier coastal (henceforth referred to as Springmount; 33°42′S, 26°03′E) sites in the Alexandria State Forest.

Vegetation at Pirie is high forest, typical of the eastern Cape (Greyling and Huntley, 1984) with dominant species including the economically important species of yellowwoods, *Podocarpus falcatus* and *P. latifolius*. Structure of the vegetation in the Alexandria State Forest varies between thicket (near the coast) and forest (further east and inland) with dominant species including *P. falcatus*, *Strychnos decussata*, *Euclea*, and *Sideroxylon inerme*.

The Pirie Forest Reserve falls within the Steppe climatic type (Kopke, 1988) with ≥8 months having temperatures >10°C and the warmest months >22.2°C. Annual rainfall is ≤1,800 mm. Both Alexandria and Springmount sites are classified as subtropical (Kopke, 1988) with monthly mean temperatures ranging from 9.2 to 25.5°C. Average annual rainfall at the Alexandria Forest Station is 934 mm (Greyling and Huntley, 1984), although the coastal site receives substantially less rain (392 mm at the Sundays River station, ca. 10 km to the west).

Diet was investigated by microscopic fecal analysis. Although this technique has several shortcomings, it is the only feasible procedure for studying the diets of secretive, nocturnal, or endangered herbivore species where observations or culling are not possible (Anthony and Smith, 1974; Loggers, 1991).

During each field survey, specimens of plants were collected in the vicinity of den trees of tree hyraxes for a reference collection. Plants were identified by comparison to material in the Ria Olivier Herbarium, University of Port Elizabeth, and in consultation with botanists familiar with the study area. Nomenclature follows Gibbs Russell et al. (1985, 1987).

The method used to remove the epidermi was modified from Storr (1961) and McAllister and Bornman (1972). Leaf material was cut into 15-mm lengths and boiled in 10% nitric acid in a flask attached to a vacuum. The cuticle layer was removed, stained lightly with haemotoxylin, and permanently mounted on a microscope

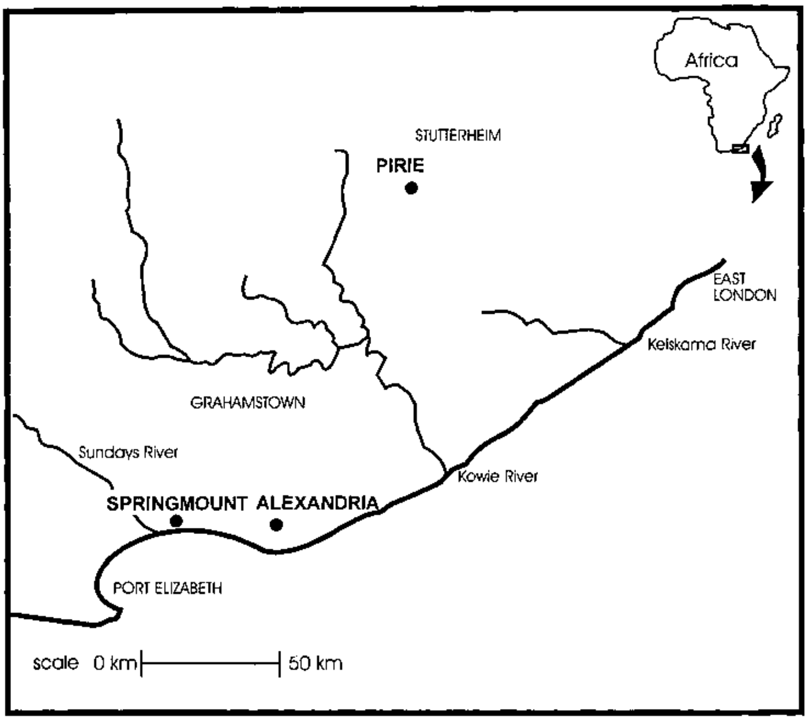

FIG. 1.—Location of the study sites in South Africa for examining diets of eastern Cape tree hyraxes by fecal analysis.

slide. Both the adaxial and abaxial surfaces of the plant cuticles were photographed, producing a reference collection of color prints.

For identification of fragments of dietary plants to species, a key to species found at the study sites was compiled using the computer program DELTA (Dallwitz and Paine, 1986). The program uses a standardized format for coding taxonomic descriptions to create printed keys and natural-language descriptions and to run interactive keys (Partridge et al., 1986). The interactive key (INTKEY) was used during the microscopic identification of fragmentary material in the fecal samples (Gaylard and Kerley, 1995).

Fecal pellets were collected seasonally on four occasions during June 1992–June 1993 at the three study sites by systematically searching for latrines of tree hyrax in hollow trees. Five randomly selected pellets from each fecal sample were broken and digested in 4 ml of concentrated nitric acid over low heat for ca. 2 min. Samples were then made up to 100 ml with distilled water, boiled, and stirred. The resulting sample was centrifuged for 15 min at 2,000 RPM and the supernatant discarded. The remaining cuticle fragments were stored in 5 ml FAA (25% distilled water, 60% absolute alcohol, 10% formalin, and 5% glacial acetic acid) until analysis.

During analysis, a subsample of prepared fecal fragments was placed on a gridded microscope slide and viewed at 400x magnification. According to Dusi (1949), a small fraction of a fecal pellet spread homogeneously under a coverslip contains all food items in the sample. A fragment could be identified positively if it contained enough characteristics for DELTA to recognize, notably shapes and sizes of cells. Fragments containing sufficient characteristics for identification, but nevertheless unrecognizable (i.e., not in the reference collection), were recorded as unknown monocotyledons or unknown dicotyledons. Fragments with insufficient characteristics for identification were recorded as unidentified monocotyledons or unidentified dicotyledons and small unidentifiable fragments were ignored. The first 100 fragments were scored in terms of their frequency of occurrence. An index of the diversity (H′) of diets was cal-

TABLE 1.—*Principal dietary species of plants (constituting ≥10% of the species identified in the diet) of eastern Cape tree hyraxes; blank = species absent from the site.*

Family	Species	Percentage consumed		
		Pirie	Alexandria	Springmount
Caesalpinoideae	*Schotia latifolia*	4.58	38.38	47.31
Celastraceae	*Cassine aethiopica*	2.0	16.13	8.31
Ebenaceae	*Euclea natalensis*	0.05	0.75	18.75
Myrtaceae	*Eugenia capensis zeyheri*	0.32	15.63	1.06
Podocarpaceae	*Podocarpus falcatus*	74.95	4.63	

culated for each site following Pielou (1975), where $H' = \Sigma P_i \ln P_i/n$.

Measuring selectivity of diet requires comparison of the relative abundances of food items available to an animal with the relative consumption of food items by an animal (Norbury and Sanson, 1992). An index of availability of plants was estimated as abundance of species of plant, expressed as a percentage of estimated cover of plants, determined using the canopy point-intercept method (Lensing and Le Roux, 1982; Mueller-Dombois and Ellenberg, 1974). At each study site four 30-m replicates were surveyed at intervals of 20 cm during June 1993. Replicates were surveyed in different areas of each study site to account for habitat heterogeneity. A preference index (percentage consumption/percentage availability) was calculated to indicate the extent of use of species of plants in relation to their availabilities. Species present in the diet but not intercepted during the point transect were assigned a value less than the minimum value measured for any species at that site. A preference index >1.0 indicates selection for that item, whereas a value of <1 indicates that the item was consumed in proportions less than its abundance in the environment would suggest. Principal food items were defined as those species that were eaten in proportions of ≥10% (Lensing, 1983), and strong selection (or preference) for a species occurred when its preference index value was >10.

RESULTS

Forty-three fecal samples (from 36 latrines, as certain latrines could be resampled in subsequent seasons if they were still active) were collected during the study period. Age of feces at time of collection could not be determined reliably and we did not consider temporal changes. Of the latrines located, 14 (19 samples) were at Pirie, 8 at Alexandria, and 14 (16 samples) at Springmount.

The reference collection of plants comprised 141 species of plants found at the study sites (Gaylard and Kerley, 1995). Of these, 21 species could not be identified reliably because they lacked fruit or flowers at the time of collection and were too rare to be encountered subsequently. These specimens were assigned reference numbers for inclusion in the identification key, were noted as dicotyledonous or monocotyledonous species, and were placed in the Ria Olivier Herbarium, University of Port Elizabeth.

Thirty-six species of plants were identified in feces of tree hyraxes in the Pirie Forest Reserve (Appendix I) with 1–16 species/sample ($\bar{X}$ = 7.2; ±1 *SD* = 4.9). A mean of 58.9% of the material was identifiable and <2% of the material comprised unknown species of plants. *P. falcatus* was the principal dietary species at Pirie, constituting nearly 75% of the diet at this site (Table 1). As a result, diversity of the diet was low (H′ = 0.8). Twenty-three species of plants (comprising 72% of the species eaten) were selected for at this site. Strongly selected species (in descending order of preference) included *Cynanchum*, *Teclea natalensis*, *C. aethiopica*, *Dovyalis rhamnoides*, *P. falcatus*, *S. latifolia*, and *S. inerme* (Table 2).

The diet of tree hyraxes at Alexandria consisted of 33 identifiable species of plants

TABLE 2.—*Percentage relative abundance and preference indices (PI) for strongly selected (PI ≥ 10) dietary plants of eastern Cape tree hyraxes; * = species present at the site, but absent from the diet, blank = species absent from the site.*

		Pirie		Alexandria		Springmount	
Family	Species	Percentage abundance	PI	Percentage abundance	PI	Percentage abundance	PI
Anacardiaceae	*Rhus*			0.00	>12.5	*	*
Apocynaceae	*Carissa bispinosa*	1.17	0.90	0.04	106.3	0.12	3.2
Caesalpinioideae	*Schotia latifolia*	0.16	28.60	0.00	>959.5	0.89	53.2
Celastraceae	*Cassine aethiopica*	0.00	>50.0	0.00	>404.3	4.90	1.7
Ebenaceae	*Euclea natalensis*	0.00	>1.3	0.00	>18.8	0.00	>312.5
	Euclea schimperi	0.60	1.3	1.73	4.3	2.19	168
Euphorbiaceae	*Acalypha glabrata*	*	*	17.83	0.00	*	*
Flacourtiaceae	*Dovyalis rhamnoides*	0.00	>50.0	3.95	0.3	0.59	0.9
Hernandiaceae	*Maerua*					0.00	>19.8
Luzuriagaceae	*Behnia reticulata*	0.12	2.6	0.00	>9.5	0.06	43.8
Oleaceae	*Chionanthus*	10.03	0.01				
Podocarpaceae	*Podocarpus falcatus*	1.61	>46.6	3.58	1.3		
Rutaceae	*Teclea natalensis*	0.00	>51.3	0.70	1.25		
Sapotaceae	*Mimusops obovata*	0.4	0.1	0.00	>90.8	0.00	>9.3
	Sideroxylon inerme	0.00	>25	0.00	>22	11.30	0.4
Vitaceae	*Cynanchum*	0.00	>147.4				
	Rhoicissus tomentosa	*	*	5.68	0.2	0.00	>10.5
Unidentified	Dicotyledon (U1)	0.00	>1.8	0.00	>22	0.00	>4.2
	Dicotyledon (U36)			0.00	>15.8		

(Appendix I), the number of species in a sample ranging from 5 to 21 ($\bar{X}$ = 12.4; ± 1 *SD* = 5.3). Unknown species accounted for 0-6.2% of the diet. *S. latifolia*, *C. aethiopica*, and *Eugenia capensis zeyheri* were the principal food plants at Alexandria with >33% of the diet comprising *S. latifolia* (Table 1). Twenty-four species of plants (comprising 80% of the species eaten) were selected for at Alexandria, with strong selectivity exhibited for nine species; *S. latifolia*, *C. aethiopica*, *Carissa bispinosa*, *Mimusops obovata*, *S. inerme*, *E. natalensis*, *Rhus*, and two other dicotyledons (U1 and U36; Table 2). Only one of these (*C. bispinosa*) was recorded during measurement of relative availability, indicating that species preferred by this population were not naturally abundant at this site. Although diversity of diet at Alexandria was higher than at Pirie (H′ = 1.8), only five species comprised >80% of the plants consumed.

Twenty-six species of plants were identified in feces of tree hyraxes at Springmount (Appendix I), the number of species in a sample ranging from 3 to 15 ($\bar{X}$ = 9.5; ± 1 *SD* = 2.8). A mean of 42.6% of the material was identifiable and unknown species of plants made up 0-3.4% of the diet. The principal food of the population at Springmount comprised only two species (*S. latifolia* and *E. natalensis*), which collectively made up 66% of the diet (Table 1). Diversity of diet was intermediate between the other two sites (H′ = 1.5). Fifteen species of plants (comprising 62.5% of the species eaten) were selected for at Springmount; *E. natalensis* being the most preferred item. Other strongly selected species were *E. schimperi*, *S. latifolia*, *Behnia reticulata*, *Maerua*, and *Rhoicissus tomentosa* (Table 2).

The proportion of monocotyledonous species eaten was low at all sites (<0.4%), and consisted almost entirely of one species

(*Protasparagus*), for which a slight preference was shown (Appendix I). A single species of grass was recorded in the sample from Springmount. No correlations were found between abundance of species of plants and their representation in the diet for any population of tree hyraxes.

Discussion

In accordance with Kingdon (1971), Skinner and Smithers (1990), and Maloiy and Eley (1992), we found the eastern Cape tree hyrax to feed almost exclusively on leaves, and there was no evidence of fruit or insects in its diet. Foraging for invertebrates, flowers, and sap by arboreal mammals is argued to be economical only for small mammals because of the small absolute size and low total biomass of the reward (Cork and Foley, 1991).

At all sites, the principal dietary plants comprised few species; one at Pirie (*P. falcatus*), three at Alexandria (*S. latifolia*, *C. aethiopica*, *E. c. zeyheri*), and two at Springmount (*S. latifolia*, *E. natalensis*). *P. falcatus* is an important timber tree that is selectively removed at Pirie during commercial-logging operations. Because *P. falcatus* is also a preferred species of den tree for this cavity-dwelling hyrax (Gaylard, 1994), removal by logging could have serious implications for the continued existence of *D. a. arboreus* in this forest.

Total number of species in the diet was highest for the population at Pirie and lowest at Springmount. This trend possibly reflects a natural shift in composition of species from a coastal to an inland forest. Similar species were eaten at all sites, with three species in common between Pirie and Alexandria (*S. latifolia*, *C. aethiopica*, and *S. inerme*), two between Alexandria and Springmount (*S. latifolia*). and *E. natalensis*), and one between Pirie and Springmount (*S. latifolia*). *S. latifolia* is clearly an important dietary item for the eastern Cape tree hyrax and, in addition, is an important tree species for denning at Pirie and Alexandria (Gaylard, 1994). This is not a commercial-timber species.

Numerous authors commented on diversity of the diet of hyracoids in East Africa (Hoeck, 1975; Sale, 1965; Skinner and Smithers, 1990; Turner and Watson, 1965). Similarly, Lensing and Le Roux (1982) reported a high diversity of food items for the rock hyrax, *Procavia capensis*, and described the species as an opportunistic feeder. In contrast, and as predicted, *D. a. arboreus* is a highly selective feeder, as is evidenced by the low diversity and species richness of plants in the diet, the high percentage of species selected, and the lack of correlation between abundance of a species and its representation in the diet. The high range and standard deviation in the number of species eaten may reflect the fact that herbivores are forced to sample new foods (even in familiar environments) due to the frequently changing nutrient content and toxicity of plants (Provenza et al., 1992). Alternatively, this could be an artifact of the relatively small sample, or due to temporal changes in diet.

The main advantage of a specialized diet is that species can develop morphological and metabolic means of exploiting resources not available to generalists (Moss, 1991). Diet selection is viewed as a major adaptive strategy and an important means of niche separation (Ellis et al., 1976). *D. arboreus* has been able to exploit the folivorous niche by means of several adaptations for a low-quality diet. Its low metabolic rate minimizes its demand for energy and nitrogen from the diet (McNab, 1978). This low metabolic rate and concomitant folivorous feeding habit are predicted to influence many of the behavioral characteristics of tree hyraxes. Its solitary nature is necessitated by the low-quality food that it consumes, because gregariousness would necessitate increased search times and energy expenditure (Eisenberg, 1978). A solitary lifestyle has led to the evolution of an extensive and characteristic vocalization system, without which this secretive species could easily be overlooked (Skead, 1987). To reduce the high energetic costs of lactation, many arboreal folivores give birth to precocial young (Janzen, 1978) and the young of *D. arboreus* are reported to eat solid food by their 2nd or 3rd day (Dorst and Dandelot, 1970). *D. arboreus* is further adapted to folivory by means of hindgut fermentation (Bauchop, 1978), which allows for digestion of the soluble fraction directly in the foregut and fermentation of cell walls posteriorly. Hindgut fermenters often practice coprophagy, and the phenomenon has been observed for the other two genera of Hyracoidea (*Procavia* and *Heterohyrax*). Although it is likely that *Dendrohyrax* also practices coprophagy, there is no such evidence to date (J. Rudnai, pers. comm.).

Dendrohyrax arboreus can compensate to a certain extent behaviorally for a low-quality diet by increasing rate of intake, consumption, or feeding time. Two factors constrain the ability of small herbivores to respond by increasing intake. First, because high-quality foods are rare, their ability to maintain high levels of intake is limited by their ability to find these foods. Second, the small herbivore is limited in its ability to expand its diet to more common, lower-quality foods (Demment and Van Soest, 1985). The relatively narrower muzzle of *D. arboreus* facilitates increased rates of intake of thorny plants, which tend to have higher crude protein and lower fiber concentrations (Cooper and Owen-Smith, 1986). Increased foraging time (both feeding and searching) is necessary to meet metabolic thresholds when feeding on a resource of poorer quality (Pellew, 1984).

Although interspecific competition has been invoked to explain selectivity in other species, *D. a. arboreus* has few arboreal vertebrate competitors. The samango monkey *Cercopithecus mitis labiatus* is mainly a frugivore and only occasionally eats leaves (Lawes et al., 1990).

The low diversity of the diet may, in fact, reflect the need for predator avoidance and the cost of arboreal locomotion, forcing *D. a. arboreus* to minimize foraging distances. This is emphasized by the fact that the principal-preferred dietary plants (e.g., *P. falcatus* and *S. latifolia*) also are largely the preferred den trees (Gaylard, 1994). We suggest that this aspect be investigated further. Because of the energetic constraints imposed by arboreal folivory, and the fact that most species eaten by *D. a. arboreus* occur naturally in relatively low proportions, removal of these plants could result in loss of dietary resources of the species, particularly if they are unable to exploit other species of plants.

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APPENDIX I

Additional species of plants consumed by *Dendrohyrax arboreus* that comprised <10% of the diet. The initial in parentheses indicates Pirie, Alexandria, or Springmount.

Dicotyledons.—Anacardiaceae: *Rhus* (A), *Rhus* 2 (P); Apocynaceae: *Acokanthera oppositifolia* (P, A, S), *Carissa bispinosa* (P, A, S); Balanitaceae: *Vepris undulata* (P, A, S); Capparaceae: *Capparis fascicularis* (S), *Capparis sepiaria* (S); Celastraceae: *Maytenus peduncularis* (P, A), *Maytenus undata* (A), *Pleurostylia capensis* (P); Ebenaceae: *Diospiros whyteana* (A), *Euclea schimperi* (P, A, S); Euphorbiaceae: *Acalypha glabrata* (A); Flacourtiaceae: *Dovyalis rhamnoides* (P, A, S), *Kiggelaria africana* (P), *Scolopia zeyheri* (S); Hernandiaceae: *Maerua cafra* (S), *Maerua* (S); Icacinaceae: *Apodytes dimidiata* (P); Iridaceae: Iridaceae (A); Loganiaceae: *Nuxia floribunda* (P), *Strychnos decussata* (A, S); Luzuriagaceae: *Behnia reticulata* (P, A, S); Meliaceae: *Ekebergia capensis* (P); Moraceae: *Ficus burtt-davyi* (A, S); Ochnaceae: *Ochna arborea* (S), *Ochna* (A); Oleaceae: *Chionanthus* (P), *Olea capensis macrocarpa* (P), *Olea europaea africana* (P, A); Piperaceae: *Peperomia* (P, A); Rhamnaceae: *Scutia myrtina* (S); Rubiaceae: *Pavetta* (P); Rutaceae: *Teclea natalensis* (P, A); Salvadoraceae: *Azima tetracantha* (A, S); Sapindaceae: *Hippobromus pauciflorus* (P); Sapotaceae: *Mimusops obovata* (P, A, S), *Sideroxylon inerme* (P, A, S); Trimeniaceae: *Xymalos monospora* (P); Ulmaceae: *Chaetacme aristata* (P); Vitaceae: *Cynanchum* 2 (P), *Rhoicissus digitata* (A), *Rhoicissus* (P), *Rhoicissus tomentosa* (A, S), *Secamone* 2 (P, A);

Monocotyledons.—Asparagaceae: *Protasparagus* (P, A, S); Poaceae: Poaceae (S).