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SPECIALIZED INSECTIVORY: BEETLE-EATING AND MOTH-EATING MOLOSSID BATS

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ABSTRACT.—The jaw structure and mechanics of insectivores have been little studied. An effort is made here to compare and contrast jaw characteristics of insectivorous bats with those of herbivores and carnivores. Further, in one particular family of bats (Molossidae) jaw modifications are such that animals that take hard-shelled insect prey can be distinguished from those that take soft-shelled insect prey. Beetle-eaters generally have thick jaws, well-developed cranial crests, and fewer but bigger teeth, whereas moth-eaters have thin jaws, little crest build-up, and more but smaller teeth.

A member of the mammalian order Insectivora should probably be referred to as an insectivoran, a mammal which may or may not be insectivorous (Van Valen, 1969, makes the same suggestion for carnivores and carnivorans). Similarly, not all insectivores are insectivorans, for example, bats. Past students of jaw structure and mechanics included insectivorous bats in the generalized, primitive, dietary category of omnivory instead of in the more specialized categories of carnivory or herbivory. Omnivory is the dietary category into which all mammals besides carnivores and herbivores usually are lumped. The representative mammals are usually omnivores of a primitive nature, such as *Didelphis marsupialis* and *Echinosorex gymnurus* (Crompton and Hiiemae, 1969, 1970; Turnbull, 1970). Although the chiropteran insectivores discussed here do share characteristics in common with these generalized, omnivorous mammals, they have features that I think are necessary for an obligatory insectivorous diet. Some insectivorous bats are further adapted to eat only certain types of insects. These specialized bats may differ as much from omnivores in degree of specialization as carnivores differ from herbivores.

All insects have a chitinous exoskeleton of cuticle of varying hardness that covers the insect's soft internal structure. The thickness of this shell may affect which mammals can prey upon the insect. Much undigested exoskeletal material is present in the feces of insectivorous mammals, but it is finely chopped. Evidence exists that an insectivorous bat has chitinase enzymes (Jeuniaux, 1961); Sheine and Kay (1977) suspect that in some small primates and tree shrews digestion of the chitinous exoskeleton must occur. The latter authors suggested that by chopping the exoskeleton more finely, the small insectivorous mammal increases its ability to digest chitinous prey. Whatever the situation may be, the question arises as to how the insectivore gets into and processes the chitin-enclosed package. I will show that, in bats of the insectivorous family Molossidae, individuals that concentrate on hard-shelled insects such as beetles can be distinguished from those which consume only soft-shelled insects such as moths.

DISCUSSION

General features.—The development of canines in insectivorous bats involves the flattening of at least one side of the tooth, forming a knife-like flange (Fig. 1). Surgeons use needles, flattened on three sides, rather than round needles because of the ease with which the triangular needles pierce the skin. Likewise, the anterior teeth of insectivorous bats probably more easily pierce the exoskeleton of insect prey.

The dilambdodont pattern of molars is one in which paracone and metacone are V-shaped cusps and together form a W-shaped ridge (ectoloph, Fig. 1). In this pattern there are at least four cutting edges instead of two on each of the upper molars. Closer
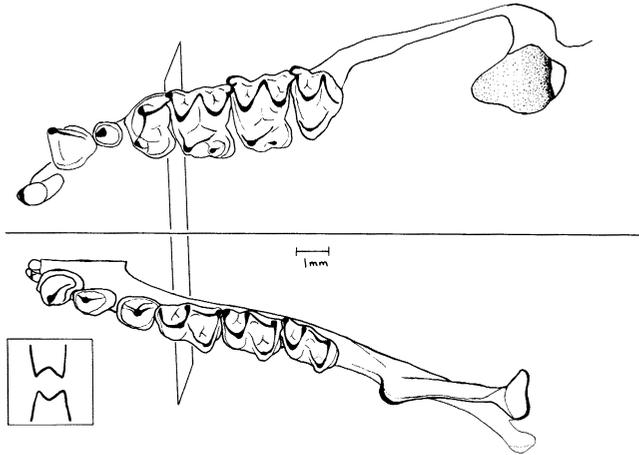
FIG. 1.—Occlusal view of the left upper toothrow showing the well-developed canine, the dilambdodont cusp pattern, the glenoid fossa, the postglenoid process, and the corresponding left lower toothrow in a molossid bat. The insert gives a transverse view of upper and lower cutting edges forming a small carnassial.

examination shows there are actually eight cutting edges because each arm of the W forms a shallow V-shaped cutting edge in the transverse plane so that the front of each tooth looks like an M. When upper and lower teeth meet, the effect is like four small carnassials on each tooth (Fig. 1, insert). Dilambdodont teeth are particularly developed in moles, shrews, insectivorous marsupials, and insectivorous bats and are "seemingly especially useful in chopping up small invertebrates" (Findley, 1974:626). The W-shaped cusp pattern has been likened to pinking shears because the teeth fit together in an interdigitating manner, a mechanism called "intercuspidation" by Gaspard (1964). The pinking shear configuration holds the item being cut on the cutting edge, and the item does not slide away as the two cutting edges come together.

How does intercuspidation by these insectivores differ from the tooth action of carnivores and herbivores? The shearing surfaces of herbivores (either artiodactyls or rodents) pass by one another in the horizontal or occlusal plane (more or less as the surfaces may be slightly tilted as illustrated by Maynard Smith and Savage, 1959). Carnivores, on the other hand, have one primary set of shearing edges, the carnassial pair, in the longitudinal or sagittal plane, which is specialized for shearing tough or tendinous food. Insectivore teeth also come together in the sagittal plane, but the triangular cusps interdigitate transversely and movement of the jaw is in a lingual-buccal axis. Each edge of each cusp of each molar forms half of a small carnassial with the lower teeth so that the food item is finely chopped or minced.

Kallen and Gans (1972) discussed the biology of mastication in *Myotis lucifugus*, an insectivorous bat, and noted how quickly and efficiently these small bats can process mealworms. Their work is an excellent description of mastication in a mammal with dilambdodont chopping teeth and long canines. Prey of *Myotis* is immobilized by numerous piercing bites with the canines and subsequently chopped up by a series (up to seven per second) of complex movements involving protrusion, retrusion, lateral translations, and rotation around three axes. By reducing the amplitude of the power stroke the bat can process small items as easily as it does larger ones.

Besides the dilambdodont molars and the large anterior piercing teeth, insectivorous bats have a characteristic craniomandibular joint. In carnivores the glenoid fossa

of the skull has a postglenoid process and often a preglenoid process, which surround the condyle. This arrangement stabilizes the joint and prevents its dislocation. The posterior process is a bony stop for the backward pull of the temporal muscle, and the anterior process is a stop for the forward pull of the masseter (Ewer, 1973). The carnivore's condyle must be held securely in the sagittal plane for the precise occlusion of the carnassials. Herbivores do not have a preglenoid process, but they do have a postglenoid protuberance. Compared to the area of the flattened glenoid fossa, however, the height of the postglenoid process is not great, and its position is only on the posteriomedial side of the fossa. Therefore, the condyle has a great deal of area in which to move around. Insectivorous bats have a well-developed postglenoid process, which is relatively tall compared to the flattened area of the fossa anterior to it, and the process occupies the posterior rim of the fossa (Fig. 1). This configuration provides a well-developed bony stop for the pull of the temporal muscle, which does the work of subduing prey via the canines or incisors or both. (Maynard Smith and Savage, 1959, discussed the specific function of the jaw muscles in carnivores and herbivores.) With insectivores this initial work must not only subdue the prey but also must pierce the exoskeleton of the prey. The flattened glenoid fossa anterior to the postglenoid process allows some freedom of lateral movement of the lower jaw in mastication or chopping up of the insect prey (Kallen and Gans, 1972). Thus, the craniomandibular joint of insectivorous bats has elements of the joints of both carnivores and herbivores.

Molossid bats.—In a multivariate study of molossid bats consisting of nearly 80 characters and 80 species (Freeman, 1977), variation in several features of the jaws and skulls indicated that some species are best adapted for hard-shelled insect prey and others for soft-shelled insect prey.

One of these features, the position of the mandibular condyle above the lower toothrow, is difficult to explain functionally. Maynard Smith and Savage (1959) pointed out that the position of the condyle affects the mechanical advantage of the temporal and masseter muscles. In carnivores, where the condyle is low and the coronoid process high, the temporal muscle moment arm is large as is the temporal muscle itself (the temporalis is the primary jaw-closing, prey-seizing muscle). The greatest pressure occurs at the back of the jaw where the carnassials are located. On the other hand, in herbivores where the condyle is elevated, the masseter muscle moment arm is large and the resulting masseter muscle, which controls grinding mastication, is large. Wolff-Exalto (1951) and Crompton and Hiiemae (1969) thought that the elevated condyle, characteristic of herbivores, provides uniform bite pressure along the toothrow. Crompton and Hiiemae further mentioned that changes in the height of the condyle are important differences between herbivores and the more primitive mammals like the opossum. Molossid bats include species with elevated mandibular condyles and species with nonelevated condyles (Figs. 2, 3). Several insectivorans have been found to have elevated condyles (Wolff-Exalto, 1951).

Greaves (1974) recently tried to clarify the functional implication of the mammalian jaw joint position. For the majority of mammals the glenoid fossa lies above the upper toothrow and this distance may be relatively similar in most cases. It is, therefore, either the lower toothrow, the condyle, or both that are variable in position. He stated that an occlusal pattern in which the lower and upper teeth meet simultaneously (like wire cutters) can be achieved by mammals with either elevated or lowered condyles, depending on whether the distance from the upper toothrow to the fossa in the skull is equal to the distance of the lower toothrow to the condyle of the mandible (as in many herbivores). If the distances are unequal the jaws close in a scissors fashion with the point of contact moving anteriorly until the jaws are completely closed (as in many carnivores). He also showed, by way of a model, that the height of the condyle
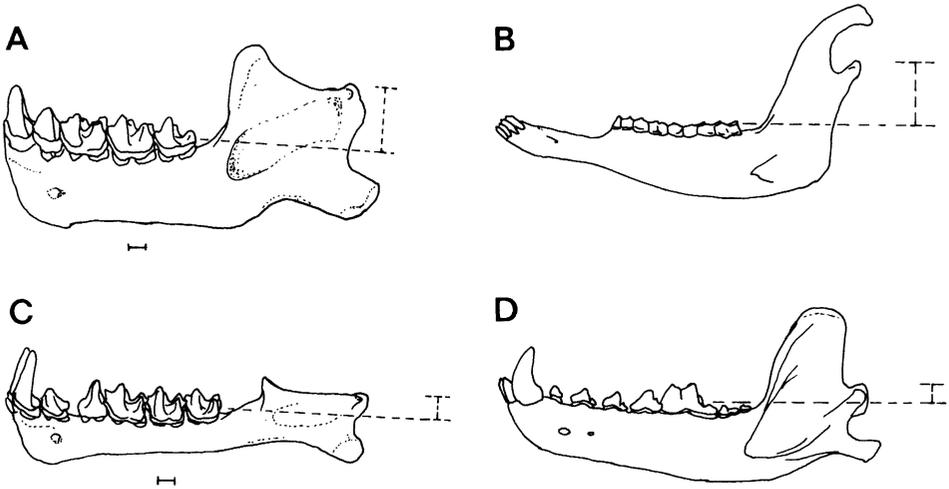
FIG. 2.—A comparison of two molossid bats (A and C) with an herbivore (B) and a carnivore (D). The line beneath the bat jaws represents 1 mm. The sheep and wolf jaws are several times larger.

can shift independently of the mechanical advantage of either temporal or masseter muscles.

The advantage for herbivores of having a simultaneous and uniform bite for the grinding of plant material, and the advantage for carnivores of having a powerful, scissor-like bite for the slicing of flesh is obvious; but the advantage of either bite for the insectivore with intercuspidate teeth is less obvious. Storch (1968) and Kallen and Gans (1972) mentioned that the elevated position of the condyle in bats changes the angle of approach of lower teeth to upper teeth to a more anterio-dorsal direction rather than a strictly dorsal direction, which occurs when the condyle is on the same level as the lower tooth row. This idea of the change of direction was advanced earlier by Wolff-Exalto (1951) and Davis (1964). Davis analyzed the elevated condyle in the giant panda, a strict herbivore. He illustrated how the lower teeth approach the uppers in a more anterior direction and that this movement is important for anterior-posterior grinding in a mammal that has a transverse cylindrical condyle, which allows almost no lateral movement. Whether insectivorous bats having greater freedom at the craniomandibular joint and dilambdodont teeth have an advantage in the processing of a food item was not made clear by either Storch (1968) or Kallen and Gans (1972). Storch (1968) reasoned that the more anterior approach of lower teeth to uppers produces a better rendering of the food and a delay in swallowing. Hildebrand (1974:634) mentioned that the oblique approach of the lower teeth "might tend to roll or slice plant food as it was crushed."

Herring (1972) reviewed advantages to mammals that have nonelevated condyles, but the advantages that have greatest relevance here are the increase in the temporalis leverage and the increase in effective gape. Both features would aid the insectivorous bat in taking large insects.

It is the complement of other jaw characteristics that co-vary with the height of the mandibular condyle in a principal components analysis of the molossid bats that lead me to believe that insectivorous bats are adapted to eating certain types of insects. The height of the condyle above the toothrow in one molossid extreme is relatively as high as that of a sheep or cow. The other extreme has a low condyle, more like that
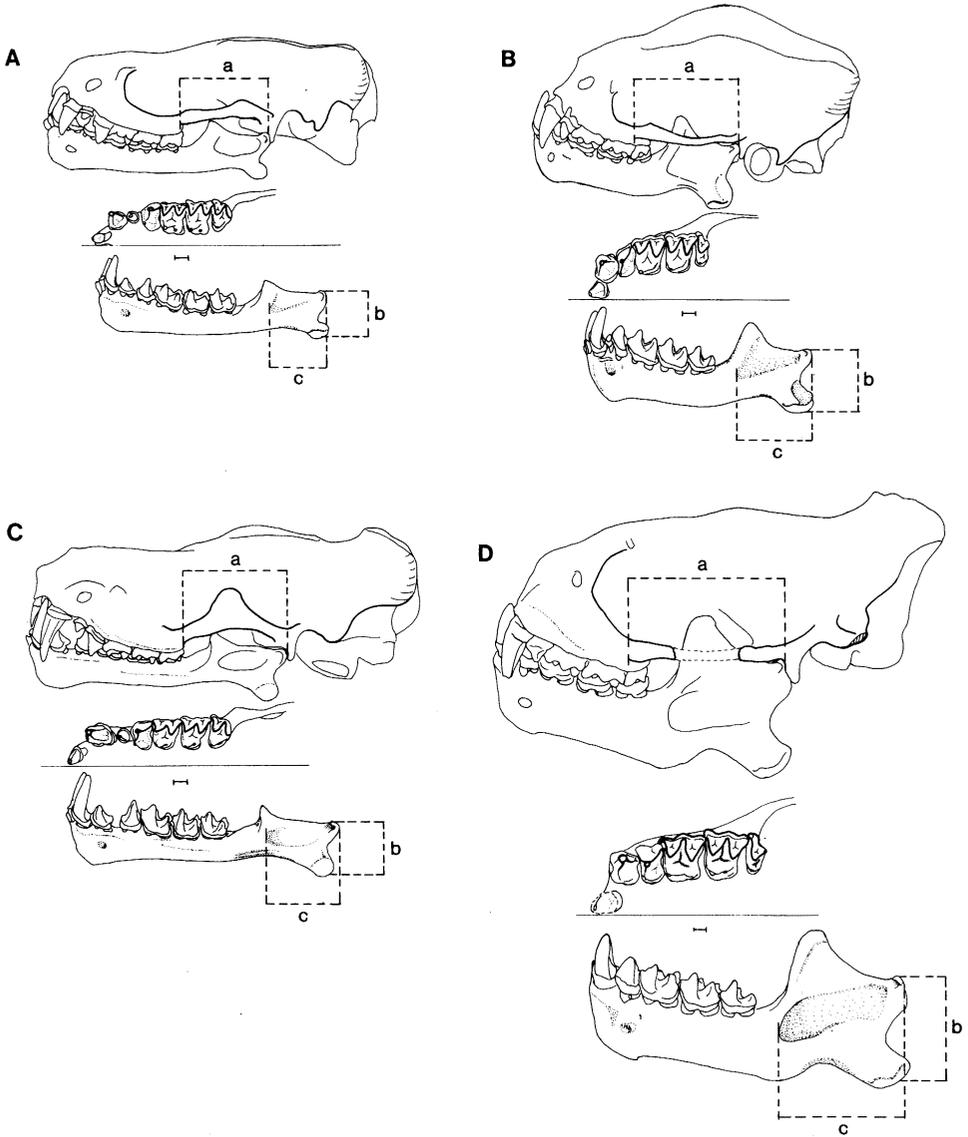
FIG. 3.—Four molossid bats in the New World (A and B) and the Old World (C and D): A) *Nyctinomops macrotis*, B) *Molossus ater*, C) *Otomops martiensseni*, D) *Cheiromeles parvidens*; a—length from joint to origin of masseter; b—length from joint to insertion of masseter (the larger the ratio a/b, the wider the gape—Herring and Herring, 1974); c—length of masseter muscle scar.

in some of the carnivores (Fig. 2). The bats with the elevated condyle also have a thicker dentary, higher coronoid process, greater sagittal crest development, and greater tooth reduction. These bats have lost PM³ and the posterior commissure of the ectoloph on M³ (giving the tooth a V-shaped pattern, Fig. 3). Opposite this extreme are molossids with the condyle on the same level as the toothrow, a thinner dentary, a lower coronoid process, a less developed sagittal crest, and relatively more teeth
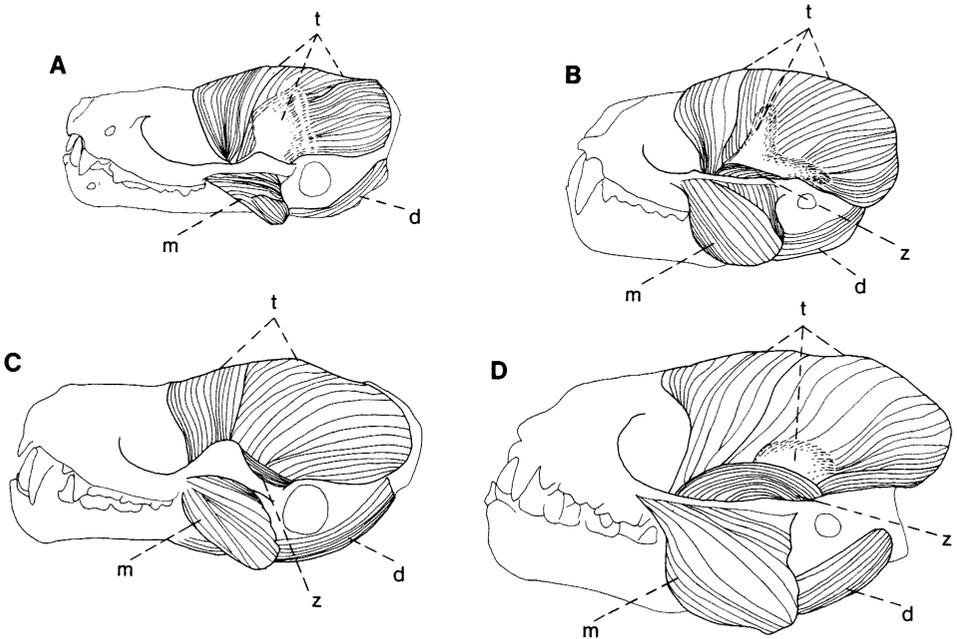
FIG. 4.—The four molossids illustrated in Fig. 3, here showing some of the jaw muscles: t—superficial temporal; m—superficial masseter; z—zygomaticomandibularis; d—digastric.

and cusps. Bats of this structural pattern retain a PM³ and a well-developed M³ (posterior commissure is present and cusp pattern is N-shaped; Fig. 3).

Dentary thickness is thought to be correlated in carnivores with the degree of prey struggling (Maynard Smith and Savage, 1959), and several authors have written on the thickening of bone in general as a response to greater stress (Washburn, 1947; Tucker, 1954; Hildebrand, 1974). The development of the coronoid process and sagittal crest allows for increases in leverage and in area and volume of jaw muscle (Figs. 3, 4). An increase in the temporalis is particularly important to the increased stress of more struggling or tougher prey and heavy canine use (Maynard Smith and Savage, 1959).

Reduction of teeth and cusps occurs in mammals as jaws get shorter, as teeth get larger, or both. This reduction is carried to an extreme in carnivores such as cats, the most specialized flesh eaters, where PM⁴ and M¹ are the large functional teeth in the upper toothrow, posterior to the canines. The molossid species with thick jaws have only shearing edges in the upper toothrow and no nonshearing surface like PM³, but the molossids at the opposite extreme retain the rather blunt, nonshearing PM³ (Fig. 3). Further, the loss of the posterior commissure on M³ in the bats with thick jaws is related to the enlargement of teeth in the upper toothrow. Whatever disadvantage is caused by the loss of the posterior shearing edge may be more than compensated for not only by the larger cusps but also by the increased advantage of having the molars closer to the fulcrum of the jaw lever and more vertically aligned under the larger masseter muscle mass. In Fig. 3 one can see the more anterior position of the anterior juncture of the zygomatic arch to the rostrum in *Molossus ater* and *Cheiromeles parvidens*. It is at this anterior juncture that much of the masseter originates.

An exception to the above trends should be mentioned. Some of the smallest molossid bats (greatest skull lengths from 13.0 to 16.0 mm) have the most elevated condyles of any molossid, but these bats have a fully developed M³. If teeth are lost they

TABLE 1.—*Skull and toothrow characteristics for four morphologically distinctive molossid bats.**

Characteristic	Nyctinomops macrotis	Otomops martiensseni	Molossus ater	Cheiromeles parvidens
Greatest skull length (GSL)	23.0[1]	27.2	21.5	30.6
Maxillary tooth row (MTR)	8.4[1]	10.2	7.9	10.6
Dentary length (DL)	15.9[1]	18.6	15.6	22.6
Sum of cusps P^4-M^3	15.2[1]	15.8	17.2	22.5
Sum of tooth areas P^4-M^3	15.1[2]	18.5	20.4	35.9
MTR/GSL	36.5[3]	37.5	36.7	34.6
Cusp row/MTR	1.8[3]	1.5	2.2	2.1
Tooth area/MTR^2	0.21[3]	0.18	0.30	0.32
Dentary thickness/DL	8.2[3]	8.6	14.1	15.5
Height condyle/DL	8.2[3]	5.4	12.8	17.7
Coronoid height/DL	20.1[3]	18.8	32.7	39.8
Masseter origin/masseter insertion (from Fig. 3)	2.0[3]	2.0	1.6	1.4
Masseter muscle scar/DL (from Fig. 3)	24.0[3]	25.0	33.0	38.0

* Data mostly from Freeman, 1977; sample size is a male and female for each species except for *C. parvidens*, which is one female only. Values given are: 1—mm; 2—mm²; 3—percent.

are lost from the anterior portion of the toothrow (either lower incisors or upper premolars or both). These small bats combine features of both molossid extremes: 1) the elevated condyle and whatever advantage it may have for insect eating; 2) complete M^3 and its additional shearing edge. Small bats should also be proportionally stronger for their size than larger bats because muscle power varies by the square of linear dimensions while volume varies by the cube.

A few characteristics of the skulls and toothrows of four morphologically extreme molossids are listed in Table 1. *Molossus ater* and *Cheiromeles parvidens* have higher condyles, thicker jaws, and fewer teeth and cusps in the upper toothrow than do *Nyctinomops macrotis* (formerly *Tadarida macrotis*; Freeman, 1977) and *Otomops martiensseni* (Fig. 3). *Molossus ater* and *N. macrotis* are New World species that are sympatric in much of the Neotropics. The latter migrates to the temperate zone annually. *Cheiromeles parvidens* and *O. martiensseni* are Old World species; the first occurring in Borneo and the Philippines, the second in central Africa. Although the species of *Molossus* and *Cheiromeles* have fewer teeth and cusps than those of *Nyctinomops* and *Otomops*, the teeth are larger and cusps longer. An additional difference between the two morphological extremes is in the gape of the jaws. *N. macrotis* and *O. martiensseni* have a greater masseter origin-insertion ratio and therefore should have a greater gape than do *M. ater* and *C. parvidens* (Herring and Herring, 1974; Fig. 3).

To explain the possible function of these two molossid extremes, perhaps a loose analogy can be drawn from Olson (1961), who describes two basic jaw systems found in rhipidistians, amphibians, and reptiles—the kinetic-inertial jaw system and the static-pressure jaw system. The action of the first is primarily that of rapid closing of the lower jaw to the upper where velocity and mass of the jaws are the effective components of the bite. Little force is exerted in or near the occlusal surface and the movement of the jaw is mostly vertical. Morphological characteristics of kinetic-inertial jaws include a long, slender dentary, small coronoid process, and adductor muscle scar ¼ or ⅕ of the total dentary length. *N. macrotis* and *O. martiensseni* have these same features as well as large gapes of the jaws. Action of the static pressure system is that of exerting pressure when the jaws are nearly closed and of overcoming resistance with both vertical and lateral movements. Characteristics of this second

TABLE 2.—*Food habit data for* Nyctinomops-*like molossid bats (7 species) and* Molossus-*like molossid bats (12 species) in both New and Old Worlds.*

Species	Sample size	Evidence	Source
1. *Nyctinomops macrotis* New World	1	100% Macrolepidoptera (Sphingidae).	Ross (1967)
	49	86.1% volume Lepidoptera in 98.0% of the bats, 6.7% Gryllidae or Tettigoniidae in 28.6% of the bats, 4.1% Formicidae in 8.2% of the bats, 1.4% unidentified Insecta in 18.4% of the bats, 1.3% Pentatomidae in 2.0% of the bats, 0.3% unidentified Coleoptera in 6.1% of the bats, 0.1% Cercopidae and Cicadellidae in 6.1% of the bats.	Easterla and Whitaker (1972)
	4	An estimated average of 83,334 moth scales per gram of fecal material (relatively great compared to *Molossus*).	Freeman (1977)
2. *Nyctinomops femorosacca* New World	2	100% Macrolepidoptera (probably Sphingidae) in one, 85% Microlepidoptera and 15% Coleoptera in the other.	Ross (1967)
	13	36.9% volume Lepidoptera in 69.2% of the bats, 3.8% Gryllidae in 23.2% of the bats, 18.8% Formicidae in 30.8% of the bats, 5.8% unidentified Insecta in 46.1% of the bats, 2.3% Pentatomidae in 7.7% of the bats, 4.6% unidentified Coleoptera in 30.8% of the bats, 6.9% Cercopidae and Cicadellidae in 30.8% of the bats, 9.6% unidentified Hymenoptera in 23.2% of the bats, 7.3% unidentified Hemiptera in 30.8% of the bats, 2.7% unidentified Diptera in 23.2% of the bats, 1.2% Chrysopidae in 7.7% of the bats.	Easterla and Whitaker (1972)
	?	Wings and hard parts of insects in guano.	Krutzsch (1944)
3. *Tadarida brasiliensis* New World	88	34% Lepidoptera (also Nepticulidae), 26.2% Hymenoptera (Formicidae), 16.8% Coleoptera (Scarabidae, Chrysomelidae), 15% Homoptera (Cicadellidae) 6.4% Hemiptera (also Corizidae) 1.6% Neuroptera (Myrmeleontidae, 25 mm)	Ross (1967)
	7	95% Lepidoptera (mostly Gelechiidae), 4% Diptera (Dolichopodidae), 1% Homoptera; most of insects from 5 to 9 mm in length, one moth 18 mm.	Ross (1961)

TABLE 2.—*Continued.*

Species	Sample size	Evidence	Source
	8	Lepidoptera in 6 of the bats, Diptera in 6, Hymenoptera in 6, Coleoptera in 4, Homoptera in 2, Odonata in 1, and Neuroptera in 1.	Sherman (1939)
	5	An estimated average of 25,753 moth scales per gram of fecal material.	Freeman (1977)
	?	95% moth; 5% carabid beetles, hymenopterous insects, and a few crane flies in a series of bats.	Bailey (1931)
	?	Over 90% moth; remains of dragonflies, true bugs, a leafhopper, several beetles, and two ants in guano samples.	Storer (1926)
	4	Remains of insects, flies, and beetles.	Grinnell (1918)
4. *Eumops perotis* New World	9	100% Macrolepidoptera (Sphingidae, up to 60 mm); lower intestine of one with 4 Homoptera, one large cicada (Cicadidae), two leafhoppers (Cicadellidae), and one planthopper (Fulgoridae). Only abdomens of moths were taken.	Ross (1967)
	18	79.9% volume Lepidoptera in 100% of the bats, 16.5% Gryllidae or Tettigoniidae in 55.6% of the bats, 0.7% unidentified Insecta in 11.1% of the bats, 2.8% Acrididae in 5.6% of the bats.	Easterla and Whitaker (1972)
	4	50% Hymenoptera (36% Halictidae, 12% Formicidae, 5% Megachilidae, 5% Anthophoridae); 11% Coleoptera (1% Scarabidae, 5% Tenebrionidae, 5% Curculionidae); 10% Lepidoptera; 10% Orthoptera (Acrididae); 10% Hemiptera (Miridae).	Ross (1961)
	1	In captivity ate only abdomens of crickets.	Freeman (1977)
5. *Tadarida australis* Old World	21	20 with Lepidoptera, 2 with Coleoptera (Scarabidae), 3 with Hymenoptera (1 Formicidae), 1 with Hemiptera.	Vestjens and Hall (1977)
	?	"When skimming the surface of a river or a large pool it will often splash into the water, presumably in pursuit of water-beetles." (p. 744)	Shortridge (1936)
6. *Tadarida ansorgei* Old World	2	Debris of wings of Formicidae, antennae of Hymenoptera, and legs of Coleoptera.	Verschuren (1957)

TABLE 2.—*Continued.*

Species	Sample size	Evidence	Source
7. *Chaerephon limbatus* (=*Tadarida pumila*)	?	Adult moths of the cotton bollworm in Africa.	Allen (1939)
Chaerephon frater (=*Tadarida pumila*) Old World	?	"stomach contents show that it feeds on insects without hard integuments" (p. 547)	Lang and Chapin (1917)
1. *Molossus ater* New World	1	85.7% Hymenoptera (60.0% Formicidae up to 8 mm, 25.7% Chalcidoidea about 2 mm); 11.5% Coleoptera (8.6% small beetles of 8 mm, 2.9% large beetles of 25 mm); 2.9% unidentified insects about 9 mm.	Pine (1969)
	1	Mixed Coleoptera, Orthoptera, Hymenoptera with a conspicuous lack of Lepidopteran remains.	Howell and Burch (1974)
	4	An estimated average of 991 moth scales per gram of fecal material (many beetle parts present).	Freeman (1977)
2. *Molossus major* (=*Molossus molossus*) New World	10	9 with coleopteran remains only, 1 with dipteran remains.	Howell and Burch (1974)
3. *Molossus bondae* New World	2	An estimated average of 492 moth scales per gram of fecal material.	Freeman (1977)
4. *Molossus coibensis* New World	15	An estimated average of 3,475 moth scales per gram of fecal material (coleopteran, hymenopteran, and dipteran parts present).	Freeman (1977)
5. *Molossus pretiosus* New World	4	An estimated average of 631 moth scales per gram of fecal material (beetle parts present).	Freeman (1977)
6. *Molossus sinaloae* New World	6	An estimated average of 1,523 moth scales per gram of fecal material (beetle parts and seeds present).	Freeman (1977)
7. *Eumops underwoodi* New World	6	47% Coleoptera (primarily Scarabaeidae 6–10 mm, some Chrysomelidae); 31% Orthoptera (Acrididae 40–60 mm); 12% Homoptera (primarily Cicadellidae 6 mm, trace of Fulgoridae 20 mm); 10% Lepidoptera.	Ross (1967)

TABLE 2.—*Continued.*

Species	Sample size	Evidence	Source
8. *Tadarida (Mops) midas* Old World	1	4 large June beetles (Scarabaeidae, 40 mm), 2 large long-horned beetles (Cerambycidae, 60 mm).	Ross (1967)
9. *Tadarida (Mops) trevori* Old World	?	"dodge and dive after small hard-shelled Coleoptera" (p. 554).	Lang and Chapin (1917)
10. *Tadarida (Mops) condylura* Old World	1	"stomach contents showed that it fed on good-sized Coleoptera" (p. 555).	Lang and Chapin (1917)
	?	Legs of Coleoptera in stomach.	Verschuren (1957)
11. *Tadarida (Chaerephon) jobensis* Old World	9	8 bats with moth remains, 3 with remains of plant bugs, and one bat each with remains of ground beetles, water beetles, leaf beetles, unidentified beetles, flies, crickets, and earwigs.	Vestjens and Hall (1977)
12. *Cheiromeles torquatus* Old World	1	In captivity, lived well on grasshoppers and moths.	Kitchener (195⅘)
	?	"exoskeletal insect fragments" in guano (beetles?)	Medway (1958)

system include a large coronoid, an adductor muscle scar that occupies more of the dentary, and well-developed posterior adductor muscles. *M. ater* and *C. parvidens* have similar features.

The analogy lies primarily in the initial action of the jaws. The complete chewing cycle of the bats' jaws is probably far more complex than that in primitive reptiles and amphibians. Molossids with thin, kinetic-inertial jaws and wide gape should be able to take large, soft items such as moths. The sharp, long canines and the snapping-shut action of the jaws should be effective in seizing soft insect prey on the wing. Molossids with thick, static-pressure jaws should have the ability to crunch hard-shelled items such as beetles. Although the beetle-eater's gape may not be as large, the well-developed canines, strong jaws, and enlarged temporal muscles should be enough to procure, puncture, and process the hard-shelled prey. Data on the food habits of molossid bats support these predictions: *Nyctinomops*-like bats eat moths and *Molossus*-like bats eat beetles (Freeman, 1977; Table 2). Data are scanty and qualitative for these night-flying, hard-to-capture mammals, but the trends of moth-eating and beetle-eating are apparent.

In conclusion, I suspect the specialized feeding habits seen in molossid bats can be found in all chiropteran insectivores. Perhaps terrestrial insectivores, shrews, moles, and insectivorous marsupials also specialize on certain portions of the insect community. Whether or not these habits can be revealed from morphology of the structure of the jaws and teeth has not yet been explored, although I am presently investigating other insectivorous bats with known food habits.

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Note added in press: Whitaker and Mumford (J. Mamm., 59:632–634, 1978) reported food data from Kenya for nine specimens of *Tadarida pumila* (=*Chaerephon pumila,* this report), which took 61.6% Hemiptera and Lepidoptera and 18.4% Coleoptera, and nine specimens of *Tadarida condylura* (=*Mops condylura,* this report), which took 63.9% Coleoptera and 32.3% Hemiptera and Lepidoptera. The first feeds primarily on soft items and the second, primarily on hard. These results support my predictions and supplement data for the same species given in Table 2.