CARNIVOROUS PLANTS

Katsuhiko Kondo

The term "insectivorous plants" was introduced by Charles Darwin in 1875 in his famous text by that name. In 1942 F. E. Lloyd called these plants carnivorous plants, since insectivorous plants digest not only insects but also small animals, like fishes, birds, and mice. Carnivorous plants are always included among those higher vascular plants which produce their own foods by photosynthesis and have trapping and digesting mechanisms. Carnivorous fungi have trapping and digesting mechanisms but lack a photosynthetic machine and are, therefore, excluded from the carnivorous plants. Some higher vascular plants which have a trapping apparatus but do not have digesting mechanisms (e.g., *Roridula, Triphyophyllum*) also are excluded from the carnivorous plants. The identifying aspects of carnivorous plants, then, are their trapping apparatus, and their digesting mechanisms which always include enzyme activities. Carnivorous plants have an enzyme system that digests small animals in a strongly acid medium which does not allow putrefaction. Thus, they can use organic nitrogen from the small animals directly as a nutrient. It seems that since these plants can obtain organic nitrogen in this way and use it directly and economically as a nutrient, they are well adapted to regions with barren soils.

Table 1 shows Lloyd's names for all kinds of traps exhibited by the carnivorous plants.

Table 1. Traps of carnivorous plants named for their obvious analogs among human devices (after Lloyd, 1942)

Kind of trap	Genus	Common Name
Pitfalls (passive traps) the pitcher plants	Heliamphora	South American pitcher plant
	Sarracenia	pitcher plant
	Chrysamphora	cobra plant
	Cephalotus	Western Australian pitcher plant
	Nepenthes	Asiatic tropical pitcher plant (monkey cup)
Lobster pot (passive trap)	Genlisea	
Bird lime or fly-paper trap		
Passive	Byblis	rainbow plant
	Drosophyllum	
Active	Pinguicula	butterwort
	Drosera	sundew
Steel-trap (active)	Dionaea	Venus' fly trap
	Aldrovanda	waterwheel plant
Mousetrap	Utricularia	bladderwort

Pitfalls do not show any active movement. Their trapping mechanisms are highly specialized structures. Most all pitcher plants have pitfalls (e.g., *Nepenthes, Sarracenia*) which produce nectar from glands located around their mouths or lids. Insects or small animals take nectar produced by the glands and move around the traps or entrances, sometimes losing their balance and slipping into the pitchers. *Sarracenia, Heliamphora, Chrysamphora,* and *Cephalotus* have well-developed downward-pointing hairs. It is very easy for prey to slip on the hairs and be forced downward toward the bottom of the pitchers.

The pitcher of *Chrysamphora* is very unusual. The tube is tapering, widening upward. At the top the tube spreads suddenly, and at the same time is bent sharply forward to form a dome, bringing the mouth into a horizontal position underneath. Small animals crawl around the mouth of the pitcher and enter inside, then they fly or go to the top of the interior of the pitcher because of translucent areas there. Finally the prey lose their way in trying to get out and fall downward into the liquid within the pitcher and die. *Nepenthes* (Figs. 3 to 7) has a little different mechanism: the pitchers do not have any downward-pointing hairs but instead have colorful, slippery mouths around the entrance. It is believed that the pitcher of the pitcher plants arises by fusion of the leaf margin. The liquid in the pitcher has a high specific gravity and is sticky thus making it doubly difficult for the victims to get out of the pitcher. Five or ten minutes after their careless mistake, they are often dead.

The lobster pot found in *Genlisea* is another passive trap which basically has the same mechanism as the pitcher plants. The trap is Y-shaped. Structurally this consists of an epidermis enclosing a very extensive intercellular air space of lysigenous origin. During elongation, each arm of the Y-shaped part of the trap becomes twisted as a result of rotatory growth: one on the right, clockwise, the other part counterclockwise. The funnel-shaped entrances are formed by the occurrence at certain distances of two large clear cells which lie one upon the other, and which may be called prop cells. They are merely the end cells of the rows of trapping hairs. There is a row of prop cells on only one edge, and the prop cell is only the middle cell of a three-celled hypertrophied trichome, the basal cell of which is much enlarged, while above it the middle cell is enormously large and ends in a small knob-shaped cell terminating the trichome. The Y-shaped part of the trap is connected with a tubular neck which makes the bulb look like a chianti flask. This bulb is the final part of the trap in *Genlisea.* Many digestive glands are located in this area. Small animals enter the mouth of the trap, and are led toward the inside of the tube by prop cells and trapping hairs. They finally reach the bulb part of the trap where with bacterial help they are killed and digested by enzymes from the digestive glands of *Genlisea.*

Bird limes or flypaper traps of carnivorous plants are of two types: the passive and the active trap. *Byblis* (Fig. 13 and 14) and *Drosophyllum* are the examples of plants with passive flypaper traps. Many glandular hairs and sessile glands are found on the leaves of these genera and they produce a sticky, acid liquid containing an enzyme. But the glandular hairs and the leaves do not show any movement in catching small animals. This explains why these structures are called passive traps or flypaper traps. Small animals are caught by the sticky liquid produced by glands on these leaves (flypaper traps) and then the prey die in the same position and are digested by a certain digestive enzyme. In contrast, *Drosera* and *Pinguicula* have active glandular hairs and leaves which move, twist, hold, fold and roll victims to the center of the leaves. Thus, these are called active types of flypaper traps. The glandular hairs consist of a tapering stalk topped by an oval gland. The stalk

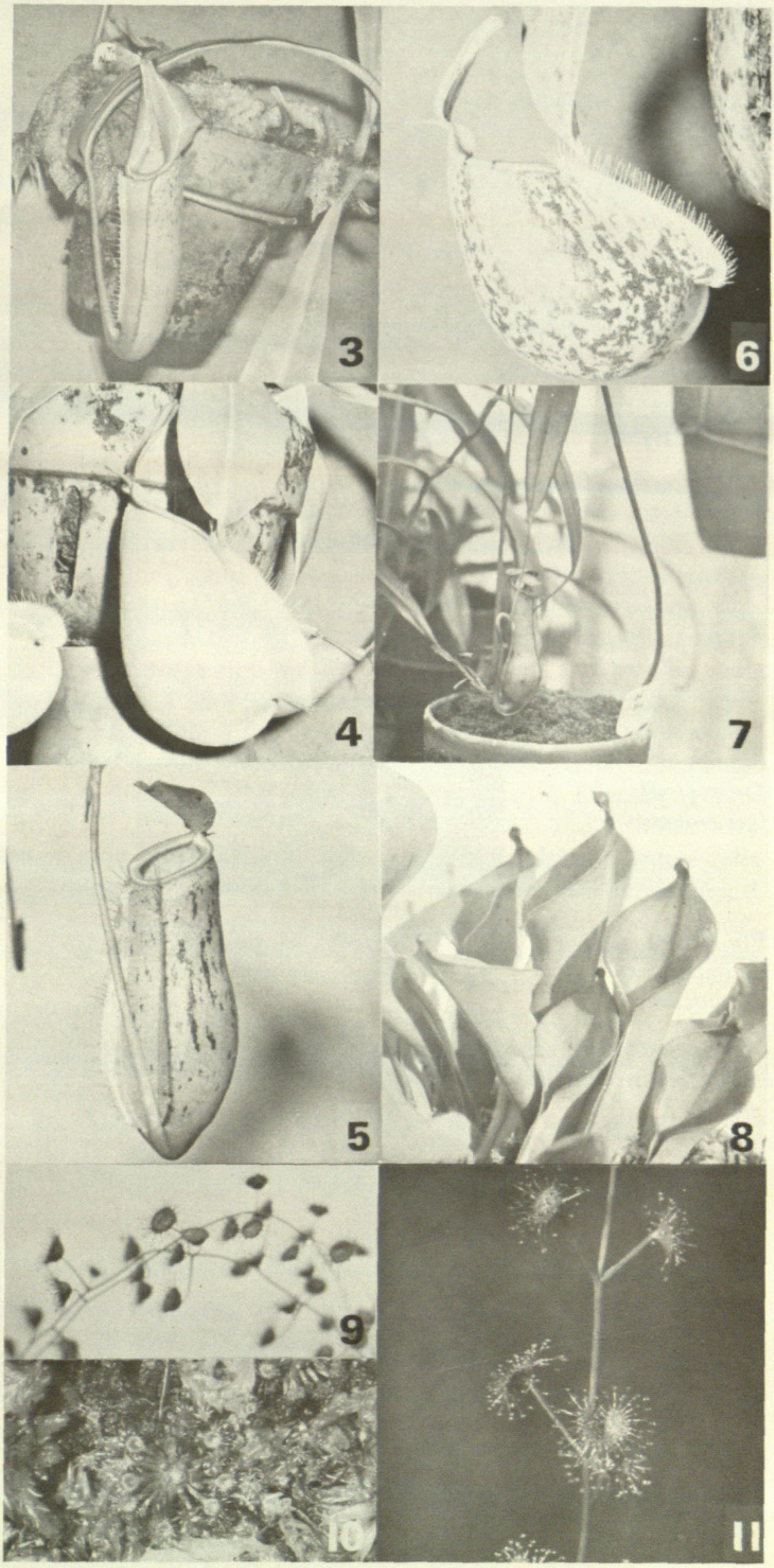


Fig. 3-8. Examples of pitfalls:

Fig. 3. *Nepenthes veitchii*

Fig. 4. *Nepenthes* x *hookeriana* (albino type)

Fig. 5. *Nepenthes* x *trichocarpa*

Fig. 6. *Nepenthes* x *hookeriana* (wild type)

Fig. 7. *Nepenthes gracilis*

Fig. 8. *Heliamphora nutans*

Fig. 9-11. Examples of active flypaper trap:

Fig. 9. *Drosera menziesii*

Fig. 10. *Drosera drummondii*

Fig. 11. *Drosera stolonifera*

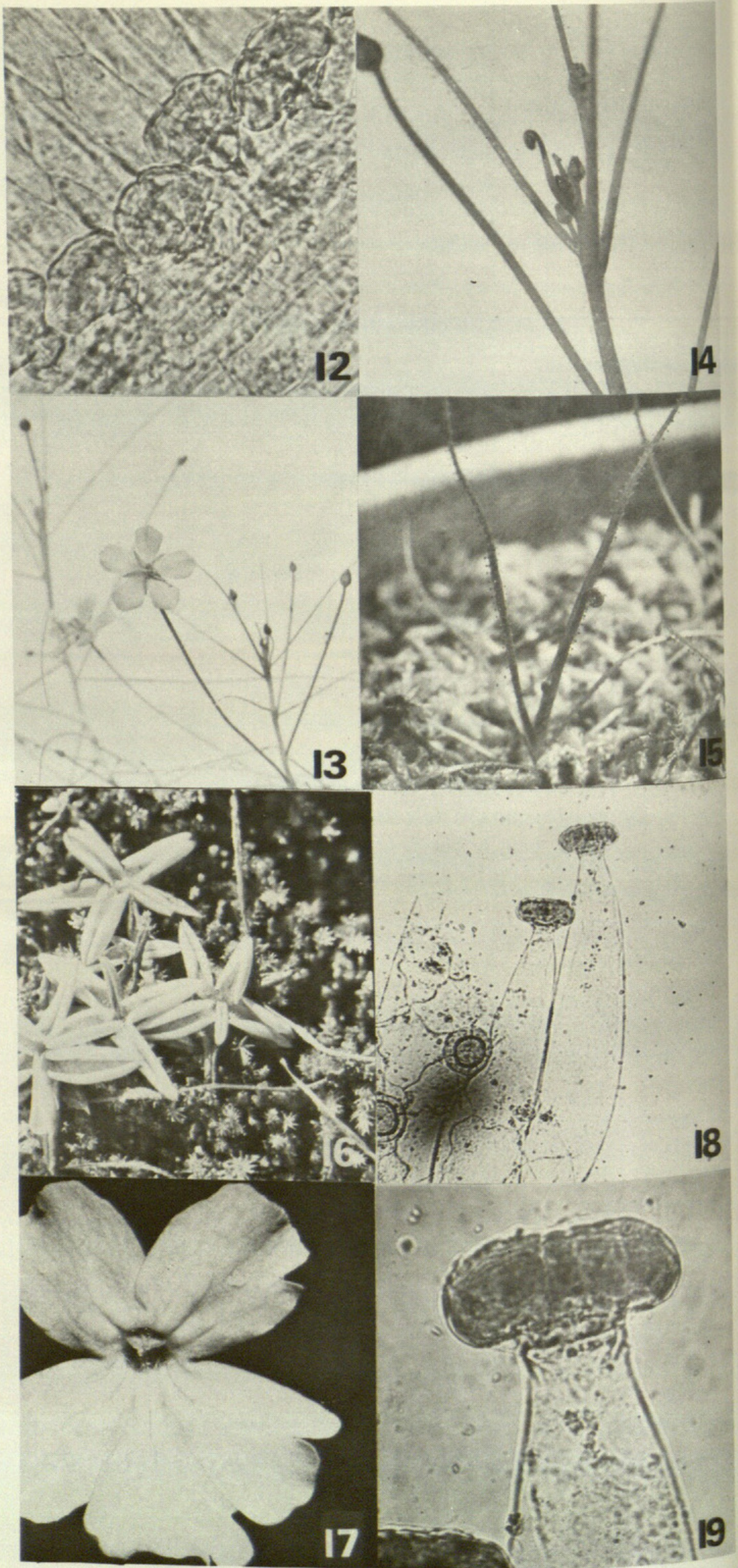


Fig. 12. Digestive glands of *Aldrovanda vesiculosa*

Fig. 13-15. Examples of passive fly paper trap

Fig. 13. *Byblis liniflora*

Fig. 14. Shoot apex of *Byblis liniflora*

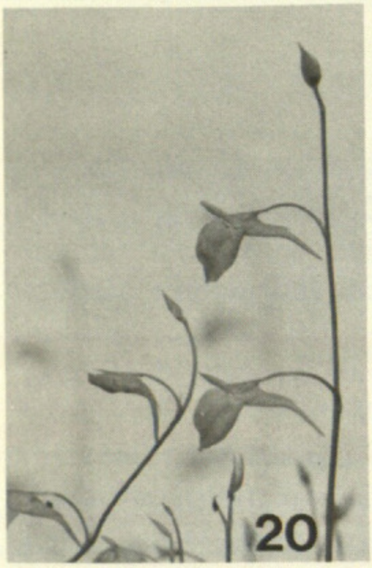
Fig. 15. *Drosophyllum lusitanicum*

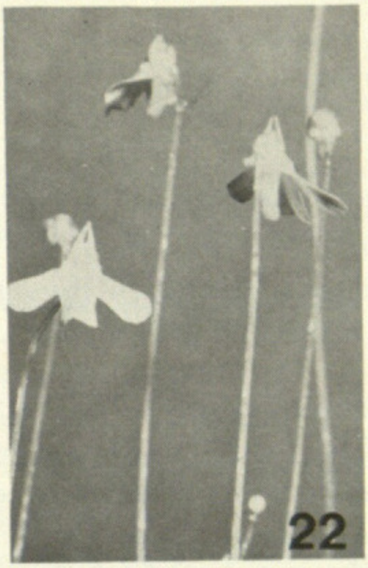
Fig. 16-19. Active fly paper trap—*Pinguicula*:

Fig. 16. Vegetative parts of *Pinguicula* (*P. lusitanica*)

Fig. 17. Flower of *P. colimensis*

Fig. 18 and 19. Glandular hairs of leaf





Examples of mousetrap (*utricularia*): Fig. 20, *U. caerulea;* Fig. 21, *U. menziesii;* Fig. 22, *U. multifida.*

arises from the leaf surface as a mass of tissue including all elements of the leaf structure — epidermis, parenchyma, and vascular tissue. Many leaves roll back on themselves from the apex toward the base. The glandular hairs are capable of movement, often being bent like a bow, a very useful movement for catching small animals. In addition to the stalked glands, there are very numerous, small, sessile glands. The origin of the sessile glands is purely epidermal. Sessile glands of the concave leaf surface are alone capable of absorption; it should be noted that those of the dorsal surface are small and usually have lost their terminal cells. The active glands display cytoplasmic changes during the absorption of nutrients. If small animals are caught around on the edge of a leaf blade, long, marginal, glandular hairs start bending and carry the prey slowly to the center of the blade. Then, the leaf slowly folds and rolls the apex toward the base. The advantage of this behavior is that the entire surface of a victim is covered and digested by enzymes from glandular hairs and sessile glands.

The steel-trap type is found in *Aldrovanda* and *Dionaea.* This trap is very active, and is the outer part of the leaf (the blade), which consists of two lobes, trapezoidal in form with fringed margins and united along the middle line by a thick midrib. The two lobes act like the jaws of a steel trap. The two lobes form an angle of 40 to 50 degrees when they are widely open. They are clothed with a distinctly firm epidermis of straight-walled cells, elongated and parallel with the veins, but become somewhat wavy toward the margins, which lends a surprising stiffness to the trap. The inner surface of each lobe in *Dionaea* is supplied with many glands and each has three trigger hairs which exhibit sensitive cells at the base. There are two physiological kinds of glands, digestive and alluring. The alluring glands are situated in a narrow zone just within the fringed margin and secrete a sweet liquor. The digestive glands are rendered conspicuous by their deep red color and are responsible for the evident red color of the inner surface of the trap. In contrast, the alluring glands contain no pigment. However, small animals seem to be attracted by the honey or sweet liquor produced by the alluring glands, and in moving around must touch the sensitive trigger hairs at least twice to *"spring the trap."* The most interesting feature of this steel-trap mechanism is the method by which water moves during the closing responses of the leaf-lobes. The movement of the lobes seems to be due to the loss of water through pores in the protoplasm. Indeed, there appears to be rows of extremely minute pores of globules in the protoplasm of the parenchyma cells of the motile tissues. The mechanism is similar to that in the pulvini of the sensitive plant, *Mimosa,* in which the leaves and leaflets fold together due to a rapid loss of turgor in the cells of the pulvini. There are two steps in the closing of the trap which may be referred to as "*shutting*" and "*harrowing.*" The first makes the initial catch of the prey, and the second more tightly clasps the victims, preventing their escape and forcing them into contact with the digestive glands (Fig. 12) near the center of the trap.

The last to be described is the mouse trap which is found in *Utricularia,* an aquatic genus. The trap is called a bladder, which it resembles in shape. The entrance is guarded by two valves, a larger, the door, and a smaller membranous one, the velum. The door is attached to the trap along a semicircular line on the dorsal part of the entrance, its free edge hanging and in contact with a firm, semicircular collar or threshold. Against these are numerous longer or shorter, stalked mucilage glands, secreting mucilage and sugar, which are said to be attractive to small animals and so act as a lure. The door bears four stiff, tapering bristles attached near the free, lower edge. These comprise the tripping mechanism. The surface of the threshold, against which the door edge rests, is covered with a pavement epithelium of glandular, sessile cells secreting mucilage. Along the outer edge of this pavement there is attached a thin but firm transparent membrane, the velum, which lies against the lower edge of the door, filling in the chink between this and the threshold. The internal surface of the trap has many glandular hairs, called bifids and quadrifids. In response to small animals touching hairs on the door, the door opens. Since the pressure inside the bladder is lower than that outside, by inward movement of water small animals are forced in to the bladder. Then the door closes. The prey are killed and decomposed with bacterial help in the bladder. Glandular hairs in the bladder produce enzymes which assist in the digestion of the animals. The soluble nitrogenous compounds are then absorbed into the plant.

I wish to discuss further the digestive enzymes produced by carnivorous plants. Formerly, the protease in carnivorous plants had been suspected to be pepsin-like, since it acts within essentially the same pH range as does pepsin. The present studies show the acid protease which carnivorous plants have is different from pepsin. The acid protease, named *nepenthesin* (Nakayama, *et al.,* 1968), is the common digestive enzyme in carnivorous plants. *Nepenthesin* is predominantly specific to aspartic acid residue at its carboxyl side or at its amino side, and is apparently specific also to tyrosine and alanine residues at their carboxyl side. The protease seems to be an endopeptidase. The mechanism of digestion involves cooperation between protease and some other enzyme, such as a chitinolytic enzyme or chitinase (Amagase, *et al.,* 1969, 1972).

It is still unknown how foods are absorbed through the cytoplasmic membranes in the glands of carnivorous plants after enzyme activity. Changes in the nitrogen content, or nitrogen movement in the leaves given protein have been observed by various methods (e.g., Sibata, *et al.,* 1972; Heslop-Harrison, *et al.,* 1971). Especially the work of Heslop-Harrison, *et. al.,* (1971) is very interesting. After placing 14C-labelled protein on the glands of a leaf of *Pinguicula,* digestion on the leaf surface and absorption of the products has been investigated autoradiographically. Within two hours, digestion products enter the leaf and move towards the margin in the vascular system. Within twelve hours movement out of the leaf begins. Thus, carnivorous plants in some ways seem to have similar digestive mechanisms as those in animal stomachs.

At least 450 species of carnivorous plants representing thirteen genera and six families are taxonomically known. All genera are shown in Table 1. Each family and each genus belonging to it are discussed below:

1. Family Droseraceae (Sundew family)

The family consists of the genera: *Drosera, Drosophyllum, Dionaea,* and *Aldrovanda.*

A). *Drosera.* Drosera consists of approximately ninety species in the world: about sixty species grow in Australia. The name "Drosera" was originated from a Greek word "droseros," which means moist with dew. Thus, the common name in English for *Drosera* is "sundew." They grow mostly in moist pinelands and sandy roadside ditches in savannahs. They thrive in acid soil (pH 3.5 to 4.0) and in air and soils with a high humidity. Figs. 9 to 11 show some examples of *Drosera.*

B). *Drosophyllum.* The name "Drosophyllum" is a compound word of "drosos" (dew) and "phyllon (leaf). However, *Drosophyllum* means leaf with dew. This genus is monotypic: the single species *Drosophyllum lusitanicum* (Fig. 15) is found only in Portugal, Spain, and Morocco.

C). *Dionaea.* The name "Dionaea" comes from the Greek word "Dione," which means Venus. The common name in English for *Dionaea* is "Venus' flytrap." This genus is monotypic and a very rare endemic: the species *Dionaea muscipula* is found only in North and South Carolina in the United States. The North Carolina state government protects this interesting plant by law.

D). *Aldrovanda. Aldrovanda* was named in honor of N. Aldrovandi, an Italian botanist. *Aldrovanda* is another monotypic genus and is distributed from Japan, Australia, through India, to Eastern Europe. It is a floating, aquatic plant.

2. Family Sarraceniaceae (Pitcher plant family)

The family consists of *Chrysamphora, Heliamphora,* and *Sarracenia.*

A). *Chrysamphora.* The name "Chrysamphora" is a compound word of "chrysos" (golden) and "amphora" (bottle). Because of its leaf shape, this plant is locally called "cobra plant." This genus is monotypic and endemic to the Siskiyou Mountains of Oregon and California.

B). *Heliamphora.* The name "Heliamphora" is a compound word in Greek of "helos" (sun) and "amphora" (bottle). This genus, which is the most primitive type in the Sarraceniacaea, consists of six species all endemic to the mountains in Venezuela and Guiana of South America. Fig. 8 shows a species of *Heliamphora, H. nutans.*

C). *Sarracenia.* Sarracenia is based on Tournefort's original description (1700) of a plant sent to him by M. S. Sarrazin in Canada. *Sarracenia* was named in honor of M. S. Sarrazin, however, and it was later adopted by C. Linnaeus (1737). *Sarracenia* consists of eight species: *S. oreophyla, S. sledgei, S. flava, S. drummondii, S. rubra, S. minor, S. psittacina,* and *S. purpurea.* Natural hybrids in the genus are very common. They are distributed in the eastern United States and Canada.

3. Family Nepenthaceae (Tropical pitcher plant family)

The Nepenthaceae consists of only one genus *Nepenthes.*

A). *Nepenthes.* Nepenthes is a compound word in Greek of "ne" (no) and "penthos" (grief). This genus is found scattered throughout the tropics of the Old World from the Philippines as far south as northern Australia and New

Caledonia, and westward to Madagascar and Seychelles. They grow only in moist situations in lateritic acid soil. Figs. 3 to 7 show some examples of *Nepenthes.*

4. Family Byblidaceae (Rainbow plant family)

The Byblidaceae consists of only one genus, *Byblis.*

A). *Byblis. Byblis,* which is endemic to Western Australia, consists of two species: *B. gigantea* and *B. liniflora* (Figs. 13 and 14).

5. Family Caphalotaceae (Western Australian pitcher plant family)

The Cephalotaceae consists of only one genus, *Cephalotus,* which is monotypic and endemic to Western Australia.

6. Family Lentibulariaceae (Bladderwort family)

The Lentibulariaceae consists of three genera, *Pinguicula, Genlisea,* and *Utricularia.*

A). *Pinguicula. Pinguicula* comes from the Latin word "pinguis," which means grease. Its common name is "butterwort." *Pinguicula* consists of 46 species scattered around the world. *Pinguicula* grows in wet places often with mosses; in chinks of wet, dripping rocks; on hummocks in swamps; on wet sand, and on other wet substrates.

Figs. 16 and 17 show some examples of *Pinguicula.*

B.) *Genlisea.* Genlisea consists of about 20 species growing in western Africa, and in Brazil and Guiana in South America.

C). *Utricularia.* The name "Utricularia" originally came from "utriculus" which in Latin means "bladder." Thus, the common name for *Utricularia* is bladderwort. *Utricularia* is found as a free-floating or anchored aquatic, or an epiphyte among mosses, or a terrestrial plant on moist to wet sandy soils. The genus consists of approximately 310 species in many parts of the world. Figs. 20 to 22 shows some examples of *Utricularia.*

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