

ELECTROMYOGRAPHY AND MECHANICS OF MASTICATION IN THE SPRINGHARE, *PEDETES CAPENSIS* (Rodentia, Pedetidae)

by

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SUMMARY

In springhares, *Pedetes capensis* (FORSTER, 1778) ingestion, transport and mastication of food are cyclic events. During these cycles, the movement of the lower jaw shows no lateral component and the activity of all muscles is bilaterally symmetrical. The temporal muscles reach a peak activity during the fast-closing stage. During the reduction stages, peak activities are subsequently reached in the maxillomandibular muscles, the medial pterygoids, the masseters, the zygomaticomandibular muscles, the posterior masseters, and the lateral pterygoids in order. During fast opening, only the digastrics fire bilaterally. Magnitude and duration show some variation for the different types of food offered. The maxillomandibular muscle reaches its maximum activity whenever the animals feed on groundnut. Food that does not require biting (*i.e.* rolled oats), produces very low muscle activity.

The Rodentia include groups with a similar gross muscular morphology but considerable differences in their masticatory patterns, whereas members of different major groups show similar masticatory patterns. Although the masticatory patterns shown by *Rattus* and *Pedetes* are similar, the forces acting on their lower jaws differ. In *Pedetes* the masseter-complex is more important than in *Rattus* as the bite force at the incisors is 68 % of the estimated muscle resultant.

Keywords : mastication, jaw muscles, electromyography, biomechanics, rodents, *Pedetes*.

INTRODUCTION

Cinematography and electromyography have substantially added to our knowledge of mammalian mastication (for review see GANS *et al.*, 1978 ; HIEMAE, 1978 ; GORNIAK, 1985). Experimental studies on rodent mastication modify the conclusion of theoretical analyses (*cf.* MAYNARD SMITH and SAVAGE, 1959) and show that masticatory mechanics differs remarkably among rodents.

Comparison of the kinematics and anatomical data on rodent mastication shows that the absence or presence of isognathia, the orientation and occlusal pat-

tern of the molar teeth, and the position of the incisors are the most important dental characteristics regulating the masticatory pattern.

Springhares, *Pedetes capensis*, are rodents that do not fit comfortably into their present systematical classification. Their characteristics do not permit placement within any of the four major rodent groups (Protrogomorpha, Sciuromorpha, Myomorpha, and Hystricomorpha) (OFFERMANS and DE VREE, 1989). Their characteristics are shared with those of groups, such as the Anomaluridae, Ctenodactylidae, Dipodidae, and Theridomorpha. Despite their substantial morphological differences, the mastication pattern in *Pedetes* is similar to that of *Rattus* (OFFERMANS and DE VREE, 1990). Both masticate bilaterally : chewing the food simultaneously on both sides.

The present paper reports on the muscular activity during ingestion and mastication of springhares. These data and quantified motion analysis have been combined in a threedimensional model that permits investigation of external forces that act upon the mandible during ingestion and mastication cycles.

MATERIALS AND METHODS

Feeding movements were studied on two adult specimens (one male of 2.5 kg and one female of 2.1 kg), placed at our disposition by the Zoo of Blijdorp (Rotterdam, The Netherlands). After the experiments, the female specimen was sacrificed for analysis of the muscle pattern. Additionally, a preserved head (State Museum, Windhoek, Namibia) and dry skulls (Mus. r. Afr. Centr., Tervuren, Belgium) could be studied.

In six experiments, the animals were studied while ingesting and masticating rolled oats and groundnuts (peanuts). The animals were not restrained as it was found that they were easily trained to accept food in the experimental setting.

Electromyography electrodes were formed of 0.076 tefloncoated stainless steel wires (Medwire Corp.), and inserted in the muscles with 16-gauge hypodermic needles through small skin incisions under general anesthesia (40 mg Ketalar/kg and 0.04 ml Rompun/kg) (GANS and GORNIK, 1980). Movements of the electrode tips were minimized by gluing the electrodes at the insertion site with histoacryl (Braun Melsungen AG). The electrodes were led subcutaneously to the back of the animal between the shoulder blades. The ends of the wires were soldered to an externally placed, 31-pole miniature connector (Amphenol, nr 222-22N31) that subsequently was attached to the skin with silicon rubber (Silastic 382 Medical Grade, Elastomer, Dow Corning) (DE GUELDRÉ and DE VREE, 1988). EMG signals were passed through Tektronix 26A2 differential preamplifiers and Honeywell Accudata 117 DC amplifiers and recorded on a Honeywell medium bandpass 96FM 14-channel tape recorder at 19 cm/sec.

Electromyography was combined with X-ray cinematography using a Siemens Tridoros X-ray flash apparatus in combination with a Siricon 2 image intensifier. Film sequences were recorded in lateral view at 50 fps with an Arriflex 16 mm camera, using Gevapan 30 negative film (80 asa). Films were projected frame by

frame on a Vanguard analyzer with a PCD projecting system. The coordinates of the markers were determined and digitized with a PCD analyzer and recorded with a IBM-AT computer.

Electromyograms were digitized with a Keithley DAS A/D converter using an IBM-AT computer. Muscle activity was described as spike number, amplitude and product of spike number times amplitude for intervals of 10 msec (two intervals per film frame). As the product of spike number times amplitude correlates best with tension (GORNIK and GANS, 1980; GORNIK *et al.*, 1982; DE GUELDRE and DE VREE, 1988), this value was used for further calculations. The muscle activities recorded with each electrode were averaged and the %EMG was expressed as a fraction of the maximum value observed for that electrode in any interval.

Wet muscle weights were determined on a freshly killed female specimen and a preserved head. The muscles were excised carefully, weighed, and fixed in 10 % formalin. To dissolve the connective tissue the muscles were immersed in 25 % nitric acid for five to six days and then placed in 50 % glycerol. Fiber lengths were measured on a Wild M5 dissecting microscope with an ocular micrometer. Physiological cross sectional areas were estimated by dividing the mean wet weight, used as measure of volume, by the mean fiber length (FICK, 1910; SCHUMACHER, 1961; WEIJS and DANTUMA, 1981; DE GUELDRE and DE VREE, 1990).

The origin and insertion of the theoretical central fibers (RAYNE and CRAWFORD, 1972) were marked on the skull and the mandible with lead markers (HIEMAE, 1971). The working lines of the muscles were determined from the coordinates in the x, y and z planes of the points of origin and insertion. To do this the skull was mounted in a stereotactic apparatus with the teeth in full occlusion. The coordinates of these points, of the teeth and the condyles were determined relative to the sagittal and occlusal planes. The changing direction of the working lines during the ingestion and mastication cycles could be established using standardized cycles (OFFERMANS and DE VREE, 1990). The origin-insertion lengths and the moment arms of the muscles could also be derived from these data.

The magnitude of instantaneous muscular force was estimated for each muscle by multiplying the value of %EMG, a measure of the degree of activity, with the physiological cross section, a measure for maximal force (WEIJS and DANTUMA, 1981; DE GUELDRE and DE VREE, 1990).

RESULTS

Anatomy

The morphology of the masticatory apparatus of the springhare has been described in detail (OFFERMANS and DE VREE, 1989). Most muscles of the masseteric complex are well separated from each other. However, the superficial masseter barely can be distinguished from the deep masseter. Therefore, these muscles were treated as a single unit for the electromyographic and biomechanical study. The zygomaticomandibular and maxillomandibular muscles form a uniform mass which

is well separated from the other muscles of the masseteric complex. The temporal muscle is small and consists of a single layer, which shows no connection with the zygomaticomandibular muscle: *Pedetes* shares this characteristic with other rodents (ALLEN, 1880). The masticatory muscles are illustrated in Figure 1 and their areas of origin and insertion of are summarized in table 1.

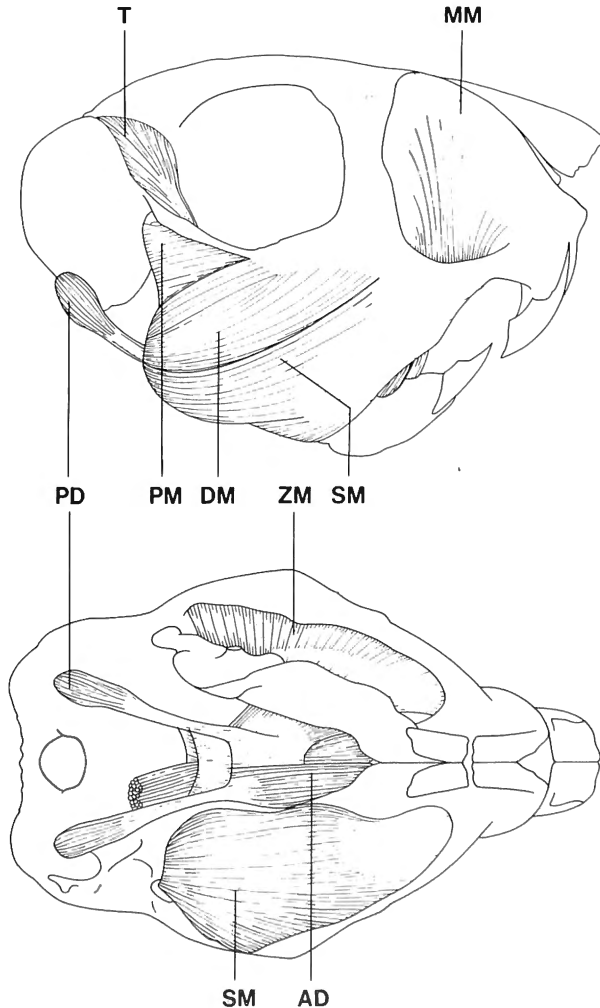


Fig. 1. — *Pedetes capensis*. Lateral and ventral view of the masticatory muscles. AD = anterior digastric muscle, DM = deep masseter, LP = lateral pterygoid muscle, MP = medial pterygoid muscle, MM = maxillomandibular muscle, PD = posterior digastric muscle, PM = posterior masseter, SM = superficial masseter, T = temporal muscle, ZM = zygomaticomandibular muscle.

TABLE 1

Areas of origin and insertion of the masticatory muscles in *Pedetes capensis*.

| Muscle | Origin | Insertion |
|---------------------------|---|---|
| Masseter-complex | | |
| M. masseter superficialis | aponeurosis of origin lateral surface of the zygomatic process of the maxillary bone | aponeurosis of insertion lateral and medial side of the angular process |
| M. Masseter profundus | medial aponeurosis of origin lateral surface of the zygoma | aponeurosis of insertion posterior edge of the angular process lateral surface of the lower jaw, dorsal to the anterior and posterior masseteric ridges |
| M. masseter posterior | lateral surface of the zygoma | lateral surface and posterior edge of the conylar process |
| M. maxillomandibularis | aponeurosis of origin maxilla and premaxilla | aponeurosis of insertion |
| M. zygomaticomandibularis | medial wall of the zygoma | aponeurosis of insertion |
| M. temporalis | temporal fossa | medial surface of the coronoid process |
| M. pterygoideus medialis | external aponeurosis pterygoid fossa | aponeurosis of insertion medial wall of the angular process |
| M. pterygoideus lateralis | lateral surface of the outer pterygoid lamina lateral surface of the maxillary bone | medial surface of the condyloid process articular capsule |
| M. digastricus | | |
| Anterior part | hyoid | medioventral edge of lower jaw |
| Posterior part | jugular process | hyoid |

Although the upper and lower toothrows lie at an acute angle with the sagittal plane, *Pedetes* is isognathic. It can keep both toothrows in occlusion during propalinal movements of the lower jaw. The upper molars slant outward from the midline and the lower ones inward at an angle of 5° . The premolars and molars are bilobed. These on the maxilla show a buccal valley. This crosses the maxillary teeth almost to the lingual margin, whereas a lingual valley crosses the mandibular teeth equally far. See FRIANT (1963), LAVOCAT and MICHOUX (1966), and WOOD (1962, 1965a) for a detailed description of dental morphology.

Movement profiles

During feeding in the springhare, two cyclic events, namely ingestion and mastication (Fig. 2) can be distinguished (OFFERMANS and DE VREE, 1990). During the ingestion cycles, the mandibular movement profile depends on the type of food ingested. During ingestion of groundnut, the lower jaw rotates with a single degree of freedom and little or no condylar translation occurs. Ingestion of rolled oats involves mandibular rotation as well as translation. During the closing stage, the jaw rotates upward and the condyle simultaneously moves backward. A marked forward translation coincides with the end of the opening stage and the beginning of the closing stage.

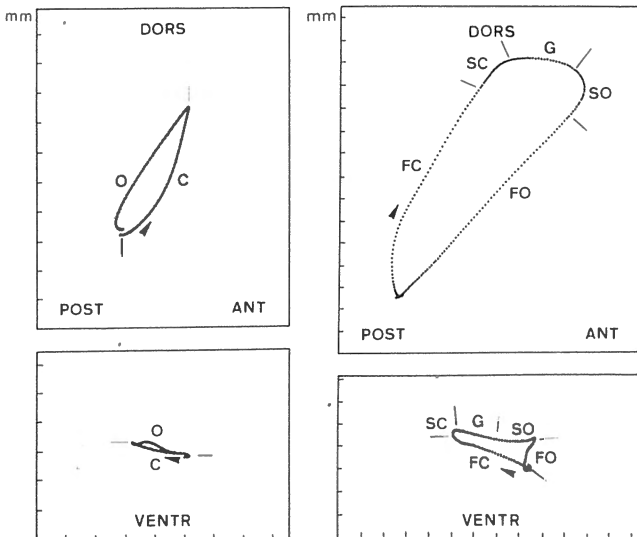


Fig. 2. — *Pedetes capensis*. Mean movement profiles of the mandibular incisor (above) and condyle (below) during ingestion (left, $N = 30$) and mastication (right, $N = 54$) of rolled oats. Data derived from cineradiographic films taken at 50 fps in lateral projection. Arrows indicate direction of movement. C = closing, FC = fast-closing stage, FO = fast-opening stage, G = grinding stage, O = opening, SC = slow-closing stage, SO = slow-opening stage.

Movement profiles during mastication are essentially the same for all food types investigated. *Pedetes* shows a bilateral, propalinal mastication cycle. This cycle can be divided into a fast- and slow-closing stage, a grinding stage, and a slow- and fast-opening stage. Fast closing of the mouth is established by an upward rotation of the jaw, accompanied by a backward translation of the condyle. The upward movement of the jaw is slowed when tooth-food-tooth contact is reached, whereas at that moment, the jaw slowly shifts forward. The forward movement of the condyles coincides with the beginning of the slow-closing stage during mastication of rolled oats. During mastication of groundnut, this forward movement starts at the end of the slow-closing stage, which results in a prolonged activity in some of the muscles during the closing stages. During the grinding stage, the lower jaw shifts forward with the molar teeth in full occlusion on both sides simultaneously. This forward movement is accompanied by a small downward rotation during the slow-opening stage. Fast opening of the jaw is a downward rotation with a single degree of freedom.

Activity in single muscles

Ingestion

The activity patterns of the masticatory muscles demonstrate a completely different ingestion for rolled oats and groundnut (Fig. 3). Rolled oats are not bitten during ingestion. Instead, the lower jaw shovels in the small food particles. Ingestion of groundnut involves biting off of small pieces. The lower incisors move more anteriorly and dorsally to grasp the food against the upper ones.

Whereas the temporal muscles fire at a level of 5 % or less, halfway into the closing stage during the ingestion of rolled oats, they are inactive during the ingestion of groundnut.

The maxillomandibular muscles show hardly any activity during the ingestion of rolled oats. However, during ingestion of groundnut the level of firing reaches 100 % early in the closing stage. This activity drops rapidly and ceases before the end of the stage. After the end of the closing phase, the activity increases again and reaches its maximum at the beginning of the next closing stage. The activity pattern of the zygomaticomandibular muscles resembles that of the maxillomandibular ones. During ingestion of rolled oats, they show no activity. During ingestion of groundnuts, firing starts halfway the opening stage to reach its maximum at a 50-60 % level at the beginning of the closing stage. However, activity decreases rapidly and ceases halfway into this stage.

The activity of the masseter muscles during the ingestion of rolled oats does not exceed the 5 % level during half of the closing stage. In contrast, firing reaches the 20 % level at the beginning of the closing phase during ingestion of groundnuts. The activity slowly decreases towards the end of this stage. Firing resumes before the end of the opening stage. The posterior masseter controls condylar movement. As there is little or no condylar translation during the ingestion of groundnut, it then shows hardly any activity. During the ingestion of rolled oats, this activity (10-

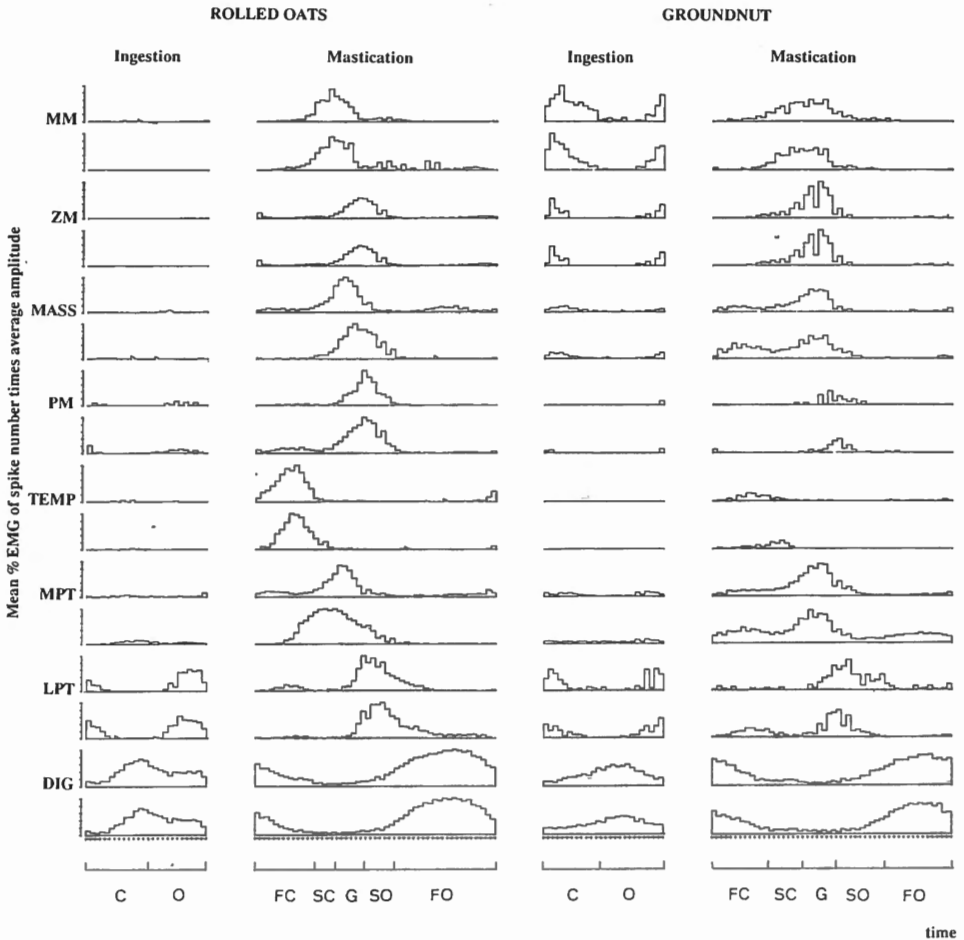


Fig. 3. — *Pedetes capensis*. Overall pattern of muscle activity during the ingestion and mastication of rolled oats and groundnut. The EMG activities are expressed as the mean % distributions of the product of spike number times amplitude. Activities of right (above) and left (below) muscle of each pair is given. C = closing stage, DIG = anterior digastric, FC = fast-closing stage, FO = fast-opening stage, G = grinding, LPT = lateral pterygoid, MASS = superficial masseter, MM = maxillomandibularis, MPT = medial pterygoid, O = opening stage, PM = posterior masseter, SC = slow-closing stage, SO = slow-opening stage, TEMP = temporalis, ZM = zygomaticomandibularis.

20 % level) coincides with the forward movement of the condyle at the beginning of closing and during the opening stage.

The activity patterns of the lateral pterygoids resemble those of the posterior masseters. The former fire at a 50 % level at the beginning of the closing stage and reach a 60 % level during the opening stage. Although there is little or no condylar translation during the ingestion of groundnut, the lateral pterygoids show a similar

activity pattern during the ingestion of this type of food. For both food types the medial pterygoids show a continuous low level activity (always less than 15 %).

The digastric muscle acts to open and retract the jaw. It is mainly active during the opening stage. However, the activity starts to build up during the closing stage, increasing rapidly during its second half and reaching peak activity at the closing-opening transition. During the opening stage activity gradually diminishes. The activity pattern is essentially the same for both food types. However, ingestion of rolled oats coincides with a higher activity level (70-80 %) than ingestion of groundnut (50-60 %).

Mastication

Not only the movement patterns of the lower jaw but also the activity sequences of the masticatory muscles are similar for the different food types investigated (Fig. 3). However, they considerably differ in their activity levels and some muscles are active for different periods. The following description is based on electromyography during mastication of rolled oats. Whenever marked differences occur during mastication of groundnut, these are mentioned.

The temporales start to fire at the end of fast opening and are mainly active during fast closing. Muscle activity increases rapidly and reaches a 100 % level (only 20-30 % for groundnut) halfway into fast closing. Activity then drops to 5-10 % during slow closing and ceases.

During fast-closing, the activity of the maxillomandibular muscles is low but increases rapidly towards the end of this stage. During slow-closing, these muscles reach peak activity at a 90-95 % level. Then, firing drops rapidly. It reaches a 10-20 % level at the end of the grinding stage and continues till the end of slow-opening. During ingestion of groundnut, the activity of the maxillomandibularis only reaches 60 %. However, firing remains at this level almost till the end of the grinding stage, then drops rapidly to 10 to 20 % and decreases slowly towards the end of slow-opening. The zygomaticomandibular muscle becomes active halfway into fast-closing. Firing reaches 10 to 20 % during this stage. Activity slowly increases during slow-closing to reach a maximum during grinding at a 60 % level (100 % for groundnut). After reaching maximum activity, firing decreases rapidly.

Whenever rolled oats are masticated, firing of the masseter reaches 10 % during fast-closing. During slow-closing, muscular activity increases rapidly and reaches a 100 % level at the end of this stage. During the grinding stage, the activity drops to 5 %, and this continues during the first half of the subsequent slow-opening stage. In mastication of groundnut firing is much more active (40-50 %) during fast-closing. However, the maximum activity reached at the end of slow-closing stays below the 70 % level. In contrast to the activity pattern for rolled oats, this maximum activity is maintained during most of the grinding stage, after which firing diminishes till halfway into slow-opening.

Reduction of rolled oats involves an activity of the posterior masseter that is similar to that of the masseter muscle. However, during the reduction stages (slow-

closing, grinding and slow-opening), the activity of the posterior masseter builds up more slowly, so that it only reaches the 100 % activity level halfway through the grinding stage. This instance coincides with the forward translation of the lower jaw. During the reduction of groundnut, the posterior masseter also achieves maximal activity coincident with the forward translation of the lower jaw. However, this translation occurs during the grinding stage and the first half of slow-opening. The maximal activity (40 %) occurs at the end of grinding.

During the closing stages, the activity of the lateral pterygoids does not exceed 10 %. Activity increases during the grinding stage and the slow-opening stage, during which the mandible is shifted forward. A maximum (100 % for rolled oats, and 70 % for groundnut) is reached at the grinding slow-opening transition, after which activity diminishes rapidly. Although the medial pterygoids show some activity throughout the entire mastication cycle, firing rapidly increases prior to the forward shift of the lower jaw (the end of fast-closing for rolled oats, and the end of slow-closing for groundnut). They reach their maximum activity in the subsequent stage (100 % for rolled oats, and 90 % for groundnut), and then become inactive.

Both during the reduction of rolled oats and of groundnut, the digastric muscles are maximally active during the fast-opening stage (100 % and 80 % respectively). Firing then diminishes, to reach a minimum at the end of fast-closing. Activity stays low during the subsequent slow-closing and grinding stages, and slowly increases during slow-opening.

Activity patterns

Ingestion

Ingestion of rolled oats does not involve biting, and most muscles have low activity, the lateral pterygoids and the digastrics forming an exception. During the beginning of the closing stage, upward rotation is accompanied by forward translation of the condyle. At that moment the digastrics show low and decreasing activity, whereas that of the posterior masseters is weak, and the lateral pterygoids fire at 50 %. Early in the closing stage, the condyles reverse their movement and the posterior masseters cease firing; also the activity in the lateral pterygoids diminishes rapidly. At the same time, the masseter muscles are weakly active. However, this activity ceases halfway the closing stage. At this time the temporal muscles start to fire. Meanwhile, the medial pterygoids and digastrics are increasingly active and are most active at the closing-opening transition. During the opening stage, these muscles remain active at a reduced level. Opening of the mouth is accompanied by a forward translation of the condyles. The posterior masseters and the lateral pterygoids become increasingly active during this stage, whereas the temporal muscles become silent.

During the ingestion of groundnuts, muscle activities are much higher than during the ingestion of rolled oats. The mouth is closed and opened by rotation at the temporomandibular joint with the condyles in their most anterior position. Early in the closing stage, the muscles of the masseteric complex show a peak activity. The maxillomandibular muscles are especially active (100 %), but the zygomatico-

mandibular muscles reach 50 % of maximal activity. Although there is little or no condylar translation during the ingestion of groundnut, during this stage the posterior masseters and lateral pterygoids are highly active. The medial pterygoids are weakly active throughout the entire cycle. However, the temporal muscles are inactive. At the beginning of the cycle, the activity of the digastrics is low, but it increases toward the end of the closing stage. At the same time, the activity of the lateral pterygoids and the muscles of the masseteric complex diminishes. It ceases at the end of this stage. During the first half of the opening stage, the activity of the digastric muscles peaks. Whereas their activity diminishes during the second half of the opening stage, the activity of the muscles of the masseteric complex and the lateral pterygoids increases.

Mastication

During mastication, the condyles lie in their most forward position at maximum opening of the mouth. Fast closure of the mouth is accompanied by a backward translation of the condyles. At the beginning of fast-closing, the digastrics show a decreasing activity. The activity of the muscles of the masseteric complex is very low, except for the superficial masseters, as well as the medial pterygoids, during the mastication of groundnut. The first muscles that become highly active are the temporales which reach peak activity halfway into fast-closing. Decreasing activity in the temporales generally coincides with low level activity in the lateral pterygoids. These bursts of activity stop before the reversal of condylar translation (beginning of slow-closing for rolled oats, and near the end of slow-closing for groundnut). When tooth-food-tooth is reached (beginning of slow-closing) the upward rotation of the mandible slows and the jaw slowly shifts forward. The muscles of the masseteric complex and the medial pterygoids become increasingly active. The maxillomandibular muscles reach their activity peak during slow-closing, closely followed by subsequent activity peaks in the medial pterygoids (closely after the beginning of the forward movement of the condyles), the masseter muscles, and the zygomaticomandibular muscles. While their activity level decreases toward the end of the grinding stage, the posterior masseters and the lateral pterygoids become increasingly active, reaching peak activity halfway through the grinding stage and at the transition between the grinding and slow-open stages respectively. As a result the mandible is shifted forward, with the molar teeth in full occlusion. This motion continues during slow-opening, accompanied by a small downward rotation of the lower jaw about the temporomandibular joint. While activity in the posterior masseters and lateral pterygoids decreases, activity in the digastrics rapidly increases, to reach a maximum halfway fast-opening. During this stage, low level activity may occur in the medial pterygoids. The condyles stay in their most forward position throughout the fast-opening stage.

Physiological cross section

Physiological cross sections are customarily assumed to provide an estimate of the maximal force the muscle can produce. However, recent analyses suggest that the aggregate mass provides a better basis of comparison (GANS and DE VREE,

1987). The muscle weights, fiber lengths and physiological cross sections of the masticatory muscles are given in table 2. These data show the importance of the muscles of the masseter-complex. Both mass and physiological cross section are largest for the zygomaticomandibularis, the masseter and the maxillomandibularis. The data suggest that the increased size and complexity of the masseter-complex is at the expense of the temporal muscle, which has the smallest physiological cross section and mass of all masticatory muscles in *Pedetes*. Whereas the medial pterygoid is relatively large, the lateral pterygoids and temporal muscles have a comparable physiological cross section.

TABLE 2

Wet weights (mg), fiber lengths (mm), and physiological cross sections (g wet/cm²) of the masticatory muscles of *Pedetes capensis*.

| Muscles | Wet Weight | Fiber length | | Cross section |
|------------------------|------------|--------------|-----------|---------------|
| | | Mean | Range | |
| Maxillomandibularis | 3208.6 | 1.43 | 1.21-1.68 | 2.244 |
| Zygomaticomandibularis | 1911.2 | 0.81 | 0.72-0.93 | 3.360 |
| Masseter | 4126.9 | 1.43 | 1.12-1.66 | 2.886 |
| Posterior masseter | 398.9 | 0.61 | 0.54-0.71 | 0.654 |
| Temporalis | 418.2 | 0.81 | 0.77-0.91 | 0.516 |
| Lateral pterygoid | 378.6 | 0.73 | 0.64-0.78 | 0.519 |
| Medial pterygoid | 1163.7 | 1.03 | 0.86-1.15 | 1.130 |
| Digastricus | 408.0 | 0.75 | 0.61-0.89 | 0.544 |

The effective force produced by the masticatory muscles not only reflects the theoretical maximum but also the three-dimensional angle of insertion, which is subject to considerable change during rotation of the jaws. Even more important (and customarily ignored) is the range of muscle shortening relative to the length-tension curve (GANS and DE VREE, 1987; WEIJS and VAN RULJVEN, 1990). As this information is here lacking (it would cost too many specimens to generate it) we provide calculations of origin-insertion lengths, angles with the antero-posterior, vertical and transverse axes, vector components along these axes and moment arms about the horizontal, vertical and bicondylar axes. These are established for 50 jaw positions during the mastication of rolled oats and groundnut, and for 25 positions during the ingestion of both types of food. Table 3 gives these data for the different masticatory muscles at occlusion during ingestion of rolled oats. Table 4 and Figure 4 give it for the equivalent position during their mastication. The difference reflects the changed direction of action by some of the muscles.

For instance during ingestion, the lower jaw is shifted forward and the mouth is slightly more opened than during mastication. The forward component of the

TABLE 3. — *Pedetes capensis*. Origin-insertion length in mm (l), angles relative to X(a), Y(b), and Z(c) axes, vector components along the horizontal (X), vertical (Y), and transverse (Z) axes, and moment arms around the Z, Y, and X axes (MXY, MXZ and MYZ for the right and MXY, MXZ', and MYZ' for the left condyle) of the masticatory muscles for the lower jaw in the most closed position during the ingestion of rolled oats.

| Muscle | l | d | a | b | c | x | y | z | MXY | MXZ | MYZ | MXZ' | MYZ' |
|-----------------------|-------|-------|--------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|
| Maxillomandibularis | 54.53 | 43.84 | 85.36 | 4.76 | 88.95 | 0.08 | 1.00 | 0.02 | 33.14 | 1.96 | 9.55 | 37.05 | 30.45 |
| Zygomatocmandibularis | 14.63 | 26.87 | 107.75 | 43.35 | 127.96 | -0.30 | 0.73 | -0.62 | 10.04 | 14.54 | 8.22 | 32.30 | 38.76 |
| Masseter muscle | 24.07 | 25.55 | 32.41 | 57.62 | 88.81 | 0.84 | 0.54 | 0.02 | 24.95 | 1.28 | 2.42 | 38.71 | 37.55 |
| Posterior masseter | 6.73 | 4.92 | 37.30 | 96.66 | 126.50 | 0.80 | -0.12 | -0.59 | 4.47 | 0.83 | 4.63 | 31.20 | 3.02 |
| Temporal muscle | 32.47 | 20.95 | 126.01 | 36.14 | 92.65 | -0.59 | 0.81 | -0.05 | 0.57 | 0.57 | 0.51 | 39.31 | 39.42 |
| Lateral pterygoid | 17.69 | 3.39 | 42.99 | 122.29 | 64.92 | 0.73 | -0.53 | 0.42 | 1.07 | 2.45 | 1.39 | 32.16 | 29.95 |
| Medial pterygoid | 22.51 | 26.68 | 68.69 | 28.57 | 71.88 | 0.36 | 0.88 | 0.31 | 6.67 | 6.80 | 14.26 | 23.60 | 23.45 |
| Digastricus | 46.68 | 45.01 | 143.30 | 55.81 | 101.74 | -0.80 | 0.56 | -0.20 | 20.47 | 11.52 | 2.67 | 27.25 | 34.94 |

TABLE 4. — *Pedetes capensis*. Origin-insertion length in mm (l), angles relative to X(a), Y(b), and Z(c) axes, vector components along the horizontal (X), vertical (Y), and transverse (Z) axes, and moment arms around the Z, Y, and X axes (MXY, MXZ and MYZ for the right and MXY, MXZ', and MYZ' for the left condyle) of the masticatory muscles for the lower jaw in the most closed position during the mastication of rolled oats.

| Muscle | l | d | a | b | c | x | y | z | MXY | MXZ | MYZ | MXZ' | MYZ' |
|-----------------------|-------|-------|--------|--------|--------|-------|-------|-------|-------|-------|-------|-------|-------|
| Maxillomandibularis | 50.57 | 43.83 | 81.47 | 8.61 | 88.87 | 0.15 | 0.99 | 0.02 | 37.90 | 4.36 | 9.51 | 35.29 | 30.48 |
| Zygomatocmandibularis | 12.04 | 26.87 | 90.00 | 48.37 | 138.37 | 0.00 | 0.66 | -0.75 | 21.00 | 21.00 | 8.64 | 21.00 | 35.21 |
| Masseter muscle | 26.62 | 25.54 | 25.62 | 64.40 | 88.92 | 0.90 | 0.43 | 0.02 | 25.48 | 1.25 | 2.48 | 38.74 | 37.49 |
| Posterior masseter | 12.22 | 4.92 | 19.72 | 94.70 | 109.11 | 0.94 | -0.08 | -0.33 | 4.31 | 0.66 | 4.37 | 37.12 | 5.34 |
| Temporal muscle | 28.26 | 20.94 | 119.7 | 29.89 | 93.04 | -0.50 | 0.87 | -0.05 | 4.47 | 0.00 | 0.55 | 39.77 | 39.38 |
| Lateral pterygoid | 22.95 | 3.39 | 31.83 | 114.45 | 70.93 | 0.85 | -0.41 | 0.33 | 1.13 | 2.62 | 1.43 | 34.71 | 29.97 |
| Medial pterygoid | 24.11 | 26.68 | 61.51 | 33.95 | 73.12 | 0.48 | 0.83 | 0.29 | 12.96 | 5.13 | 14.25 | 29.04 | 25.50 |
| Digastricus | 43.62 | 45.01 | 144.47 | 57.40 | 102.58 | -0.81 | 0.54 | -0.22 | 16.49 | 9.99 | 2.18 | 28.65 | 34.90 |

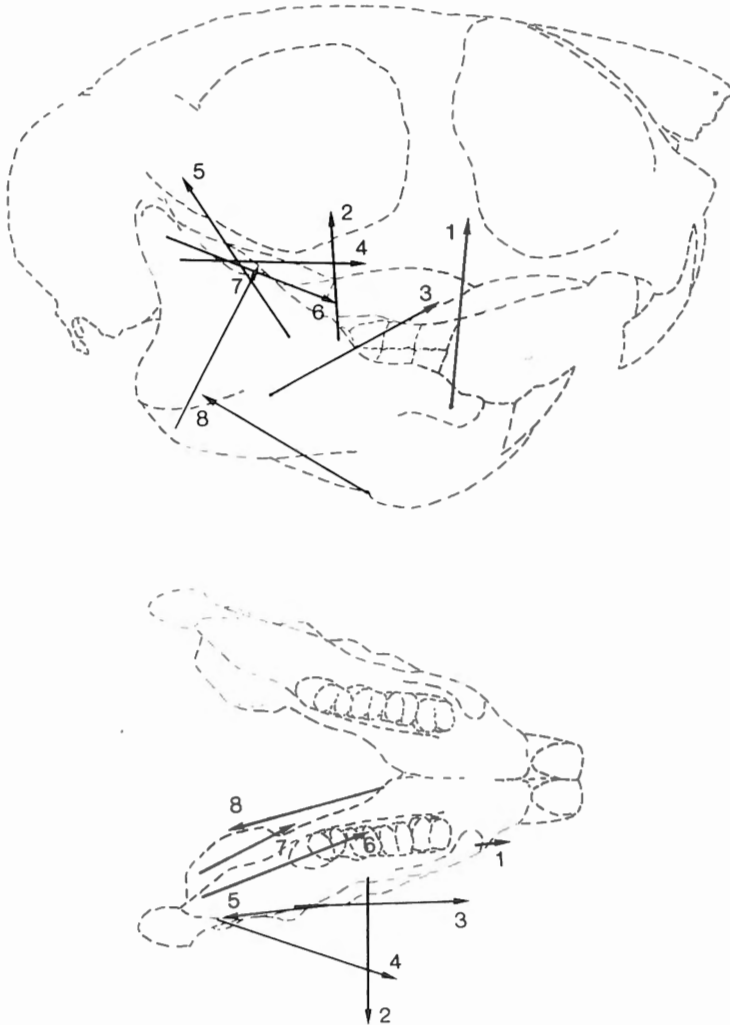


Fig. 4. — *Pedetes capensis*. Working lines of the masticatory muscles during the mastication of rolled oats with the lower jaw in the most closed position. 1 = Maxillomandibularis, 2 = Zygomaticomandibularis, 3 = Masseter, 4 = Posterior masseter, 5 = Temporalis, 6 = Lateral pterygoid, 7 = Medial pterygoid, 8 = Digastric muscle.

muscles of the masseter-complex (except for the posterior masseter) and the medial pterygoids decreases, and may even reverse to a backward component (zygomaticomandibular muscles). The vertical component on the other hand, increases, whereas the transverse component remains unchanged. The forward component of the pull of the posterior masseter and lateral pterygoids, both protractors of the lower jaw, decreases due to the forward position of the jaw, whereas their upward component increases as the mouth is more opened. Whereas the changes in the directional pull

TABLE 5. — *Pedetes capensis*. Changes in the origin-insertion length (l) and vector components along the horizontal (X), vertical (Y), and transverse (Z) axes during the different stages of groundnut ingestion. a-beginning closing stage; b-halfway closing; c-closing-opening transition; d-halfway opening.

| Muscle | l | | | | x | | | | y | | | | z | | | |
|-----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | a | b | c | d | a | b | c | d | a | b | c | d | a | b | c | d |
| Maxillomandibularis | 57.35 | 55.84 | 54.66 | 56.05 | 0.10 | 0.07 | 0.05 | 0.07 | 1.00 | 1.00 | 1.00 | 1.00 | 0.02 | 0.02 | 0.02 | 0.02 |
| Zygomatocmandibularis | 15.90 | 15.56 | 15.41 | 15.60 | -0.28 | -0.35 | -0.41 | -0.34 | 0.77 | 0.74 | 0.70 | 0.74 | -0.57 | -0.58 | -0.58 | -0.58 |
| Maseter muscle | 24.79 | 23.64 | 22.59 | 23.81 | 0.84 | 0.83 | 0.82 | 0.83 | 0.55 | 0.56 | 0.57 | 0.56 | 0.02 | 0.02 | 0.02 | 0.02 |
| Posterior maseter | 5.64 | 5.51 | 5.28 | 5.54 | 0.69 | 0.68 | 0.64 | 0.68 | -0.12 | -0.13 | -0.14 | -0.13 | -0.71 | -0.73 | -0.76 | -0.72 |
| Temporal muscle | 33.42 | 33.51 | 33.68 | 33.49 | -0.58 | -0.60 | -0.62 | -0.60 | 0.81 | 0.80 | 0.78 | 0.80 | -0.04 | -0.04 | -0.04 | -0.04 |
| Lateral pterygoid | 16.46 | 16.44 | 16.31 | 16.44 | 0.68 | 0.68 | 0.67 | 0.68 | -0.57 | -0.57 | -0.58 | -0.57 | 0.46 | 0.46 | 0.46 | 0.46 |
| Medial pterygoid | 22.33 | 22.11 | 21.89 | 22.15 | 0.39 | 0.34 | 0.29 | 0.35 | 0.87 | 0.89 | 0.90 | 0.88 | 0.31 | 0.32 | 0.32 | 0.32 |
| Digastricus | 46.22 | 47.23 | 48.15 | 47.09 | -0.77 | -0.80 | -0.81 | -0.79 | 0.60 | 0.57 | 0.55 | 0.58 | -0.21 | -0.20 | -0.20 | -0.20 |

TABLE 6. — *Pedetes capensis*. Changes in the origin-insertion length (l) and vector components along the horizontal (X), vertical (Y), and transverse (Z) axes during the different stages of groundnut mastication. a-beginning fast-closing stage; b-beginning slow-closing; c-beginning grinding stage; d-end grinding stage; e-beginning fast-opening.

| Muscle | l | | | | | x | | | | | y | | | | | z | | | | |
|-----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | a | b | c | d | e | a | b | c | d | e | a | b | c | d | e | a | b | c | d | e |
| Maxillomandibularis | 59.85 | 54.74 | 53.17 | 52.39 | 55.14 | 0.13 | 0.08 | 0.06 | 0.03 | 0.04 | 0.99 | 1.00 | 1.00 | 1.00 | 1.00 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| Zygomatocmandibularis | 16.74 | 14.76 | 14.36 | 14.61 | 15.81 | -0.21 | -0.31 | -0.37 | -0.45 | -0.43 | 0.82 | 0.73 | 0.69 | 0.65 | 0.70 | -0.54 | -0.61 | -0.63 | -0.62 | -0.57 |
| Maseter muscle | 26.19 | 24.05 | 23.01 | 21.68 | 22.37 | 0.84 | 0.84 | 0.84 | 0.82 | 0.81 | 0.54 | 0.54 | 0.54 | 0.57 | 0.59 | 0.02 | 0.02 | 0.02 | 0.02 | 0.02 |
| Posterior maseter | 5.38 | 6.57 | 6.53 | 5.77 | 4.87 | 0.66 | 0.78 | 0.78 | 0.70 | 0.55 | -0.11 | -0.12 | -0.13 | -0.15 | -0.15 | -0.74 | -0.61 | -0.61 | -0.69 | 0.82 |
| Temporal muscle | 33.63 | 32.60 | 32.52 | 33.12 | 34.13 | -0.55 | -0.59 | -0.61 | -0.64 | -0.63 | 0.83 | 0.81 | 0.79 | 0.77 | 0.78 | -0.04 | -0.05 | -0.05 | -0.05 | -0.04 |
| Lateral pterygoid | 16.02 | 17.53 | 17.60 | 16.91 | 15.79 | 0.66 | 0.73 | 0.73 | 0.70 | 0.65 | -0.59 | -0.54 | -0.54 | -0.56 | -0.60 | 0.47 | 0.43 | 0.43 | 0.44 | 0.48 |
| Medial pterygoid | 22.40 | 22.48 | 22.24 | 21.85 | 21.74 | 0.45 | 0.36 | 0.32 | 0.25 | 0.28 | 0.84 | 0.88 | 0.89 | 0.91 | 0.91 | 0.31 | 0.31 | 0.31 | 0.32 | 0.32 |
| Digastricus | 44.91 | 46.56 | 47.54 | 48.76 | 48.79 | -0.74 | -0.80 | -0.82 | -0.84 | -0.81 | 0.64 | 0.56 | 0.54 | 0.51 | 0.55 | -0.21 | -0.20 | -0.20 | -0.19 | -0.20 |

of the digastrics are relatively small, the pull of the temporal muscles shows an increased backward and decreased upward component.

During mastication, the maxillomandibular muscle acts upward, and has a small forward and inward component. The zygomaticomandibular muscle also shows a mainly upward directed pull, but has no forward component, whereas the transverse component is directed outward. In the masseter muscle, the vertical component is the largest. It also shows an upward and small inward component, as does the maxillomandibular muscle. Starting from their area of origin, the muscle fibers of both the posterior masseters and the lateral pterygoids run in a dorsocaudal direction. Therefore, the direction of their pull is forward and downward. Whereas the transverse component of the lateral pterygoids is directed inward, the posterior masseters pull outward. The gross directional pull of the temporal and digastric muscles is upward and backward, with a small outward component, whereas that of the medial pterygoid resembles that of the maxillomandibular muscle.

Tables 5 and 6 show the changes in the length of the muscles, and in the direction of their working lines for respectively ingestion of groundnut and for their mastication.

Forces

The force applied to the lower jaw during ingestion and mastication has been calculated by vectorial addition of the maximal forces estimated for the individual muscles. The instantaneous force of the muscle has been estimated by multiplying the value of % EMG with the physiological cross section (WEIJS and DANTUMA, 1981; DE GUELDRE and DE VREE, 1990), (Fig. 5).

During the ingestion of groundnut, the lower jaw rotates with a single degree of freedom. During the ingestion of rolled oats, this rotation is accompanied by a translation. The ingestion of oats does not involve biting, thus the resultant forces then are only 10 % of those during the ingestion of groundnut.

The ingestion cycle of rolled oats is divided into closing and opening stages. Early in the closing stage the horizontal component (X) is protractive (Fig. 5), whereas the vertical component (Y) is close to zero: hence the condyles move forward. Throughout the entire cycle, the transverse components (Z) generated by the ipsilateral, contralateral, and resultant forces are zero. Backward shift of the lower jaw is achieved by an increase of the upward and retractive components of the retracting resultants. These reach their maximum before the end of closing and decrease during opening. During the second half of the opening stage, the resultant force is protractive only.

During the ingestion of groundnut, the resultant is large and upward at the beginning of the closing stage, as well as relatively small and anteriorly directed. Both components decrease slowly, to reach their minimum at the end of the closing stage. At the start of closing, the muscles of each side generate a minor outwardly directed component, but those of the two sides cancel each other. During the first half of the opening stage, the resultant force is upward and retractive. The upward

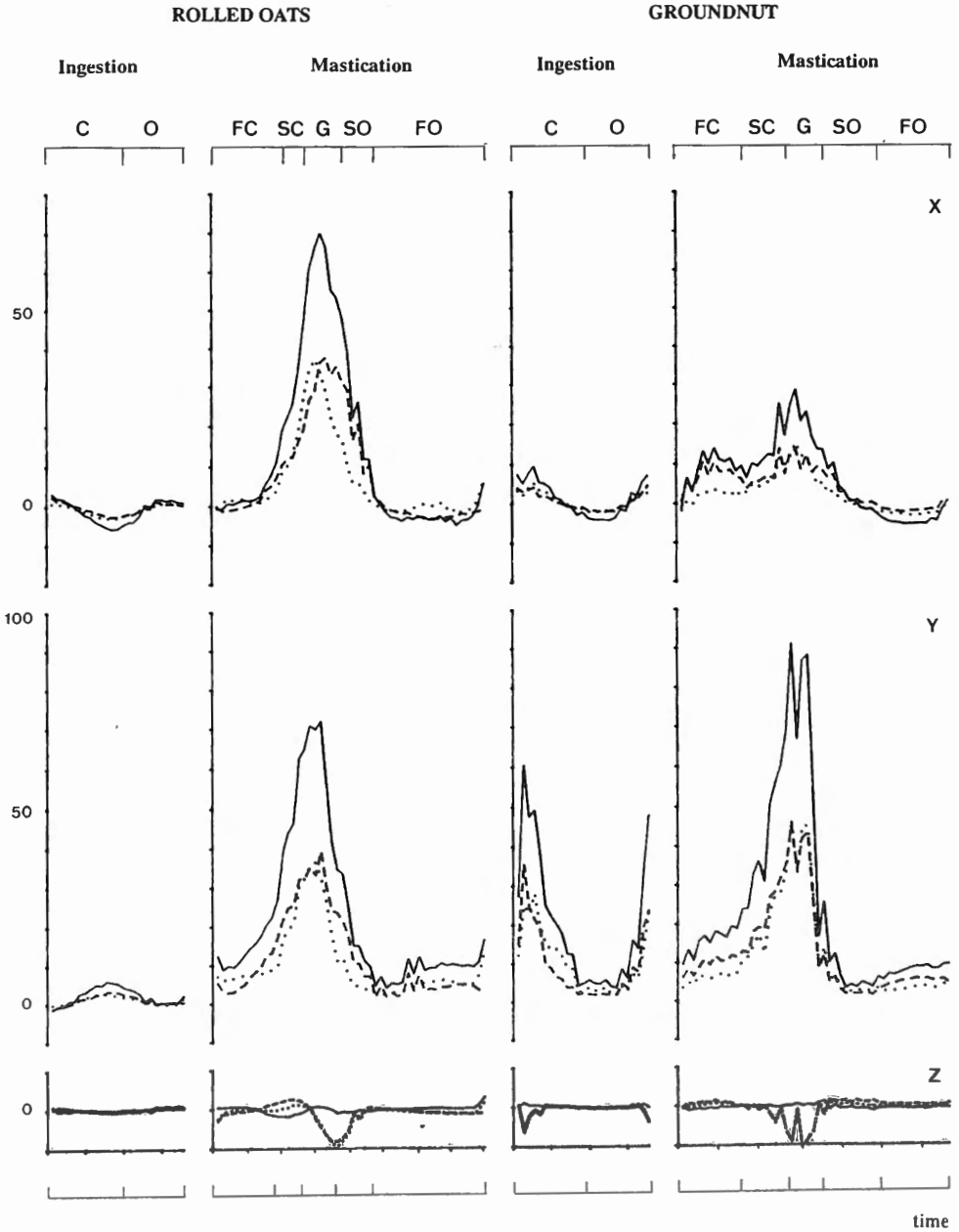


Fig. 5. — *Pedetes capensis*. Estimates of the horizontal (X), vertical (Y), and transverse (Z) components of the resultant force during ingestion and mastication of rolled oats and groundnut. Force estimates are expressed in kgf if an absolute force of 10 kgf/cm² is accepted. Solid lines = bilateral resultant force, dashed line = resultant of right side muscles, dotted line = resultant of left side muscles.

component increases significantly thereafter as the horizontal component becomes protractive.

The horizontal component of the resultant muscular force is protractive during the closing stages, the grinding stage and the slow-opening stage in a mastication cycle. At the start of closure, this component is absent during feeding on rolled oats. The component increases rapidly at the end of fast-closing, and reaches a maximum at the beginning of the grinding stage. The protractive component decreases rapidly toward the end of slow-opening. During the mastication of groundnut, the protractive component appears at the beginning of fast-closing, but reaches a much lower maximum during the grinding stage. The horizontal component of the resultant force during the fast-opening stage is retractive for both food types.

The vertical component is similar for rolled oats and groundnut. It is directed upward throughout the entire cycle. During fast-closing, it is relatively low, but then increases rapidly to reach a maximum at the beginning of the grinding stage. Thereafter it decreases rapidly to reach a minimum halfway slow-opening (groundnut) or at the end of this stage (rolled oats). During the fast-opening stage, the upward component slowly increases.

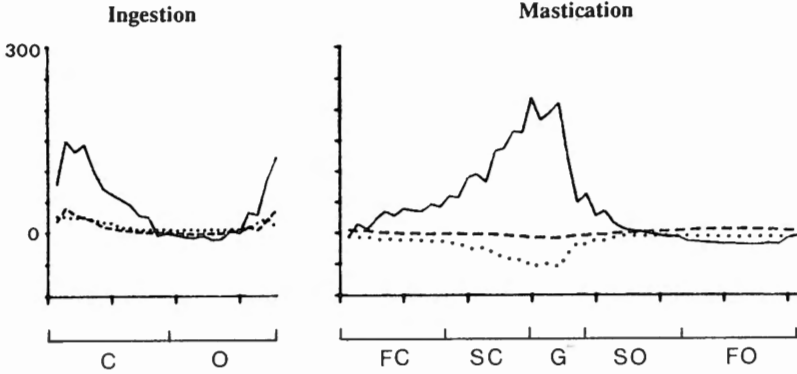
During the mastication cycle, there usually is no net transverse component. However, this component is relatively large and directed outward during the grinding stage. As the forces are similar on both sides and act in opposite directions, the net effect is zero.

Torques

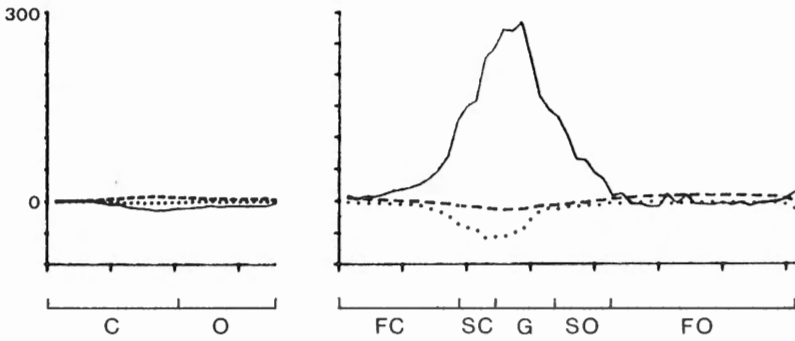
The changing proportions of the protractive, adductive and transverse components of the resultant force change the rotational forces about the bicondylar, vertical and horizontal axis. Figure 6 gives the moments around the three axes. Moments are calculated using the right condyle as centre of rotation, the X-axis directed to the snout, the Y-axis to the top of the skull and the Z-axis directed medially. During closing, the moment about the bicondylar axis is positive and negative during opening. In a mastication cycle, the moment increases during fast- and slow-closing, and reaches a peak value at the beginning of the grinding stage. It then decreases toward the end of slow-opening (groundnut) or halfway through this stage (rolled oats). At the end of slow-opening and during fast-opening the moment around the bicondylar axis is slightly negative. When rolled oats are ingested, the value stays close to zero throughout the entire cycle. During ingestion of groundnut, the moment peaks early in the closing stage. It then decreases, becoming negative during the opening stage.

The moment around the Y-axis is generally low in all cycles studied. During mastication, it is slightly positive in the first half of fast-closing and during fast-opening. A negative peak occurs at the end of slow-closing (rolled oats) or at the beginning of the grinding stage (groundnut). Thus, during the reduction stages (slow-closing, grinding and slow-opening), both lower jaws tend to be rotated

GROUNDNUT



ROLLED OATS



time

Fig. 6. — *Pedetes capensis*. Estimates of the moments around the transverse (Z, solid line), vertical (Y, dashed line), and horizontal (X, dotted line) axis, with the right condyle as the centre of rotation. Moments are expressed in kgf.m if an absolute force of 10 kgf/cm² is accepted.

laterally. During the ingestion of groundnut, the moment around the Y-axis is relatively large, and tends to pull the condyles medially.

The moment around the X-axis is negative in all cycles, except in the ingestion cycle of rolled oats. The positive values reflect the dominant activity of the maxillo-mandibular and zygomaticomandibular muscles and the low activity of the medial pterygoids. The peak negative values of moments around the X-axis coincide with peak negative values around the Y-axis.

TABLE 7

Pedetes capensis. Estimates of the maximal amplitude of the bite force components (R_x , R_y) at the incisor, and the components of the joint reaction forces (r_x , r_y) at the condyles during ingestion of rolled oats and groundnut. Reaction forces at left and right condyle are assumed to be equal. Forces are in kgf if an absolute force of 10 kgf/cm² is accepted.

| | | R_x | R_y | r_x | r_y |
|-------------|---------------|-------|--------|-------|-------|
| Rolled oats | Closing stage | 1.74 | 1.00 | 1.09 | -3.10 |
| | | 2.52 | 0.82 | 1.03 | -2.95 |
| | | 2.82 | 0.92 | 1.24 | -3.53 |
| | Opening stage | 3.42 | 1.06 | 1.19 | -3.41 |
| | | 3.38 | 0.98 | 1.13 | -3.23 |
| | | 2.78 | 0.82 | 0.92 | -2.64 |
| Groundnut | Closing stage | 2.24 | 0.86 | 0.85 | -2.43 |
| | | 1.82 | -10.42 | -1.72 | -4.92 |
| | | -2.00 | -8.96 | 1.56 | -4.45 |
| | Opening stage | -2.52 | -3.78 | 1.53 | -4.37 |
| | | -2.32 | -3.30 | 1.59 | -4.53 |
| | | 1.34 | 0.24 | 0.78 | -2.23 |
| | 0.32 | 0.04 | 0.86 | -2.46 | |
| | 1.76 | 0.20 | 0.96 | -2.77 | |

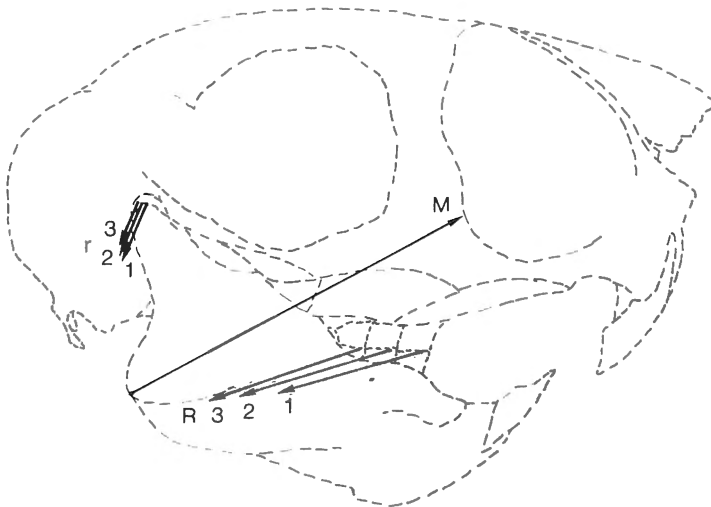


Fig. 7. — *Pedetes capensis*. Resultant muscular force (M), bite force (R), and joint reaction forces (r) for three different bite points during the mastication of rolled oats. 1 = premolar biting, 2 = first molar biting, 3 = second molar biting. Forces are in kgf if an absolute force of 10 kgf/cm² is accepted.

TABLE 8

Pedetes capensis. Estimates of the maximal amplitude of the bite force components (Rx, Ry) at the premolar, the first and second molar, and the components of the joint reaction forces (rx, ry) at the condyles during mastication of rolled oats and groundnut. Reaction forces at left and right bite point and condyle are assumed to be equal. Forces are in kgf if an absolute force of 10 kgf/cm² is accepted.

| | | Rx | Ry | rx | ry |
|-------------|--------------|--------|--------|-------|--------|
| Rolled oats | Premolar | -29.71 | -18.23 | -3.50 | -10.00 |
| | | -23.70 | -9.09 | -2.86 | -8.18 |
| | | -17.34 | -6.21 | -2.22 | -6.33 |
| | First molar | -30.51 | -20.53 | -2.70 | -7.70 |
| | | -24.09 | -10.21 | -2.47 | -7.06 |
| | | -17.60 | -6.95 | -1.96 | -5.59 |
| | Second molar | -31.29 | -22.75 | -1.92 | -5.48 |
| | | -24.47 | -11.29 | -2.09 | -5.98 |
| | | -17.85 | -7.66 | -1.71 | -4.88 |
| Groundnut | Premolar | -2.81 | -18.20 | -5.64 | -16.10 |
| | | -8.82 | -17.60 | -5.50 | -15.70 |
| | | -4.17 | -23.10 | -7.32 | -20.90 |
| | | -5.04 | -3.44 | -1.69 | -4.83 |
| | First molar | -3.47 | -20.1 | -4.98 | -14.2 |
| | | -9.47 | -19.4 | -4.85 | -13.8 |
| | | -5.00 | -25.5 | -6.49 | -18.6 |
| | | -5.17 | -3.82 | -1.56 | -4.45 |
| | Second molar | -4.09 | -21.8 | -4.36 | -12.5 |
| | | -10.1 | -21.2 | -4.24 | -12.1 |
| | | -5.77 | -27.7 | -5.72 | -16.3 |
| | | -5.30 | -4.18 | -1.43 | -4.09 |

Statics

Instantaneous, static reaction forces were calculated at both condyles and the incisors for ingestion cycles, and at both condyles and left and right molars for mastication cycles since *Pedetes* chews at both tooththrows simultaneously. Reaction forces were assumed to be equally large at both sides and transverse reaction force components could not be calculated. Reaction forces were calculated for lower jaw positions close to the close-open transition (ingestion cycles) and for the end of slow-closing, grinding and the beginning of slow-opening (mastication cycles), whenever the lower jaw may be assumed to be in static condition. The results are given in table 7 (ingestion), and table 8 and Figure 7 (mastication).

During an ingestion cycle, the reaction forces at the incisors are directed vertically, but have a small backward component. Closer to the closing-opening transition, the downward component decreases, whereas the backward component increases to the magnitude of the vertical component. At the condyles, the reaction forces then show a downward component and a smaller forward one. At the beginning of the opening stage, both the vertical and horizontal components of these action forces at the incisors are positive, which seems to have little meaning. As there is no tooth-food-tooth contact, and the lower jaw is accelerating, the forces cannot be calculated assuming static relationships. Also during the ingestion of rolled oats, the calculated reaction forces have little meaning, as tooth-food-tooth contact and therefore a semi-static condition is never established.

At the end of the slow-closing stage of a mastication cycle, the reaction forces at the molar teeth are especially directed downward, but show a considerable backward component. Whenever rolled oats are masticated, the horizontal component may even become dominant. When groundnut is reduced, the horizontal component stays relatively low, whereas the vertical component is large. For groundnut the reaction forces at the condyles are much higher during the grinding stage, than they are during the mastication of rolled oats. For both food types the reaction forces at the condyles are directed downward and backward.

DISCUSSION

General

The incisors of rodents and lagomorphs enable them to reduce a great variety of foods. They are open-rooted and grow throughout life to meet the constant wear of their tips. This incisive specialisation has divided the masticatory apparatus into two separate regions. Gnawing requires a more anterior position of the lower jaw than does mastication. The increased importance of the incisive function has led to an anterior displacement of the masseteric complex, which became the most important muscle group (WOOD, 1955, 1965b, 1985; TURNBULL, 1970). Furthermore, the anteriorly open glenoid fossa permits anteroposterior movements. The Rodentia are a highly specialized group (BECHT, 1953; SCHUMACHER, 1961; TURNBULL, 1970). However, the different lines appear to have evolved in parallel under the influence of similar selective pressures (WOOD, 1959). Although the morphology of their masticatory musculature represents variations of but a few basic patterns, the mechanics of chewing differs remarkably among rodents. In a comparative survey, OFFERMANS and DE VREE (1990) show that dental characteristics greatly influence the movement pattern of the lower jaw. The absence or presence of isognathia, the orientation of the molar teeth, the occlusal pattern, and the position of the incisors in relation to the molars are the most important dental characteristics influencing the movement pattern.

Muscle activities in the Rodentia

Muscle activities in Rodentia have been studied on three members of the Myomorpha (*Rattus*, WEIJS and DANTUMA, 1975; *Mesocricetus*, GORNIAK, 1977; *Tachyoryctes*, MEIRTE, 1986), and one member of the Hystricomorpha (*Cavia*: DE VREE, 1979; BYRD, 1981). The activity of the masseter of *Aplodontia rufa* has been briefly discussed (DRUZINSKY, 1985).

In the Myomorpha, movement of the lower jaw during the grinding stage ranges from purely propalinal (*Rattus*; WEIJS, 1975) over oblique (*Tachyoryctes*) to purely transverse (*Mesocricetus*). As in *Pedetes*, the masticatory muscles in *Rattus* fire symmetrically. In *Tachyoryctes* and *Mesocricetus*, the shift of the lower jaw toward the balancing side is brought about by the asymmetrical or asynchronous activity of some of the masticatory muscles. Muscle activity is also asymmetric in the hystricognathous, hystricomorphous *Cavia*, whereas the masseter muscles of the primitive *Aplodontia* also fire asymmetrically.

Although the presence of the transverse component in the movement pattern of the lower jaw and the symmetry and synchronization of the muscular activity are correlated, a lot of variation occurs in the sequence of activity. In *Pedetes*, the temporal muscle reaches a peak value halfway into fast-closing, and activity ceases at the end of this stage. During the reduction stages, peak activities are subsequently reached by the maxillomandibular muscles, the medial pterygoids, the masseter muscles (slow-closing), the zygomaticomandibular muscles, the posterior masseters and the lateral pterygoids (grinding stage). This momentum conserving mechanism of successive but overlapping contractions of different muscle groups (KALLEN and GANS, 1972) is also found in *Rattus*. However, none of the muscles reaches peak activity during fast-closing. The temporales are the first muscles to reach a peak activity at the beginning of the reduction stages, followed by the infra-orbital part of the zygomaticomandibular muscle, and the masseters. Both the lateral and medial pterygoids reach a maximum level, shortly after the masseters.

Variable activity is also found in rodents in which the masticatory pattern shows a lateral component. In *Mesocricetus*, the lateral translation at the top of the orbit is produced by retrusor (temporal muscle) activity on the balancing side and protrusor (superficial masseter and medial pterygoid) activity on the working side. Furthermore, the working side anterior digastric and lateral pterygoid fire before those of the balancing side. They thus produce an additional force which drives the lower jaw to the balancing side. During the downstroke, the lower jaw is returned to the midline by the continued activity of the lateral pterygoid of the balancing side. In *Tachyoryctes* and *Cavia*, which chew unilaterally with alternating cycles, the tip of the lower jaw is shifted laterally towards the working side whenever the mouth is maximally opened. The translation of the mandible toward the balancing side in *Tachyoryctes*, is not accomplished by the temporales (which fire symmetrically), but by the asymmetrical activity of the masseters and zygomaticomandibular muscles. During the opening stages, the excursion of the mandible toward the balancing side reflects mainly activity of the working side lateral pterygoid. In *Cavia*, activity in the temporales is asymmetric during the closing stage. Lateral

translation is produced by the balancing side temporal muscle and the working side lateral pterygoid. Simultaneously, the protrusors fire asymmetrically producing a closing force with a significant anteromedial translation. Initially, the mandible returns to midline by asymmetric activity of the digastrics at the start of opening, but this movement is reversed at the end of this stage by the unilateral firing of the lateral pterygoid at the working side.

The search for patterns in the muscular activity of masticating mammals is an ongoing activity. Mammalian mastication has been studied in American opossum (CROMPTON *et al.*, 1977), tenrec (ORON and CROMPTON, 1985), shrews (DÖTSCH and DANTUMA, 1989), bats (*Myotis*: KALLEN and GANS, 1972; *Pteropus*: DE GUELDRE and DE VREE, 1988), rabbits (WEIJS and DANTUMA, 1981; WEIJS *et al.*, 1989; SCHWARTZ *et al.*, 1989), miniature pigs (HERRING, 1976; HERRING and SCAPINO, 1973; HERRING *et al.*, 1979), pygmy goats (DE VREE and GANS, 1976), cats (GORNIAK and GANS, 1980), dogs (DESSEM, 1989), macaques (MCNAMARA, 1974; LUSCHEI and GOODWIN, 1974; BYRD and GARTHWAITE, 1981; MILLER *et al.*, 1982; HYLANDER *et al.*, 1987) and man (AHLGREN, 1966; MÖLLER, 1966; HANNAM *et al.*, 1977; HANNAM and WOOD, 1981; STOHLER, 1986; WIDMALM *et al.*, 1987). Trends in the currently available data (HIEMAE, 1978; GORNIAK, 1985) are confused by diversity, raising questions about the reality of a generalized sequence of muscular activity. Certainly, no generalized muscle activity pattern is obvious in the Rodentia. This is not surprising. After all, rodents display considerable variation in masticatory pattern in spite of similarity in gross muscular morphology, whereas other rodents belonging to different major groups show similar masticatory patterns.

Biomechanics

GORNIAK (1985, p. 334) commented that understanding the differences in the muscular activity of mammals requires establishment of the time that the muscle is active during its three-dimensional movement pattern, of that portion which is active at the time, of the time at which activity starts and stops relative to the activity of the other muscles, and of the magnitude of the activity relative to movement, food placement, and action of the other muscles. An important question to add to this series is: what is the effect of the activity of a muscle on mandibular movement, and what is the total effect of all muscles?

The effect of the muscles on the mandible has been studied mainly by static, anatomical analysis of jaw mechanics on representatives of different taxa (KÜHLHORN, 1938; ARENDSSEN DE WOLFF-EXALTO, 1951; BECHT, 1953; MAYNARD SMITH and SAVAGE, 1959; SCHUMACHER, 1961; SCHUMACHER and REHMER, 1962; CROMPTON, 1963; SCAPINO, 1965; TURNBULL, 1970; GREAVES, 1978, 1982, 1988). Such studies generally assume that the masticatory muscles simultaneously contract maximally or to the same extent. Furthermore, the components of the resultant force are subject to considerable changes during the jaw movements. Although several biomechanical studies include either mandibular displacements or changing muscular activities (CARLSÖ, 1952; LEMIRE-BELMONT, 1966; AHLGREN, 1966;

AHLGREN and ÖWALL, 1970; HIEMAE, 1971; GASPARD, 1972; BARBENEL, 1972; HERRING and HERRING, 1974; HYLANDER, 1975, 1978; BARON and DEBUSSY, 1979, 1980; HERRING, 1985), few have combined anatomical data with quantified movement analysis and electromyography (BARBENEL, 1974; WEIJS and DANTUMA, 1975, 1981; WEIJS *et al.*, 1987; OTTEN, 1987; DE GUELDRÉ and DE VREE, 1990).

The three-dimensional model here used to study the jaw mechanics of *Pedetes* is essentially similar to that used in the biomechanical studies on the rat and the rabbit (WEIJS and DANTUMA, 1975, 1981; WEIJS *et al.*, 1987) and *Pteropus* (DE GUELDRÉ and DE VREE, 1990). It estimates the resultant force at any interval of the chewing cycle. In *Pteropus*, the estimated resultant force of the masticatory muscles has a small anterior component early in the opening stage, but this is generally directed posteriorly. During the entire cycle, the resultant force remains close to the midsagittal plane. Rabbits show a resultant force with substantial vertical and forward components. The transverse component is initially directed toward the working side, but decreases to the end of the closing stage. During reduction, it is directed toward the balancing side.

Both *Rattus* and *Pedetes* chew bilaterally, and the resultant muscular force is generally directed upward and forward. Whereas in *Pedetes* the mandibular symphysis is immovable, the mandibular symphysis in *Rattus* allows independent adjustment of the two mandibular sides. As a result, the lower jaw in *Pedetes* stays close to the midsagittal plane, whereas that of *Rattus* incorporates a transverse component that is close to zero during the closing stage. During the reduction stages, the muscles tend to turn the lower border of the mandible inward and press the rami against each other in the symphysis.

Rattus and *Pedetes* chew bilaterally and both require an upward and protractive resultant force during reduction. Muscle (sequence) activity however, shows a lot of differences. Partially, this can be explained by the differences in the relative mass of the masticatory muscles. In *Rattus*, the masseteric complex accounts for 56.6 % of the masticatory muscles, whereas it accounts for 87.5 % in *Pedetes*. Consequently, the relative weight of the temporal muscle is 23.8 % in *Rattus* and 2.9 % in *Pedetes*. However, the proportional differences of the masticatory muscles are accompanied by differences in the components of their working lines (Table 9). In *Rattus*, the temporal muscle is divided in an anterior part with a dominant vertical component and a posterior part with a large retractive component. The temporal muscle of *Pedetes* consists of a single layer the fibers of which lie mainly vertically but do slope forward. Most masticatory muscles are directed more vertically in *Pedetes* than in *Rattus*. The zygomaticomandibular muscle shows no or few anteroposteriorly directed fibers. The masseteric complex on the other hand, shows a distinct posterior part in *Pedetes* that should generate substantial protraction.

These differences in proportion and direction of the working lines of the masticatory muscles, require that the muscles be activated differently in order to produce similar masticatory patterns. Although the overall resultant force shows an upward and protractive component in both species, it derives from quite different

TABLE 9

Comparison of the vector components along the horizontal (X), vertical (Y), and transverse (Z) axes of the masticatory muscles of *Pedetes* and *Rattus* halfway the grinding stage.

| | <i>Rattus</i> | | | <i>Pedetes</i> | | |
|----------------------|---------------|-------|-------|----------------|-------|-------|
| | x | y | z | x | y | z |
| Superficial masseter | 0.94 | 0.28 | 0.19 | } 0.90 | 0.43 | 0.02 |
| Ant deep masseter | 0.57 | 0.82 | -0.05 | | | |
| Post deep masseter | 0.64 | 0.67 | -0.37 | | | |
| Posterior masseter | | | | 0.94 | -0.08 | -0.33 |
| Maxillomandibularis | 0.45 | 0.89 | -0.09 | 0.15 | 0.99 | 0.02 |
| Zygomandibularis | | | | 0.00 | 0.66 | -0.75 |
| Medial pterygoid | 0.52 | 0.71 | 0.49 | 0.48 | 0.83 | 0.29 |
| Lateral pterygoid | 0.68 | -0.25 | 0.69 | 0.85 | -0.41 | 0.33 |
| Ant temporalis | -0.24 | 0.97 | 0.07 | } -0.50 | 0.87 | -0.05 |
| Post temporalis | -0.88 | 0.41 | 0.24 | | | |

forces. In the rat, the resultant force traverses (in sagittal projection) the middle of the molar row and the temporomandibular joint remains unloaded. In *Pedetes*, reaction forces occur at the joint, and the bite force is smaller than the resultant force. *Pedetes* is similar to rabbits and rats, in having reaction forces with vertical and large posterior components. As expected, the reaction force increases as the bite point moves posteriorly, as also noted earlier (GOSEN, 1974; PRUIM *et al.*, 1980; WEIJS *et al.* 1987; DE GUELDRE and DE VREE, 1990).

During biting, *Pedetes* produces relative smaller reaction forces at the temporomandibular joint than *Rattus* in which the incisors counteract the forward component of the resultant, whereas the vertical component is resisted mainly in the temporomandibular joint. *Pedetes* directs the resultant force more vertically during biting. At the incisors, the bite force shows a large vertical component, reaching 68 % of the resultant force applied by the muscles.

Muscle activity differs substantially among those mammals thus far studied. Differences in the proportions and direction of the working lines of their muscles can explain these differences in forms with a similar masticatory pattern. Furthermore, the jaw apparatus has more muscles than degrees of freedom for movement. Therefore, the same force can be generated by different combinations of jaw muscle forces (WEIJS and VAN RUIJVEN, 1990). Variation in muscle activity results in a different masticatory pattern in forms with a similar muscle configuration. Three-dimensional models including data on movement patterns and muscle activity may explain the effects of this variation on the forces which act on the lower jaw (KOOLSTRA and VAN EIJDEN, 1992; VAN EIJDEN *et al.*, 1990). However, these models are scarce and not available for closely related forms.

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