The Comparative Anatomical Study of the Masseter of the Mammal (II)

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I. Introduction

The authors already reported the lamination of the masseter of the insectivora (mole), the rodentia (albino-rat), the lagomorpha (rabbit), the carnivora (dog and cat), the perissodactila (horse), the artiodactila (pig, sheep, goat and cattle) in 1961; the primate (crab-eating monkey, organg-utan, gorilla and man) in 1962; the chiroptera (flying-fox, long-winged bat and pipistrelle) in 1962; the ruminantia (deer, nilgai and camel) in 1962; and the cetacea (humpback whale) in 1963.

In this paper, some of the remaining animal, which include the kangaloo, galago, squirrel-monkey, chimpanzee, guinea pig, bear and elephant, will be described to supplement the above reports.

To understand the laminal structure of the masseter, it is most recommendable to investigate the improper masseter group which consists of the maxillomandibular and zygomaticomandibular muscles by removing the zygomatic arch after the exact recognition of the proper masseter group which includes the first superficial, second superficial, intermediate and deep masseters. The terms of these muscular layers were adopted after the old usage of various authors with a slight modification. The maxillomandibular and zygomaticomandibular muscles which were firstly mentioned by Toldt (1905) have escaped singularly the exact recognition by various authors, owing probably to the vague definition. Toldt regarded the zygomaticomandibular muscle as a part of the temporal muscle. He overlooked the second superficial masseter after Yoshikawa et al. (1961).

After all, inspite of the marvellous development of the modern anatomy, the muscular mass behind the zygomatic arch remains as
the mass of enigma, which has escaped the thorough investigation of the anatomist. The present authors expect especially the cleft identification of the maxillomandibular and zygomaticomandibular muscles in the near future.

While the investigation of the authors has been taken place, Schumacher (1961, a and b), Schumacher-Rehmer (1962) and Heinz e (1963, a and b) reported independently the structure of the masseter of the various mammals. Although they succeeded to describe the new tendon which corresponds to the second superficial masseter after Yoshikawa et al. (1961), they regarded the masseter as the polypenniform muscle. The German anatomist overlooked the division of the proper and improper masseter groups. This is the most fundamental reason which they failed to recognize the salient feature of the masseter. Heinz e (1963, a) insists to deny to call every layer of the masseter the muscle. To avoid the confusion, the authors propose that the muscular layer is synonymous with the 'element' which composes the masseter. So the first superficial element may be used instead of the first superficial muscle, etc. In the investigation of the masseter, there are cases, in which the muscular layer can be separated with or without difficulty. In the carnivora and ungulate, the expression such as the dissection by violence (eine gewaltsame Trennung, Heinz e) may be used in the separation of every muscular layer of the masseter. But the compact adherance of the muscular layers may be due to the secondary fusion. In various regions except the masseter, there are many muscles, the separation of which is largely artificial, e.g., the longissimus dorsi etc. in the horse.

II. Materials and Method

Except the fresh chimpanzee and adult elephant, the other has been preserved in the formalin or alcohol solution.

So far the experience of the authors is concerned, the investigation of the masseter of the carnivora is the most difficult, because the development of the tendon is not good, inspite of the full development of the muscular substance. In such a case, the separation must be deliberate. The separation, however, must not be too deliberate to cause the incomplete removal of the muscular substance, which causes another confusion. To reach the clear conclusion, it is better to use the new-born material after fixation as the control, because the fresh material is very soft and the secondary
fusion of the muscular layer does not yet occur.

In order to avoid the misdissection, the authors recommend to cut the muscular substance of every layer along the terminal line. When the muscular substance is cut in this way, the tendon of the underlying layer is easily found and the overlying layer can be separated completely by scraping along this tendinous sheet. There is the reversal relation of the tendon and the muscular substance between the succeeding layers of the proper masseter. The cutting of any tendon must be avoided, because it leads to the misdissection of the underlying layer. By this method every layer which composes the proper masseter group can be followed easily. The remaining dorsoanterior muscular mass represents the improper masseter group, every layer of which terminates with the tendon on the mandible. In the proboscidea and ungulate, however, the maxillomandibular muscle adopts the laminar structure, differentiating into several layers under the reversal relation of the tendon and the muscular substance. The complete removal of the zygomatic arch is necessary to observe exactly the improper masseter group.

III. Description

1. The red kangaroo, *Macropus rufus* Desm. (Figs. 1 and 2). Female, infant.

The orbit and the temporal fossa are continuous. In the mandible, the coronoid process develops better than the glenoid process. The short angular process protrudes at the posterior extremity of the curved free border of the mandibular branch, which bends inwards in a large degree. The incisura vasorum is not conspicuous.
Fig. 2. The lamination of the masseter of the red kangaroo.

The deep masseteric fossa extends from the oblique line to the glenoid process and contains not only the deep masseter, but also the maxillomandibular muscle as described below. The zygomatic arch is very broad.

The tendon of the first superficial masseter takes its origin from the anterior half of the ventral border of the zygomatic arch and terminates with the muscular substance on the long line which extends from the free border of the mandibular branch to the angular process. The tendon which originates from the anterior extremity of the zygomatic arch makes an especially good development, while the muscular substance which terminates along the mandibular angle is very thin. The muscular layer which appears near the glenoid process is the intermediate masseter. Another muscular layer spreads along the lateroventral half of the zygomatic arch. Later, this is found to be the dorsal portion of the first layer of the deep masseter.

The second superficial masseter originates along the ventral
side of the anterior extremity of the zygomatic arch with the thin muscular substance and terminates with the tendon along the terminal line of the first superficial masseter.

The intermediate masseter is also thin. It takes its origin with the tendinous sheet from the whole ventral margin of the zygomatic arch and terminates obliquely near the ventral margin of the masseteric fossa.

As already mentioned, the deep masseter originates from the lateral ventral half of the zygomatic arch with the thin muscular substance, terminating with the tendinous sheet along the ventral margin of the masseteric fossa. The deep masseter can be divided into the pars anterior and pars posterior by the masseteric nerve which appears from the anterior third of the deep masseter. This pars posterior corresponds to the first layer of the deep masseter. The second layer is also divided into the pars anterior and pars posterior by the masseteric nerve. Under the latter, the third and fourth layers are found. Near the mandibular notch, the fifth layer terminates with tendon, showing the dorsal limit of the fossa. These muscular layers of the pars posterior become smaller as the layer deepens and alternate their tendon and muscular substance.

After the complete removal of the proper masseter group, the improper masseter group makes its appearance. Along the lateral surface of the slender coronoid process the maxillomandibular muscle is found, while the zygomaticomandibular muscle along the oblique line. Both layers attach along the medial aspect of the broad zygomatic arch.

The superficial temporal muscle is slender, terminating upon the oblique line and the top of the coronoid process with the muscular substance. The deep temporal muscle terminates upon the medial surface of the coronoid process, the strong tendon of which terminates upon the top of the process.

2. The galago or pigmy bushbaby, Galagoides demidovii Fisher (1808) (Figs. 3 and 4).

The first superficial masseter is the thick rectangular muscular plate which originates from the whole ventral margin of the zygomatic arch with the tendinous sheet, extending towards the ventrocaudal direction and terminates along the free border of the mandibular angle with the muscular substance. Along the anterior margin, the strong tendon develops especially. When the muscular
Fig. 3. Galago or pigmy bushbaby, *Galagoides demidovii* Fisher (1808).

Fig. 4. The lamination of the masseter of the galago or pigmy bushbaby.

Substance is cut through along the mandibular margin, the tendinous sheet of the underlying layer is discovered, along which the first superficial masseter is removed. Then the second superficial masseter makes its appearance. This is also the rather thick muscle, extending over the lateroventral surface of the zygomatic arch. When the muscle is removed from the zygomatic arch, the intermediate masseter appears. It originates from the ventral margin of the arch with the tendinous sheet, terminating with the muscular substance over the mandibular branch. As the tendon of the first layer of the deep masseter spreads along the ventral margin of the deep masseteric fossa, the intermediate masseter can be scraped off along this sheet. The second layer protrudes along the posterior margin of the first layer. It originates with the tendon along the
zygomatic arch and fills up the masseteric fossa with the rich muscular substance. The third layer cannot be recognized. In front of the pars posterior, the pars anterior which consists of the muscular substance only and is separated by the masseteric nerve from the pars posterior extends dorsoventrally, the ventral margin of which occupies the same level with that of the second layer of the pars posterior.

Then the zygomatic arch is removed to investigate the improper masseter group. The thick tendinous fascia covers the temporal muscle. After removal of this temporal fascia, the adipose cushion is found, spreading along the posterior wall of the orbita. Along the dorsal margin of the zygomatic arch, the transverse muscular bundle protrudes. Under the fascia the superficial temporalis spreads and the tendon of the deep temporalis can be recognized along the dorsal side of the acoustic foramen.

Under the pars anterior of the deep masseter, the narrow and strong tendinous string extends along the lateral side of the mandible, running dorsoventrally. Tracing this tendon dorsally, the tendon dives under the zygomatic arch. Its muscular substance turns posteriorly along the posteroventral surface of the orbita, a portion of which continues to the muscular bundle which runs transversely along the dorsal margin of the arch (side supra), while the remaining portion adheres along the medial wall of the arch. Between this muscle and the pars anterior, another small and narrow muscle is found, which runs along the former muscle and terminates upon the medioventral side of the arch. The latter is the maxillomandibular and the former the zygomaticomandibular muscle.

The superficial temporalis is composed of the rich muscular substance, terminating upon the lateral side of the coronoid process, occupying the place which extends from the oblique line to the dorsal side of the terminating line of the maxillomandibular muscle. The deep temporalis terminates with the strong tendon on the medial side of the top of the coronoid process.

3. The squirrel-monkey, Saimiri sciurea Linneus (1775) (Fig. 5).

Though the masseter and the temporalis of the squirrel-monkey are very small, compared with the enormously large cranium, six layers of the masseter can be mentioned as in the other mammal.

The first superficial masseter originates from the anterior three fourths of the zygomatic arch and terminates as if it to cover the mandibular angle. The development of the tendon is not good.
the careful observation, the tendon is recognized on the side of the zygomatic arch. As the difference between the tendon and the muscular substance is small, it is difficult to search for the second superficial masseter. By removing carefully the muscular fibers of the first layer with the small forceps, the tendon of the second layer makes its appearance. This layer originates along the whole zygomatic arch and terminates with the weak tendon along the mandibular angle, spreading in the triangular form. The posterior portion which contacts with the acoustic foramen protrudes along the posterior margin of the first layer.

When the second superficial layer is removed by cutting the muscular substance along the ventral border of the zygomatic arch, the intermediate masseter makes its appearance, the tendon of which is recognized in a small quantity on the side of the arch.
By turning over the muscular substance which spreads over the mandibular branch, the deep masseter is recognized. Though it is the weak muscle, the masseteric nerve divides it into the pars anterior and pars posterior.

By cutting away the zygomatic arch, another two muscles can be found under the pars anterior which contacts with the masseteric nerve. They are the maxillomandibular and the zygomatico-mandibular muscles. Besides the originating portion along the arch, the latter makes the semicircular plate over the superficial temporalis, into which a special branch of the masseteric nerve distributes.

Both temporales, superficial and deep, show the same counter. The former terminates with the muscular substance, while the latter with the tendon along the whole margin of the coronoid process.

4. The chimpanzee, *Pan troglodytes* Blumenbach (1799) (Fig. 6).

Female, 10 years old, 65.2 kg weight.

The first superficial masseter takes its origin from the ventral border of the anterior half of the zygomatic arch with strong tendon. The rather thick muscular substance terminates along the mandibular angle. The central portion which corresponds to the underlying intermediate masseter bulges out and the anterior and posterior margins spread as the thin layer. After cutting the muscular substance along the mandibular angle and scraping off the first layer along the underlying tendinous sheet, the second superficial masseter makes its appearance, attaching with muscular substance along the whole length of the ventral margin of the zygomatic arch. The underlying intermediate masseter arises from the anterior half of the arch, the dorsal half of which is occupied by the tendinous sheet. The intermediate masseter occupies the broad inserting area upon the mandible. This is one of the characteristics of the masseter of the higher primate. When the intermediate masseter is removed from the mandible, the deep masseter makes its appearance, which is divided into the pars anterior and pars posterior by the masseteric nerve. From the ventral border of the former, the thin tendon spreads over the mandible. The pars posterior consists of three layers. The first layer is narrow, the tendon of which develops on the mandibular side. Under the first layer, the broad and thick second layer spreads. After the removal of the thick muscular substance from the masseteric fossa, the small and thin third layer is found near the mandibular notch.
It is easily ascertained by the tendon which develops on the mandibular side. The maxillomandibular muscle, first layer of the improper masseter group, spreads under the pars anterior of the deep masseter, originating from the medial aspect of the zygomatic arch.

The remaining zygomaticomandibular muscle is the center of interest in the present study. After removal of the thick temporal fascia, the muscle of the temporal area appears, which is divided into the anterior and posterior portions by the oblique muscular fold. The former presents a little concaved area and the adipose cushion spreads over the surface, extending under the zygomatic arch. From the whole temporal line, the slender tendinous strings extend along the muscular fibers which converge to the coronoid process. This is one of the characteristics of the superficial temporalis. Along the muscular fold, the anterior and posterior area can be easily separated except the distal portion near the temporal line. The fusion is regarded to be secondary. The posterior area is occupied by the rather thick superficial temporalis, which terminates upon the lateral side of the coronoid process. The muscular portion which spreads on the anterior side of the muscular fold is the zygomaticomandibular muscle, which is covered with the thin superficial temporalis. It arises from the originating line which includes not only the lateral portion of the supraorbital torus, but also the anterior part of the temporal line and terminates upon the anterior margin of the coronoid process with strong tendon. This is the first layer of the zygomaticomandibular muscle. The narrow second layer which originates with small tendon from the lateral extremity of the supraorbital torus and terminates upon the retromolar surface with the muscular substance.
The strong tendinous sheet of the deep temporalis extends under the massive layer of the zygomaticomandibular muscle and terminates upon the top and the posterior margin of the coronoid process. In this way, the zygomaticomandibular muscle spreads between the superficial and deep temporales. The superficial temporalis, however, which spreads over the zygomaticomandibular muscle is very thin.

5. The guinea pig, *Cavia cobaya* Schreber (Fig. 7).

Among the muscular laminae which compose the masseter of the guinea pig, the first superficial masseter is the most complicated and peculiarly developed layer. Toldt (1905) already described that the superficial masseter consists of two portions, anterior and posterior. The former passes over the ventral margin of the mandible and the latter is called the pars reflexa (Tullberg) or Faisceau réfléchi (Alezaïs). The superficial masseter after Toldt corresponds to the complex muscle which includes the first super-

![Fig. 7. The lamination of the masseter of the guinea pig.](image-url)

The first superficial masseter consists of the pars anterior and the pars posterior. The pars anterior originates with the strong tendon from the anterior extremity of the zygomatic arch, the detail of which will be described later. The posterior portion originates with the thin tendinous sheet from the whole ventral margin of the arch and covers the pars anterior. The tendinous sheet is transformed into the thick muscular substance and terminates at the top of the angular process. The pars posterior covers not only the pars anterior, but also the remaining masseter.

When the muscular fibers of the pars posterior of the first superficial masseter is cut away from the top of the angular process, the terminating tendon of the second superficial masseter makes its appearance, which attaches to the ventral margin of the angular process, reflecting in the U-form. The muscular fibers attach not only along the whole border of the arch except the ventral margin of the infraorbital foramen, but also spread over the tendon of the pars anterior of the first superficial masseter, extending further over the ventral margin of the mandibular branch. By cutting this layer along the ventral margin of the posterior half of the zygomatic arch, the tendon of the intermediate masseter can be easily observed. The deliberate procedure is necessary to remove the portion which extends to the pars anterior of the first superficial masseter. The muscular substance of the intermediate masseter terminates on the mandibular branch in a rather small area. Along the anterior margin the pars anterior of the deep masseter can be observed. Between both layers the masseteric nerve runs out.

The muscular substance which intervenes between the pars anterior of the deep masseter and the pars anterior of the first superficial masseter seems to be overlapped by that of the second superficial masseter. The separation of both layers is the most difficult process. If the whole muscular substance is removed, a mere thin tendinous sheet remains along the pars anterior of the superficial masseter, covering the anterolateral angle of the bone crest of the mandible.

It is rather better to remove the whole deep masseter and the zygomatic arch to ascertain the arrangement of the improper masseter group. In the rodentia, the infraorbital canal is transformed into the foramen. A muscle which passes through the foramen
forms the broad tendinous plate on the distal side of the foramen and terminates on the anteromedial side of the bone crest (crista lateralis, Schumacher) as the narrow tendon. Another muscle which originates from the almost whole length of the arch and terminates in the narrow sulcus between the bone crest and the alveolar process. Being innervated by the common branch of the masseter, both muscles are regarded as the maxillomandibular muscle. Toldt (1905) and Schumacher (1961, b) and Schumacher-Rehmer (1962) called the muscle which passes through the infraorbital foramen only the maxillomandibular muscle and the muscular plate which arises from the arch and terminates in the mandibular sulcus the zygomaticomandibular muscle. The zygomaticomandibular muscle after the authors, however, is a vestigial muscle which originates from the posteromedial part of the arch and terminates on the bone platelet which spreads on the posterior side of the glenoid process. This muscle is also shown clearly in the masseter of the albino-rat (Yoshikawa et al., 1961).

The pars anterior of the first superficial masseter arises with the strong tendon from the anterior extremity of the arch and is transformed into the tendinous plate at the anterolateral surface of the mandibular branch. In the intact masseter, it can be observed through the tendon of the pars posterior (side supra) and is movable by the touch of the finger like the patella of the knee. It bifurcates at the incisura vasorum. A portion is the slender muscle which reaches to the top of the angular process, running along the ventromedial side of the angular process. Another portion forms the small tendinous plate to pass over inwards the incisura vasorum and runs towards the glenoid process along the anterior border of the medial pterygoid muscle. There is a long sulcus to accept this muscle.

6. The Yezo brown bear or Higuma, Ursus arctos yezoensis Lydekker 1897 (Fig. 8).

New-born male, body length 18 cm.

The wide first superficial masseter arises from the ventral border of the zygomatic arch, running towards the ventrocaudal margin of the mandibular branch. From the ventral border of the anterior extremity of the arch, which is sometimes called the tuberculum massetericum anterior the specially strong tendon develops. The second superficial masseter protrudes along the anteromedial margin, while the remaining portion which is covered by
The first superficial masseter is rather short, terminating in the horizontal line. Near the glenoid process, the underlying intermediate masseter can be observed. After removing the second superficial masseter by cutting along the ventral margin of the arch, the well developed maxillomandibular muscle and the intermediate masseter make their appearance, being separated by the masseteric nerve. The latter is pressed posteriorly by the former, which belongs to the improper masseter group. Under the intermediate masseter, the deep masseter can be observed which is divisible into the pars anterior and pars posterior by the masseteric nerve, occupying the deep masseteric fossa. According to the observation after removing the zygomatic arch, the maxillomandibular muscle is found to originate from the anterior half of the zygomatic arch and to terminate upon the mandible, forming the inverted triangle. The zygomaticomandibular muscle runs transversely along the zygomatic arch, connecting the lateral surface of the coronoid process with the posterior half of the zygomatic arch. Schumacher (1961, b) names this muscle the pars suprazygomatica of the temporal muscle.
7. The Japanese black bear or Tsuki-no-wa guma, *Selenarctos thibetanus japonicus* Schlegel 1857 (Fig. 9).

The adult male.

The first superficial masseter arises from the ventral border, especially from the anterior extremity of the zygomatic arch with the strong tendon and terminates at the angular process, running almost horizontally. There is a deep arterial sulcus for the facial artery. Along the dorsal border of the zygomatic arch, the strong zygomaticomandibular muscle runs transversely. The thick temporal muscle contacts with the contralateral along the dorsal sagittal line. On the lateral side of the dorsocaudally protruded portion of the temporalis, the deep impression of the auricle is noticed. The

![Fig. 9. The lamination of the masseter of the black bear.](image)
second superficial masseter occupies almost the same area with the first, except the posterior part, where the tendon does not extend to the top of the angular process. When the second superficial masseter is removed, cutting along the ventral border of the arch, the peculiar muscular arrangement, which the authors have not encountered in the other carnivora is observed. The muscular arrangement is divided into the anterior and posterior halves, inserting the masseteric nerve between them. The posterior half corresponds to the intermediate masseter. When the dorsal half of the former and the intermediate masseter are removed, the greater muscular plate makes its appearance, which resembles with the anterior half in the muscular constitution, being continuous with it at the anterior margin. This is the maxillomandibular muscle which originates along the whole medial aspect of the zygomatic arch. The development of the reflected portion in the adult is not advantageous to the polypenniform theory of the masseter. The deep masseter group takes its origin from the posterior medial aspect of the zygomatic arch and terminates in the deep masseteric fossa, forming the pyramidal form. This is divisible into the pars anterior and pars posterior by the masseteric nerve. The latter is the muscular mass, which consists of rich tendons and muscular substances. Further subdivision, however, cannot be expected.

8. The Indian elephant, *Elephas maximus* L. (Figs. 10 and 11).

The infant male of one and a half years old and the female adult of eight years old are used.

The mandibular angle is very thick. At the roots of the coronoid and glenoid processes, the comparatively deep masseteric fossa is recognized. There is a shallow notch between the glenoid process and the caudal extremity of the mandibular angle. Over the temporalis, the disk-shaped temporal gland is found, at the center of which the excretory canal is recognized.

The first superficial masseter takes its origin from the ventral border of the anterior half of the zygomatic arch with the tendinous sheet and spreads over the rounded mandibular angle with the thin muscular sheet. Along the posterior margin the second superficial masseter protrudes, while the anterior margin retards than the first layer. This retardation due to the remarkable development of the maxillomandibular muscle, one of the improper masseter group, the detail of which will be more clear in the later description. Under the second superficial masseter, the intermediate
masseter spreads and covers the deep masseter. When the intermediate masseter is removed, the dorsal half of the masseteric fossa is found to be occupied by the deep masseter group, while the ventral half by the venous plexus derived from the v. transversae faciei. The deep masseter seems to be divided into the pars anterior and pars posterior by the intervening masseteric nerve. The further lamination of the pars posterior cannot be followed exactly in the infant. In the adult (Fig. 11), however, three layers differentiate and the supposed pars anterior is found
to be a part of the maxillomandibular muscle.

The maxillomandibular muscle originates perpendicularly from the medioventral side of the anterior half of the zygomatic arch and terminates in the anterior part of the masseteric fossa. Even in the infant, it makes a good development and is divisible into four muscular bundles, the most anterior bundle of which spreads
ventrally and covers the remaining bundles. The tendon does not differentiate in the infant. The observation of the adult shows that the maxillomandibular muscle differentiates into the second, third and fourth layers at the level of the deep masseter under the reversal relation of the tendon and the muscular substance, the last layer of which is, in the infant, misinterpreted as the pars anterior of the deep masseter. The analogous example of such a good developed maxillomandibular muscle is sought in the horse only. The zygomaticomandibular muscle arises from the medial dorsal half of the middle third of the zygomatic arch and terminates along the root of the coronoid process under the second and third layers of the maxillomandibular muscle.

IV. Consideration

From the beginning of the investigation (1961), the authors divided the masseter into the proper and improper masseter groups. The former occupies the posteroventral side, while the latter the anterodorsal side of the mandibular branch. They are covered by the first superficial masseter, one of the proper masseter group. So the two groups cannot be distinguished superficially.

The function of the masseter is divided into 1) the chewing movement and 2) the movement of wide opening and firm closure of the mouth. The former is performed by the proper masseter group, while the latter by the improper masseter group.

So far the investigation is concerned, the arrangement of the proper masseter is rather uniform, while that of the improper masseter differs greatly as the order of the mammal varies and can be divided as follows:

1) the case in which the maxillomandibular and zygomaticomandibular muscles develop in the same degree,

2) the case in which the zygomaticomandibular muscle is stronger than the maxillomandibular muscle and

3) the case in which the maxillomandibular muscle makes the far better development than the zygomaticomandibular muscle.

The case 1) is found in the chiroptera and the carnivora, which can open the mouth widely. In the primate, the lower primate belongs to the case 1), while the higher primate to the case 2). In the latter the zygomaticomandibular muscle changes its position from the zygomatic arch to the lateral part of the torus supra-orbitalis. The cetacea belongs also to the case 2). The case 3) is
found in the rodentia, the lagomorpha, the proboscidea and the ungulate, in which the perissodactila is provided with the most developed maxillomandibular muscle.

According to the lamination theory of the masseter, the function of the improper masseter is easily explained by the lever and forceps models. In the lower mammal, the small coronoid process stands perpendicularly to the mandible. When it evolves to the larger size as in the carnivora, the process inclines a little caudally. In both cases, the improper masseter moves the mandible in the ‘lever style’ to open and close the mouth. In the ungulate, the coronoid process approaches too near to the glenoid process to function as the lever style. In the latter case, it is more advantageous to raise the mandible in the ‘forceps style’, because the forceps can be easily closed by pressing its side by the finger. This is the reason why the maxillomandibular muscle changes its position from the lateral side of the coronoid process to the anterolateral side of the mandibular branch. The higher primate and the cetacea belongs also to the forceps style.

When the improper masseter consists of the well-developed muscular substance, the animal opens not only the mouth widely, but also closes the mouth firmly by the strong contraction of the muscle. In the evolitional development, the tendon comes to make a good development in the strong muscle and is advantageous to contract the muscle strongly. The extensor and flexor of the leg in the ungulate are the good example. So is the case in the masseter.

The muscular layers which belong to the proper masseter group constitute a series of muscles which alternates the tendon and the muscular substance. On the other hand, the maxillomandibular and zygomaticomandibular muscles which constitute the improper masseter group terminate with the tendon on the mandible. So the reversal relation of the tendon and the muscular substance cannot be applied to the improper masseter group. In the proboscidea and ungulate, however, the improper masseter increases the efficiency, differentiating into many layers under the reversal relation of the tendon and the muscular substance. Usually the maxillomandibular muscle and the pars anterior of the deep masseter are not connected by the above mentioned reversal relation. In the ungulate, the new precursory maxillomandibular muscle (Yoshikawa et al., 1961, 1962, d) develops between them and comes to constitute a larger series of muscles which connects the
proper and improper masseter groups. This is one of the important characteristics to support the lamination of the masseter.

As already stated, German anatomists, Tolldt (1905), Schumacher (1961, a and b), Schumacher-Rehmer (1962) and Heinze (1963, a and b) overlooked the difference between the proper and improper masseter groups in the study of the masseter. In the ungulate, Schumacher and Heinze regarded erroneously the tendons of the second superficial masseter and of the maxillomandibular muscle after Yoshikawa et al. (1961) as the single tendinous sheet, because both tendons terminate on the mandible side by side. Furthermore, Heinze (1963, b) regarded the first superficial masseter and the second maxillomandibular muscle after Yoshikawa et al. (1961) of the horse as the single layer, because their tendons develop on the side of the zygomatic arch and undergo the secondary fusion in the U-form in cross section.

In the horizontal section of the masseter of the cattle, Heinze divided the tendons of the masseter into

a) the lateral originating tendon,
b) the lateral terminating tendon, which is subdivided caudally into b') the lateral lobe and b'') the medial lobe,
c) the intermediate originating tendon,
d) the medial terminating tendon and
e) the medial originating tendon,

while in the goat and sheep, the d) layer is changed into the originating tendon and e) layer into the terminating tendon, embracing the medial lobe (b'') between them. At any rate, there is the reversal relation of the originating and terminating tendons in the above division after Heinze. The interchange of the originating and terminating tendons in the d) and e) layers shows that the definite scheme cannot be applied in the ungulate. In the scheme of the transverse section of the masseter, the f) layer is mentioned (Heinze, 1963, a, Abb. 2). It is not, however, mentioned in the scheme of horizontal section, being included in the medial lobe (b'') of the lateral terminating tendon (b). The lateral lobe (b') of the lateral terminating tendon must be separated from the lateral terminating tendon (b). The former corresponds to the second superficial masseter, while the latter to the massive maxillomandibular muscle after Yoshikawa et al. (1961). On the other hand, the medial lobe (b'') of the lateral terminating tendon is the continuation of the maxillomandibular muscle, the caudal portion of which, however, belongs to the pars posterior of the deep masseter.
In other words, the original maxillomandibular muscle is represented by the main portion of the medial lobe (b'), while the larger muscle which corresponds to the lateral terminating tendon (b) is the later differentiated portion of the maxillomandibular muscle. Therefore, the strong tendon of the latter extends anteroposteriorly, spreading a little over the anterior portion of the tendinous sheet of the second superficial masseter after Yoshikawa et al. (1961). This misinterpretation took its origin already from Toldt (1905) and still survives among the recent German anatomist.

Without the division of the proper and improper masseter groups the muscular elements of the masseter can not be interpreted reasonably. Any functional advantage is not expected from the polypenniform theory of the masseter.

V. Summary

In all mammals described in this report, the masseter consists of the proper masseter group which includes the first superficial, second superficial, intermediate and deep masseters and the improper masseter group which consists of the maxillo- and zygomaticomandibular muscles. These muscular elements can be identified exactly in every animal investigated. The special features are described as follows:

1) In the red kangaroo, the first superficial, second superficial and intermediate masseters are thin, though broad. The deep masseter group makes especially a good development, namely, the pars anterior is identified in the first and second layers and the pars posterior can be divided into the first-fifth layers. The improper masseter group which includes the maxillo- and zygomaticomandibular muscles makes a good development, which is comparable to those of the carnivorous animal.

2) In the primate, the transitional change of the zygomaticomandibularis from the zygomatic arch to the supraorbital torus is pursued from the lower to the higher forms. In the galago, the muscle takes its origin from the zygomatic arch. In the squirrel-monkey, it originates not only from the zygomatic arch, but also spreads over the superficial temporalis, making the semicircular plate. In the chimpanzee, the muscle spreads between the superficial and deep temporales, connecting the lateral portion of the supraorbital torus with the coronoid process as in the human masseter.
3) The masseter of the guinea pig makes a complicated development. The first superficial masseter is divided into the pars anterior and pars posterior. The former corresponds to the pars reflexa (Tullberg), bifurcating into two branches. The maxillomandibular muscle consists of two parts as in the rat (Yoshikawa et al., 1961). One of them passes through the infraorbital foramen and the other originates chiefly from the zygomatic arch and terminates in the long sulcus in the mandible. The latter corresponds to the zygomaticomandibularis after Toldt (1905), Schumacher (1961, b) and Schumacher-Rehmer (1962). The real zygomaticomandibular muscle is vestigial as in the rat (Yoshikawa et al., 1961). It develops between the posterior part of the zygomatic arch and the root of the glenoid process.

4) In the bear, the maxillo- and zygomaticomandibular muscles make a specially good development. In the adult form, the former reflects under the second superficial masseter, taking the anterior position to the intermediate masseter. The pars posterior of the deep masseter makes the well developed pyramidal form with rich tendons, the lamination of which, however, cannot be followed.

5) In the Indian elephant, the development of the maxillomandibular muscle is remarkable as in that of the horse. The pars anterior of the deep masseter cannot be identified.

Literatures


Schrier, A. M. and J. E. Schrier (1963). Is it Saimiri sciureus or Saimiri sciurea?

Editors' note. Laboratory primate newsletter. Vol. 2, No. 1, 111.
The Comparative Anatomical Study of the Masseter of the Mammal


Explanation of the abbreviation in the figures

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>intern.</td>
<td>M. masseter intermedins</td>
</tr>
<tr>
<td>maxil.-mand.</td>
<td>M. maxillomandibularis</td>
</tr>
<tr>
<td>prof. ant.</td>
<td>M. masseter profundus, pars anterior</td>
</tr>
<tr>
<td>prof. post.</td>
<td>M. masseter profundus, pars posterior</td>
</tr>
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<td>pt. int.</td>
<td>M. pterygoideus internus</td>
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<tr>
<td>sup. 1</td>
<td>M. masseter superficialis, lamina prima</td>
</tr>
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<td>sup. 2</td>
<td>M. masseter superficialis, lamina secunda</td>
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<td>temp. superf.</td>
<td>M. temporalis superficialis</td>
</tr>
<tr>
<td>temp. prof.</td>
<td>M. temporalis profundus</td>
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<tr>
<td>zyg.-mand.</td>
<td>M. zygomaticomandibularis</td>
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<td>n. masset.</td>
<td>N. massetericus</td>
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