Comparative Anatomy of the Larynx and Related Structures

JMAJ 54(4): 241–247, 2011

Hideto SAIGUSA*[1]

Abstract

Vocal impairment is a problem specific to humans that is not seen in other mammals. However, the internal structure of the human larynx does not have any morphological characteristics peculiar to humans, even compared to mammals or primates. The unique morphological features of the human larynx lie not in the internal structure of the larynx, but in the fact that the larynx, hyoid bone, and lower jawbone move apart together and are interlocked via the muscles, while pulled into a vertical position from the cranium. This positional relationship was formed because humans stand upright on two legs, breathe through the diaphragm (particularly indrawn breath) stably and with efficiency, and masticate efficiently using the lower jaw, formed by membranous ossification (a characteristic of mammals).This enables the lower jaw to exert a pull on the larynx through the hyoid bone and move freely up and down as well as regulate exhalations. The ultimate example of this is the singing voice. This can be readily understood from the human growth period as well. At the same time, unstable standing posture, breathing problems, and problems with mandibular movement can lead to vocal impairment.

Key words Comparative anatomy, Larynx, Standing upright, Respiration, Lower jawbone

Introduction

Animals other than humans also use a wide range of vocal communication methods, such as the frog's croaking, the bird's chirping, the wolf's howling, and the whale's calls. However, only some reptiles and mammals produce sound from their vocal cords. The majority of other reptiles and amphibians do not vocalize. Frogs generate sound from tracheal ridges in their tracheae and birds produce sound from the syrinx right above the tracheal bifurcation, but the muscles that control these movements are primarily controlled by the hypoglossal nerve. This is different from the larynx of humans and other mammals.

The larynxes of many mammals consist of cartilages and intrinsic laryngeal muscles that are almost the same as those of humans. In animals that actively vocalize, the layered structure specific to the vocal cords that makes it possible for vocal cord's mucous membranes to wave tends to have a morphology that closely resembles that of humans, but the interior of the thyroarytenoid muscles—i.e., the vocal cord muscles—tend to be poorly developed in animals that do not vocalize much.[1,2] Moreover, primates, which primarily lead an arboreal life, have better developed false vocal cords and laryngeal ventricles than quadrupeds, and humans, which are also primates, show a similar tendency.[3,4] In addition, primates have laryngeal saccules, which further inflates the upper portion of the laryngeal ventricle, but there have been many reports of laryngeal saccules in humans such as those involved in heavy physical work and wind instrument performers.[5] Morphologically, the human larynx is not decisively different from the larynx of other mammals and, in particular, other primates.

So in what way is the human larynx decisively different from that of other animals? Before

*1 Department of Otolaryngology, Head and Neck Surgery, Nippon Medical School, Tokyo, Japan (s-hideto@nms.ac.jp).
This article is a revised English version of a paper originally published in the Journal of the Japan Medical Association (Vol.139, No.4, 2010, pages 803–808).

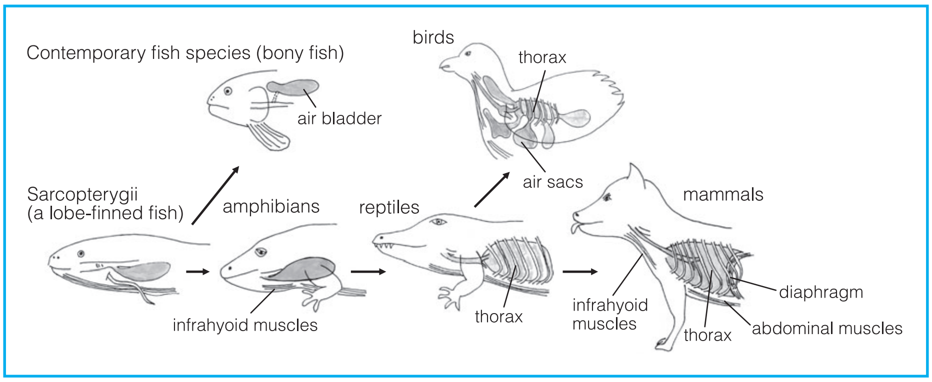

Fig. 1 Differentiation of lungs and respiration in vertebrates

exploring this, we will discuss the vocal impairments specific to humans.

What Vocal Impairments Are Specific to Humans?

Malignant neoplasms and recurrent nerve paralysis in the larynx can occur in animals as well as humans, and can be recreated in laboratory models. There have not been any reports of observations of vocal cords due to abnormal changes in animals' vocalization, so it is impossible to determine whether animals can develop vocal cord polyps, vocal cord nodules and polypoid vocal cords. However, animals' voices do not become hoarse as a result of excessive chirping or howling. Neither do animals lose the ability to vocalize when they are breathless from running. The timbre of their voices changes in various circumstances, such as reproductive activities, but they certainly do not lose the ability to say even a single word due to nervousness when the beloved appears before their eyes, nor do their voices quaver or rise.

Animals vocalize when they stick out or raise the cervical region together with the lower jaw, or as part of energetic physical expression, such as movements of the tail or trunk. Vocal behavior on its own is very unusual. In other words, animals' vocalization is an integral part of the animal's feelings and physical action, and is not compelled nor taken to the point of exhaustion, neither is it a reaction to the fetters of mental tension.

So how does human vocalization work? Every person has experienced a situation in which they are unable to speak as they intend, for example when their name is called in class, they see the object of their unrequited love, or they stand at a podium, their voice quavers or becomes stuck in the throat. Many people have also experienced hoarseness after supporting one's team at an athletic meet, or working too hard or campaigning when one has a cold. We have all had the experience of being unable to speak with the rise and fall of the larynx after running 100 m until our breath has normalized or until we have drunk a glass of water.

Moreover, there are not only functional vocal impairments that cause vocal abnormalities without any vocal cord impairments, but there are also strange disorders that puzzle doctors. This is a phenomenon not seen in animals. Human vocalization is not necessarily an integral part of their feelings and physical actions. In other words, vocalization is subject to emotions and can cause stress and be forced, and can also be impacted by unsteady breathing.

Comparative Anatomy of the Larynx (Fig. 1)

We find the primitive form of the larynx in the Sarcopterygii of the Devonian period. Exposure of the Sarcopterygii to a harsh environment in which the salt water dried up led to the formation of lung buds by the ventral side of the foregut. The sphincter deriving from the branchial arch that closes the aperture serving as the lung's entrance as if it were a drawstring bag was the larynx's archetype. This primitive larynx enabled the Sarcopterygii to accumulate air in the lungs.

In addition, simply accumulating this air without actively ventilating kept the lining of the lungs moist and enabled the Sarcopterygii to exchange gas in the lung buds at a leisurely pace. Of the Dipnoi who still use the lungs formed in the Sarcopterygii, over 90% of the lung fish native to Africa and South America, which continue to experience harsh dry seasons, breathe through their lungs, and frequently rise to the surface while exhaling air bubbles in order to draw air into their lungs.[6] Their lungs extend from the side of the esophagus to the back, and there are dilator muscles in the larynx as well as sphincter muscles, enabling the fish to more actively draw in air and store it. However, while the fish can draw in air, they exhale only by putting pressure on the lungs through physical movement.[7]

At the same time, this function of taking air into the lungs through the larynx was further specialized in teleostean fish, which are differentiated by their avoidance of shallow waters and their underwater habits, so that the lungs are separated from the foregut and used as an air bladder.[7,8] Amphibians who made it onto land compensate for inadequate lung respiration by breathing externally through the skin and lining of the mouth. The nostrils extend into the oral cavity and the amphibians constrict the infrahyoid muscles, which are the parietal muscles in the neck region, while the mouth is still closed to create negative pressure by moving the floor of the oral cavity up and down. This produces intake air and enables the amphibian to take in air more actively.[7] The start of air intake implies that the amphibian has acquired olfactory senses in the air, and arytenoid cartilage and cricoid cartilage are formed to stand in for specialized sphincter muscles and dilator muscles so that the accumulated air is not released due to the negative pressure and the amphibian can store air more actively.[3]

The cartilages of the larynx and the intrinsic laryngeal muscles are even more differentiated in reptiles whose habitats are away from the water, and in addition the thorax is formed and the reptiles breathe using the infrahyoid muscles and thoracic motion, but they merely store the air in their lungs, and exhale by wriggling their bodies left and right. Birds, the "most advanced reptiles," have the optimum morphology for holding in air, thanks to many air sacs branching off from the lungs that even penetrate bones throughout the body. These air sacs are also connected.[7]

Meanwhile, in mammals, alveoli, which are the dead ends of the respiratory tree, are blind ending, but a diaphragm exclusively for air intake was formed from the infrahyoid muscles, which were the source of air intake during the age of amphibians. Gas exchange takes place with the vertical movements of the diaphragm and the exhalation achieved by the elasticity of the lungs/thorax and the internal intercostal muscles. This also means that mammals do not have to wriggle their bodies to exhale, and can exhale vigorously by constricting their abdominal muscles. In other words, the exhaled air became actively involved in the respiration process, which had merely taken in air and stored it. As a result, the larynx that had stored air thus far now began to modurate exhalation. When the exhalation flow is narrowed as a result of the constriction of the glottis, the pressure on the undersurface of the vocal cords rises, but when the glottis completely closes, intrapleural pressure and intraperitoneal pressure also heighten, which helps in bowel movement, urine, and childbirth. Moreover, since the thorax becomes rigid when intraperitoneal pressure rises due to the breath hold, the shoulders above the thorax also become immobile, which stabilizes the upper extremity's fulcrum and enhances the upper extremity's efficiency of movement.[3] Vocalization is one part of this regulation of respiration using the vocal cords.

This historical background shows that the larynx was differentiated as a branchial organ to store air in the lungs, and even during the biological evolution resulting from the subsequent shift to land, the larynx was simply differentiated to take in air. However, in mammals, once the diaphragm—the muscle dedicated to respiration—was differentiated from the parietal muscles of the neck region, the larynx became engaged in regulating respiration. This laid the groundwork for vocal movement.

However, as indicated by the regular movements of the gills in fish, the branchial organ must move continuously, keeping a steady rhythm. In other words, the primitive larynx that appeared in the Devonian period have had a steady rhythm and admirable congruence between the primitive larynx derived from the gills and trunk movement. As living organisms were subsequently specialized, breathing modes were specialized in

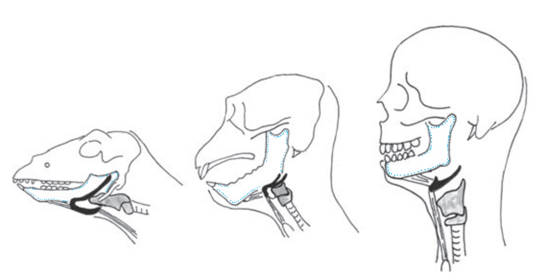

Fig. 2 The physical relationship of the cranium, lower jawbone, hyoid bone and larynx in mammals

The medial margin of the lower jawbone is indicated by a blue dotted line, the hyoid bone is highlighted in black and the larynx in grey.

various ways, but the rhythm of the respiration was maintained at a steady level. This respiratory rhythm has been sustained as the larynx has come to play the key role in regulating breathing and the nerve center for respiration was situated in the medulla oblongata with the motor nucleus concerning the intrinsic laryngeal muscles.

On the other hand, humans tend to store air without consciously exhalation in their breath or catch their breath in amazement, and even compel other people to hush by saying “shh.” Regulating respiration primarily in the larynx on a daily basis is a major problem that is contrary to the history of respiratory specialization.

Presence of Larynx in Humans

So how is the human larynx different than in other mammals? First, we will look at the larynx’s shape overall. **Figure 2** shows the physical relationship of the cranium, lower jawbone, hyoid bone, and larynx in mammals, including humans. However, part of the lower jawbone is not shown so that the positions of the hyoid bone and the larynx can be clearly depicted.

In the Japanese serow (a goat-antelope), a grass-eating quadruped, its lower jawbone extends far forward together with its cranium, and its hyoid bone connects to the inner back of the lower jawbone. Grass-eating animals grind their food finely and powerfully with a lateral movement of their lower jawbone, which resulted in the masseter muscle. At the same time, a hyoid bone attached to the suprahyoid muscles developed to depress the lower jawbone. The upper part of the hyoid bone also connects to the cranium. The larynx is closely attached to the inner part of the hyoid bone. Since the hyoid bone is connected to the lower jawbone, the infrahyoid muscles move not only the parietal muscles of the neck region, but also when opening as the neck region movements and when inhaling. In other words, in mammals, the lower jawbone, hyoid bone, and larynx are integrated horizontally to support and enable the functions of the lower jawbone, which was newly acquired due to membranous ossification (the cartilaginous lower jaw is transformed into the auditory ossicles). The lower jawbone protrudes forward, so that the masseter muscle is driven forward and adheres to the cheek bone. Of the maxillomandibular muscles and the zygomaticomandibular muscles, non-specific masseter muscles which support the lower jawbone and were previously located in the rear of the malar arch, the maxillomandibular muscles are separate from the cheek bone in higher grass-eating animals and adhere to the facial crest.[10] The temporal muscle is more developed in meat-eating quadrupeds than the masseter muscle, but the masseter muscle’s direction of travel is similar.

Gorillas, which are partially bipedal, the cranium and lower jawbone do not protrude forward as much, and the physical relationship of the lower jawbone, hyoid bone, and larynx is diagonal and almost vertical, but they remain connected. As with the Japanese serow, the infrahyoid muscles function when opening significantly as a result of movement in the neck region and inhaling. Moreover, primates can move freely their neck region because they are bigger and hardier than the Japanese serow. In higher primates such as the partially bipedal gorillas and chimpanzees, of the non-specific masseter muscles that support the lower jawbone, it is the zygomaticomandibular muscles that are separate from the malar arch and attached to the exterior posterior edge of the supraorbital ridge. By suspending it vertically,[10] the lower jawbone, which has greater freedom, is supported.

Unlike other mammals, in humans the lower jawbone, hyoid bone, and larynx are separate from each other and are suspended vertically from the cranium by muscles. By further decreasing the forward protuberance of the lower jawbone, the masseter muscle is almost vertical and the zygomaticomandibular muscles which sup-

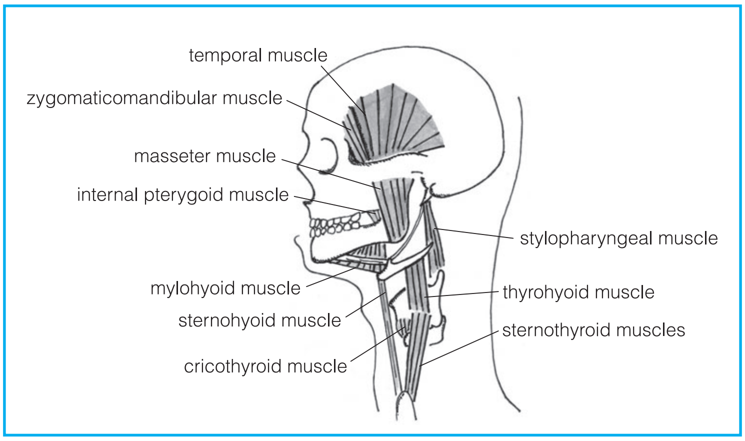

Fig. 3 Support structure for the human larynx

port the lower jawbone from the cranium also sit vertically[10] (**Fig. 3**). The digastric muscle and the mylohyoid muscle suspend the front of the hyoid bone to the lower jawbone, while the posterior belly of digastric muscle hangs the back of the hyoid bone from the cranium. The thyrohyoid muscle suspends the front of the larynx from the hyoid bone, and the stylopharyngeal muscle suspends the back of the larynx from the cranium. Of the infrahyoid muscles, the sternohyoid muscles adhere to the hyoid bone, and the sternothyoid muscles adhere to the thyroid cartilage, with the hyoid bone and larynx pulled downward. However, these muscles are thin compared to those in other mammals and barely function normally. This is an advantage for humans, who are the only animal suffering from dysphagia as well as vocalization impairment, since the larynx is impeded from elevating in an anterosuperior direction during swallowing and swallowing becomes difficult if the infrahyoid muscles are working hard.[11]

The cranium itself, in which the lower jawbone, hyoid bone, and larynx are suspended, is supported by the spine, which thickens as it descends, and its S-shaped curvature, as well as the vertical spine, made possible by the erector spinae muscles. Standing upright is reinforced by the righting reflex, which enables the two eyeballs positioned next to each other on the surface of the face to always see straight ahead. As a result, the lower jawbone is not involved in movement in the neck region and inhalation, and can move on its own. Vertical running of the zygomaticomandibular muscles supports against gravity the lower jawbone, which the articular process only loosely ties to the cranium fossa. In addition, the larynx is similarly independent of movement in the neck region and inhalation, as well as lower jaw movement. Subsequently, the intrinsic laryngeal muscles, which is surrounded by the thyroid cartilage and acquired for the first time by mammals, also began to move independently, but the thyroid cartilage was separated particularly far from the cricoid cartilage and the cricothyroid muscle activity became efficient. Corresponding to this, the trachea extending from below the larynx expands and contracts like a spring.

Once humans began to walk upright on two legs and the cervical region and the mouth cavity/nasal cavity sat at right angles to the cranium, the larynx moved downward and the pharyngeal cavity lengthened. It is often asserted that this led to the birth of language.[3,4] However, the physical relationship of the lower jawbone, hyoid bone, and larynx is almost vertical and they are connected to each other in gorillas, which are partly bipedal. Accordingly, walking upright on two legs did not suddenly cause the lower jawbone, hyoid bone, and larynx to separate in humans. The current physical relationship of them was likely acquired by upright humans over millions of years.

This can be easily understood by the human's growth process. The larynx is just below the soft palate after birth, but begins to descend when the infant begins to hold up his/her neck, is weaned

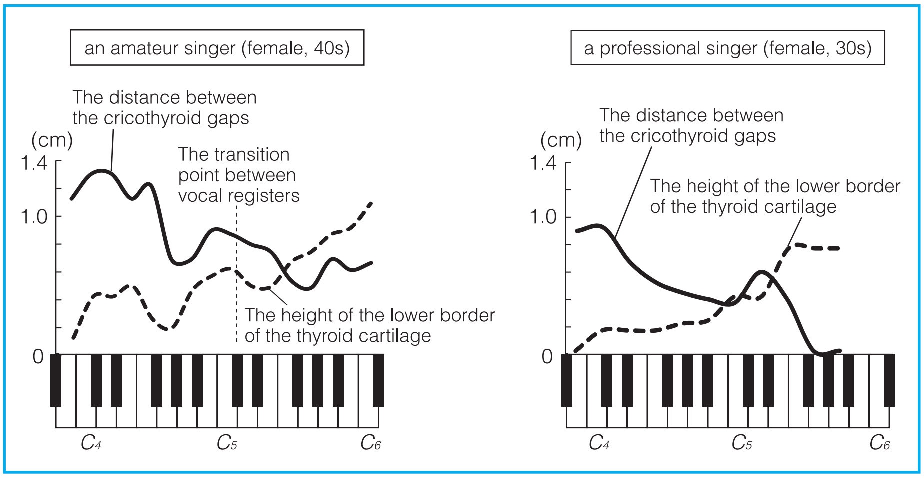

Fig. 4 The distance between the cricothyroid gaps and the changes in the height of the lower border of thyroid cartilage when singing the vowel "a"

The distance between the cricothyroid gaps as an indicator of cricothyroid muscle activity and the height of the lower border of thyroid cartilage as an indicator of the upper movement of the larynx were measured with an ultrasonic waveprobe fixed on the neck. The vertical axis shows the actual result, and the position of the thyroid cartilage at the pitch of the first sound is set at 0. As the sound becomes high, the distance between the cricothyroid gaps narrows and the height of the lower border of thyroid cartilage rises.

and begins to eat food, and walks on two legs. By the age of ten or so, the larynx reaches the same level as an adult. In addition, as a person walks upright, the unstable thorax is also rigid and inhalation becomes efficient as the diaphragm is used.

However, when the event that a person is unable to keep his/her neck steady, keep his/her own trunk upright for some reason, or swallow without chewing and depend on only tube feeding, the physical relationship of the lower jawbone, hyoid bone, and larynx remain connected, even as an adult. In other words, once a person walks upright, chews food and breaths efficiently by primarily using the diaphragm, the lower jawbone, hyoid bone, and larynx begin to separate from each other. The songs that a young children sings are monotonous with a limited range, even if the child opens his/her mouth wide, but this range expands once the child reaches the third or fourth grade of elementary school. This is easily apparent when one recalls the impressive signing at elementary school music festivals.[12] Subsequently, as a person ages and it is more difficult to remain upright, which happens for men around the age of 70, and the larynx drops as low as one vertebral body of the spine, which makes it difficult to swallow.

This demonstrates that standing upright did not simply lead to vocalization and language, but that standing, chewing, and diaphragmatic breathing led to the current shape of the larynx in humans.

Considering the Human Voice from the Position of the Larynx

To sum up, the vertical suspension of the larynx from the cranium via the lower jawbone and hyoid bone in humans freed the human larynx from body wall movements, inhalation movements, and lower jaw movements due to the infrahyoid muscles, and enabled true diversity of vocalization movements, which are stimulated by exhalation. However, this was only realized for the first time when erect positions and respiration stabilized, and these ensured free movement of the lower jawbone. If these are upset, vocalization is easily impaired. Moreover, emotional difficulties and coercion affect the muscles derived from the body wall more than the muscles derived from the branchia, which can have a negative impact on human vocalization since this disturbs posture and respiration and induces tension in the infrahyoid muscles.

Figure 4 shows the distance between the cricothyroid gaps and the changes in the height of the lower border of thyroid cartilage when an amateur singer and a professional singer sing scales using the vowel "a" at a high region. They were instructed to keep their neck and mouth in the same position. Singers with almost the same body type, height, and size of larynx were chosen. The distance between the cricothyroid gaps indicate the contraction of the cricothyroid muscle and the height of the lower border of the thyroid cartilage indicates the change in the position of the larynx. In general, as the note rises, the distance between the cricothyroid gaps narrows and the height of the lower border of the thyroid cartilage rises, but the fluctuations in both parameters are greater as the note rises in the amateur singer. In particular, the lower border of the thyroid cartilage fell significantly, showing that the trajectory as the note rises is not smooth. Moreover, the cricothyroid gaps did not narrow enough when high notes were sung, and the transition point between vocal registers left a clear auditory impression. Once the singer moved into higher notes, the falsetto voice became a piercing shriek.

In contrast, the professional singer had few fluctuations in both parameters, and the trajectory was smooth. In addition, the cricothyroid gaps narrowed sufficiently when high notes were sung. In terms of the auditory impression, the transitions between vocal registers were not obvious. In the amateur singer, the position of the larynx moved up as the musical interval rose, and occasionally moved up and down with intensity. The suprahyoid muscles, and occasionally the infrahyoid muscles become involved, which constrain the freedom of the lower jawbone via the hyoid bone. Moreover, the resulting constraint on the freedom of the thyroid cartilage, which is suspended from the hyoid bone, prevents the cricothyroid muscle from efficiently regulating the vocal cord's tension. The professional singer had little fluctuation in the position of the hyoid bone and the freedom of the lower jawbone was maintained, so that the cricothyroid muscle was able to efficiently regulate the vocal cord's tension. Indeed, singers are told not to move the position of the larynx in accordance with their singing voice and to make sure that the transition between vocal registers does not stand out.

Conclusion

A truly "good voice" is possible once a person stands upright, has stable respiration and is able to move the lower jawbone freely, in addition to being able to modulate exhalation appropriately without forcing it and while constrained by emotional tension to some extent. This can be acquired by a person's growth and learning, and indeed singing is an extension of this. Actions that frustrate this are the cause of problems unique to the human voice.

References

1. Harrison DFN: The Anatomy and Physiology of the Mammalian Larynx. Cambridge: Cambridge University Press; 1995.
2. Toyozumi T. Comparative dissection and phyletic evolution of vocal organs in vertebrates. Otologia Fukuoka. 1985;31:47–68. (in Japanese)
3. Negus VE. The Comparative Anatomy and Physiology of the Larynx. New York: Hafner Pub; 1949.
4. Hayama, S. Origins of human vocal organs. In: Shibatani, A, Nagano T, Yoro T, eds. Evolution; Lecture 4 on Evolution: Evolution based on Morphology. Tokyo: University of Tokyo Press; 1991:173–198. (in Japanese)
5. Holinger LD, Barnes DR, Smid LJ, et al. Laryngocele and saccular cysts. Ann Otol Rhinol Laryngol. 1978;87(5Pt1):675–685.
6. Tannowa S, Taki Y, eds-in-chief; Imaki A, Kawamoto A, eds. Pre-historic Fish Surviving in Present: Fascinating World of Fish. Tokyo: Tokyo University of Agriculture Press; 2008. (in Japanese)
7. Portmann, A. Shimazaki S, trans. Comparative Morphology of Vertebrates. Tokyo: Iwanami Shoten; 1979. (in Japanese)
8. Romer AS. The Vertebrate Body. 4th ed. Philadelphia: WB Saunders; 1970.
9. Miki S. Nature Studies of Life Forms. Volume 1 of Essays on Anatomy. Tokyo: Ubusuna Shoin; 1989. (in Japanese)
10. Yoshikawa T. New masseter theory. Chiba Medical Journal. 1976;52:49–59. (in Japanese)
11. Saigusa H. Swallowing mechanism: morphological consideration of relationship between upright position and a person's swallowing. JOHNS. 2005;21:1718–1724. (in Japanese)
12. Kirikae I, Sawashima M. Physiology of the voice. In: Iwabuchi E, Hatano K, Naito J, et al. Creation of Words: From First Cry to Age Five. Tokyo: Nippon Hoso Shuppan Kyokai; 1968. (in Japanese)