

Functional Morphology and Adaptive Features of the Jaw Apparatus in Puffins (Fraterculini, Alcidae, and Charadriiformes)

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Abstract—Comparative descriptions and drawings of the jaw apparatus of the genera *Fratercula* and *Cerorhinca* as compared to *Uria* have been made. During the evolution of puffins, the shape of the high and laterally compressed bill was affected by the necessity to squeeze items forcefully, which is primarily related to digging burrows (by biting the soil, which is usually dense turf), and to some extent, by sexual selection. Narrower jaws in the transverse plane exert a higher pressure during grasping and extrude a more limited water volume when the mouth is closed helping the birds to catch small crustaceans. The need to align obliquely the external adductor muscle has determined the major traits of the head in these birds, namely, a modified layout of the external adductor muscle with the prevalence of its medial portion, reduction of the postorbital part of the superficial portion, and the clinorhynch of the skull. There is an abutment of the mandible against the cranial base, which prevents the mandible from retreating when the bird presses the bill into soil (turf) during digging. The morphology of the skull and jaw apparatus of the Atlantic puffin (*Fratercula arctica*) is assumed to be fundamental for the genus. In the tufted puffin (*F. cirrhata*), maximal development of the aponeurotic framework in the jaw muscles is observed, as is a decreased range of cranial kinetics due to the complication of the pseudotemporalis profundus muscle, which increases its available force to the detriment of the contraction amplitude. The horn billed puffin (*Cerorhinca monocerata*) shows a secondarily despecialized state.

Keywords: Alcidae, *Fratercula*, *Cerorhinca*, morphology of jaw apparatus, functioning of jaw apparatus, despecialization

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INTRODUCTION

The morphology of the jaw apparatus of birds reflects to a greater or lesser extent the principal possibilities of its use. In this connection it is of interest to study the detailed structure of the jaw apparatus in order to reconstruct its mechanical properties and functioning as the primary tool for item squeezing and biting. This article discusses the genus *Fraterculini* of the family Alcidae, including marine diving birds with a mixed diet represented by fish and plankton components in various proportions (Nettleship, 1996). The functional morphology of the jaw apparatus of murres and auks has been studied previously (Badikova et al., 2014); this work continues study of the trophic adaptations of auks.

The genus *Fraterculini* includes four species: the Atlantic puffin (*Fratercula arctica*), the tufted puffin (*F. cirrhata*), the horned puffin (*F. corniculata*), and the horn billed puffin (*Cerorhinca monocerata*) (Hudson et al., 1969; Bédard, 1985; Sibley and Ahlquist, 1990; Moum et al., 1994; Baker et al., 2007; Pereira and Baker, 2008). Auklets is a sister group in relation to the puffin (Friesen et al., 1996). Strauch (Strauch, 1985) considered the genus as sister to all other

Alcidae. Sister relationships were found between *F. arctica* and *F. corniculata* (Moum et al., 1994). Some authors consider the horn billed puffin as the fundamental species for the genus (Friesen et al., 1996), and the tufted puffin as a sister species for the rest of *Fratercula* (Watada et al., 1987; Friesen et al., 1996).

The food composition for these birds has been studied well; the most comprehensive review was made by Nettleship (Nettleship, 1996). The adult birds of all four species eat invertebrate marine and small fish in varying proportions, and chicks are fed almost exclusively with fish, which are carried in a bill with several items (up to 20).

The Atlantic puffin eats fish, such as capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), mackerel (*Scomber scombrus*), Atlantic herring (*Clupea harengus*), and cod hatchlings (*Gadus morhua*), and more rarely crustaceans (copepods, euphausiids), polychaetes (Nereids), and squid. The length of the fish caught is 35–157 mm (Barrett, 2002). The average weight of portion of food brought to chicks is 8–12 g (Couzens, 2013). The species composition of food for the tufted puffin is similar to those for the puffin; it also includes pollock (*Theragra chalcogramma*),

mackerel (*Pleurogrammus monopterygius*), and goby fish (*Hemilepidotus jordani*). The diet of the horned puffin consists of fish (48%), cephalopods (31%), crustaceans (8%), and polychaetes (12%). The diet of the horn billed puffin is represented by 52% fish (hatchlings of gerbil, capelin, pollock, mackerel, saffron cod (*Eleginus gracilis*), and goby fish), 38% squid, 7% crustaceans, and 3% polychaetes.

In addition, puffins are able to dig into the soil of dense dry turf in their nesting habitats, biting and loosening the turf with their bills, raking soil away using their bills and legs (Kozlov, 1957; Yudin, 1965; Ushakov, 2007). A typical burrow of the Atlantic puffin has a diameter of 13–18 cm and reaches a length of 1–2 m; both sexes are involved in the construction of burrows (Couzens, 2013).

MATERIALS AND METHODS

We used heads of the Atlantic puffin (adult and chick), puffins, tufted puffins, horned puffins, and horn billed puffins fixed in alcohol or formalin and the skulls of puffins (a total of 31 skulls) and thick-billed murre (*Uria lomvia*) and common murre (*U. aalge*; 34 skulls of both species) from the collection of the Department of Zoology of Vertebrates, Moscow State University; the Russian Academy of Sciences and the Museum of Paleontology, Russian Academy of Sciences; and the Scientific Zoological Museum of Moscow State University. The anatomy of the jaw muscles was studied, the drawings of successive layers up to the cleaned skulls were made, and the following measurements were taken: total length of the skull from the tip of the bill to the back of the head, length of maxilla from the tip of the bill to the front end of the mesethmoideum and the palatal height from the lower surface of the palatine bone to the upper part of the ridge. The measurement results were statistically processed and compared with those obtained for murre.

RESULTS AND DISCUSSION

During the study of the morphology of the jaw apparatus in representatives of the genus *Fratereculini* and the search for its functional interpretation, the following results were obtained.

Skull. Skulls of the genera *Fraterecula* and *Cerorhinca* (Figs. 1a–1c) differ in some parameters: in *Fraterecula* there is convergence of branches of the lower jaw behind the symphysis that is absent in *Cerorhinca* (Guthrie et al., 1999).

The cranial structure of typical auks was previously described by Kozlova (1957) and Yudin (1965), so we will focus on the traits of the skull of puffins (Fig. 1; Guthrie et al., 1999: skull of a horned puffin).

(1) The skull is pneumatic, which makes it easier for the birds to dive into the water. Occipital crests and the cerebellar protrusion are well expressed on the skull. Differences in the form of the latter (it protrudes

more in the Atlantic puffin) may be related to differences in the arrangement of the inner ear. Signs of spongy tissue were observed only in the Atlantic puffin in the back of the outgrowth on the ridge, which may indicate a somewhat lighter bill to provide for its significant increase in size.

(2) Bone support is absent under the nasal glands (*glandula nasalis*), which is associated with a high placement of eyes, pressing the nasal gland above the forehead.

(3) Both jaws are wider in the sagittal plane to a greater (tufted puffin) or lesser (horn billed puffin) extent and narrow in the horizontal (front) plane, thereby significantly improving their breaking strength.

The height of the bill increases due to the formation of a vertical ridge on the premaxillary bone and also due to the vertical expansion of branches of the mandible. Interestingly, in the Atlantic puffin and the horned puffin, the upper jaw is maximized in its rear part, and the lower jaw is bigger in the front (Fig. 1a), whereas the upper jaw in the tufted puffin is maximized in the front, while the lower jaw is almost all equally wide—it is only slightly wider in the rear part (Fig. 1b). The tufted puffin appears as though the premaxilla is underdeveloped, which is compensated by the rhamphotheca. The jaws are slightly widened in the horn billed puffin (Fig. 1c).

The enlarged and, moreover, brightly colored bill is more noticeable and can have a significance in the intraspecific interactions by performing a signaling function related to the mating ritual. The signaling role is confirmed, firstly, by the changing nature of the rhamphotheca (which is subject to age (Peretsen, 1976) and seasonal variability, because in winter it is smaller than in summer (Konyukhov, 1995)), and, secondly, by the existence of a purely dermal ridge in the horn billed puffin, without a specifically high bill (Ushakova, 2007).

Vertical widening of the bill may be associated phylogenetically with its narrowing as this compensates for bone mass providing the necessary strength of the bill. This narrowing of the bill, as well as its narrow tip in loons (Korzun and Dzerzhinsky, 1975), almost eliminates the risk of expulsion of small items sensitive to viscosity from the mouth with water when the jaws are closing.

This flattening of the bill in the sagittal plane primarily affects its strength and, consequently, the quality of the tool used for soil digging and for foraging. The first can be considered as a key adaptation trait of puffins. Although not necessarily for burrowing, it is important to have the capability of the independent construction of nesting shelters, i.e., to be able to do it in principle; it is important that there is the potential possibility for them to dig due to increased pressure applied to the item (high power and small area of contact with the object that is used for biting turf). This

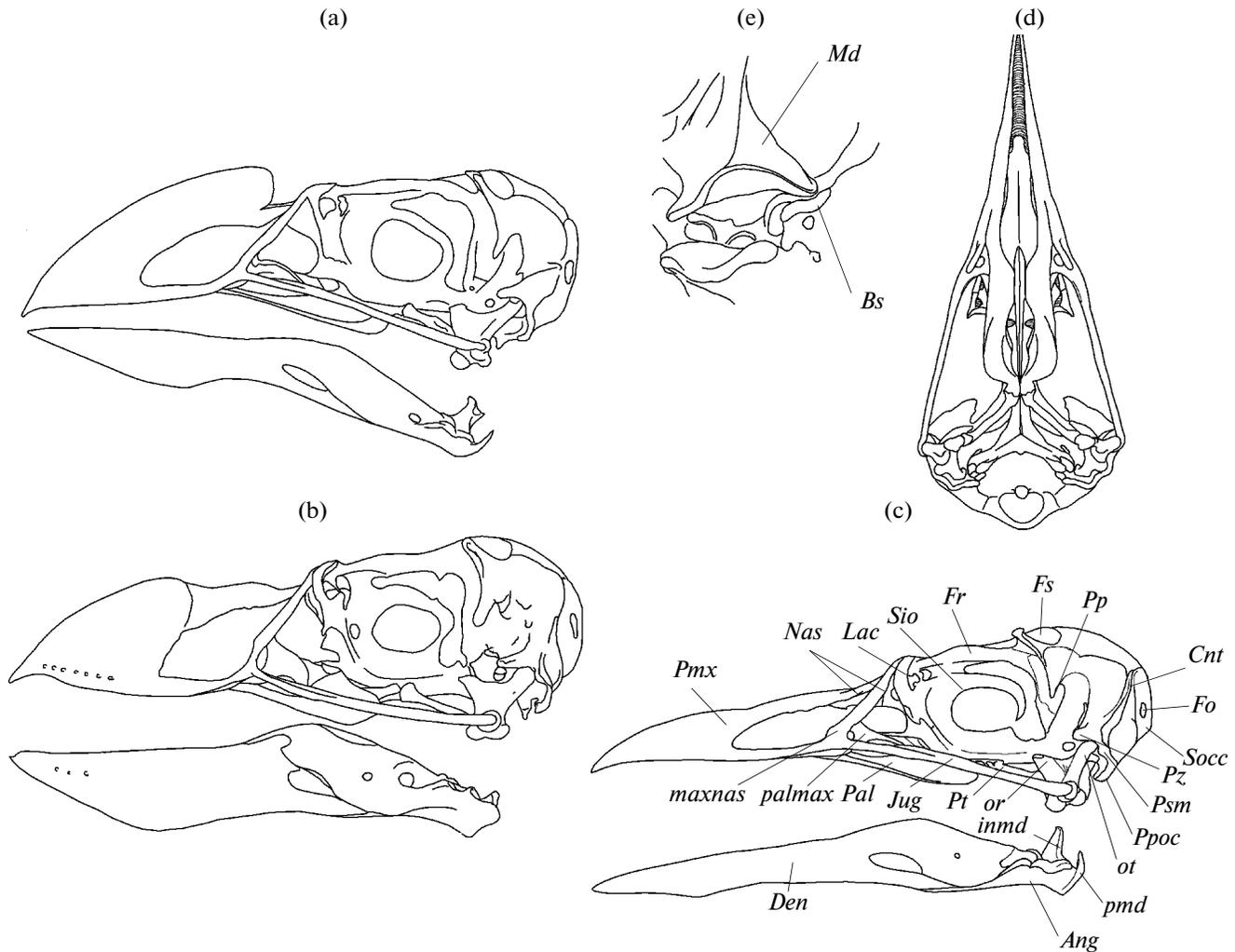


Fig. 1. Skull. Lateral view: (a) the Atlantic puffin (*Fratercula arctica*), (b) tufted puffin (*F. cirrhata*), (c) horn billed puffin (*Cerorhinca monocerata*). Bottom view: (d) horn billed puffin (*C. monocerata*), (e) abutment of the lower jaw on the cranial base (parasphenoid part) of the tufted puffin (*F. cirrhata*).

possibility is likely to have become fundamental for the genus, but more importantly, it was suitable for catching fish. In the horn billed puffin, the bill is slightly wider than in the typical *Fratercula*, and, therefore, it is less efficient as “clippers” to cut the roots in the turf.

Thus, a bill that is relatively narrow in the horizontal plane performs two opposing tasks, i.e., grasping larger, moving and escaping food items and picking up very small and passive ones. The main conditions for effective catching of prey are easily seen, on the one hand, in the increased biting strength due to better articulation and, on the other hand, in the change of the bill into a kind of fine forceps to minimize resistance and the negative effect of sharply closed jaws in the aquatic environment. Vertical widening of the upper jaw raises its breaking strength, the necessity of which arises when digging burrows and grasping food items.

(4) The Atlantic puffin’s skull (Fig. 1a) is characterized by clinorhynch (downward orientation of the bill), which increases the articulation efficiency of the lower jaw, which is longer and, therefore, generally weaker (including in murre) than the upper jaw. The palatine bones transmitting lowering (retraction) force to the upper jaw are noticeably shifted ventrally from the subocular arch, which is stronger than in the murre. It brings substantial articulation benefits for the upper jaw.

Shortening of the bill, seemingly obvious for the heads of the birds discussed as compared to murre (Badikova et al., 2014), is not confirmed by measurements. Thus, the length of the maxilla comprises about 46% of the whole length of the skull, while in the common murre it is 50%. In the thick-billed murre, it is the same at 46%. The *t*-test for independent variables gives similar results and indicates no difference between the

thick-billed murre and puffins ($p < 0.05$) and differences between the common murre and puffins ($p = 0.46$).

There is a noticeable difference in the palatal attachment height of maxilla to the skull in the ratio to the length of the maxilla. For murre, this ratio is 23% and for puffins it is 32%, which is also confirmed statistically ($p < 0.05$). This indicator directly defines the mechanical benefit of the maxilla, i.e., its articulation properties. The larger it is, the better the compression of an object with the jaws.

(5) In puffins, especially in the Atlantic puffin and tufted puffin, there is an abutment of the mandible against the cranial base ("secondary jaw joint"; Bock, 1960; Fig. 1d), which may prevent the lower jaw back from moving when the bird presses its bill into the soil during digging.

Jaw muscles. The jaw musculature of auks was described in detail in the example of the thick-billed murre (Badikova et al., 2014). For the tufted puffin and puffins, the general plan of the structure of the musculature is maintained. All four species (Fig. 2) have gaps between the muscles filled with connective tissue layers, which facilitate their mutual sliding. This gap is found within the external adductor, between the powerful development of the zygomatic and rudimentary postorbital part of the superficial portion; it is especially deep in the Atlantic puffin and the tufted puffin.

We note the differences between species in the structure of the jaw musculature.

(1) The bulk of the external adductor, namely, the superficial and medial portions, is located under the eye allowing the cheek to project laterally more than the eye, and their fibers are oriented very obliquely, almost horizontally.

(2) The prevalence of the medial portion and the presence of a large aponeurosis *alm* increase the number of muscle fibers and, consequently, the force of contraction. There is no assimilation of the superficial portion of the outer layer of the medial portion by the zygomatic part detected in murre (Badikova et al., 2014).

(3) Double attachment of the superficial portion of the external adductor to the skull wall (through postorbital and zygomatic projections). In the horn billed puffin, the horned puffin (Fig. 2b), and the tufted puffin (Figs. 2a, 3a), the aponeuroses of the superficial portions are completely fused to form a complex *apoms-Lz*. In the Atlantic puffin (Fig. 2c), the aponeurosis *apo* remains free and *ams* and *Lz* are fused to each other and with the postorbital ligament *lig. postorbitale Lp* forming a complex *ams-Lz-Lp*.

(4) Hypertrophy of the zygomatic part of the superficial portion and reduction of the postorbital section. It turns out that the postorbital part of the superficial portions, which was absent in primitive Charadriiformes and became new in gulls and auks (Yudin,

1965), used a new and higher point of attachment for the portion and became unnecessary in puffins.

(5) Accreting of the terminal aponeuroses of the external adductor (*asa + asp*). In the Atlantic puffin and the puffin (Fig. 3a), there is a longitudinal thickening at the point of their convergence. Initially, these aponeuroses are derivatives of a single *as*, but the presence of a suture may be indicative of the secondary nature of fusion.

(6) Maximum development of the aponeurotic framework of muscles (new aponeuroses development and formation of additional crests on those existing) is observed in the tufted puffin (Figs. 3–4).

Its zygomatic part became more complicated and three-layered. This happened, firstly, due to an unusually long aponeurosis *amr* (Fig. 3c), which usually covers only the inner side of the rostral part of the deep portion. The *amr* aponeurosis is not flat, as in others, and bears the dorsolateral ridge upward on its side. Secondly, there is an additional aponeurosis *asa'* (also in the Atlantic puffin), on which the fibers come from *ams* outside and from the crest *amr* from inside. It is important that blade *asa'* is not associated with either *ar* or *asa*. It complicates the pennate structure of the superficial portion adding two more layers from both sides of *asa*. Thus, we can expect a particularly high effort from the rostral part of the deep portion during contraction.

Crests also develop on aponeuroses *aci* of the external adductor (Figs. 3b, 3c), *alo'* of the pterygoid muscle (Figs. 4b–4d; also in the Atlantic puffin) and *ad* of the depressor (Fig. 3a).

(7) Similarly to murre and auk, the *amq* aponeurotic creep from the quadrate bone to the zygomatic process of the skull occurred, which somewhat removed the force vector from the joint and increased muscle articulation.

(a) In the tufted puffin, *amq* partially fuses with the ventral edge *amq'*, which, in turn, is fused to the inner surface of the keel *am* resulting in the formation of two bladed structures (Figs. 3b, 3c); i.e., the initial aponeurosis of the caudal part of the deep portion in the tufted puffin is represented by a complex *amq-amq'*–keel *am*. Formation of a complex instead of a set of individual aponeuroses may be due to increased oblique orientation of fibers of the portions *Aem* and *Aec* to the orientation of the zygomatic arch during adaptation to an increased contribution to the retraction force.

(b) In the horn billed puffin, corresponding fibers come as a narrow fan from large *amq'*. It forms a short extra blade *asc* in front, which also comes from the zygomatic process of the skull, from its very top.

(c) In the Atlantic puffin, *amq'* starts from the base of the zygomatic process and *asc* also comes from below, but more distally.

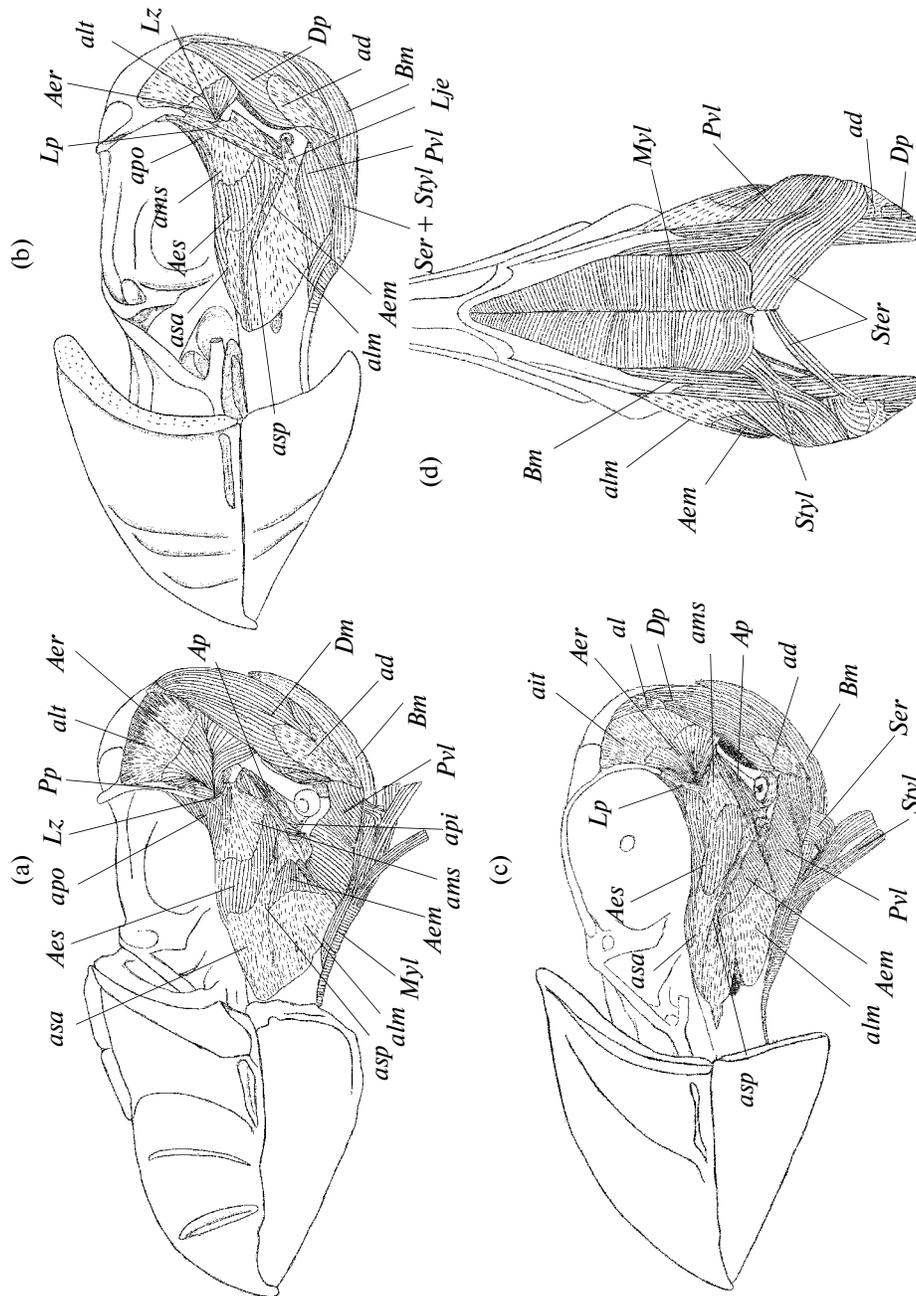


Fig. 2. The surface of the muscles of the head after removing the skin and removing the zygomatic arch. Lateral view: (a) tufted puffin (*F. cirrhata*), (b) horned puffin (*F. corniculata*), (c) Atlantic puffin (*F. arctica*). Bottom view: (d) horn billed puffin (*C. monocerata*).

(8) The complication of the deep pseudotemporalis profundus muscle in puffins indicates limited cranial kinetics.

Pseudotemporalis profundus muscles in birds reliably arose as a result of the division of a single muscle (Dzerzhinsky, 1983). Passing to the lower jaw from a long jaw joint (process of the quadrate bone), deep

pseudotemporalis profundus muscle should provide a significant amplitude of contraction. Therefore, it is usually formed by long relatively few fibers, has no complicated pennate structure, and does not use its opportunities to build up strength.

The Atlantic puffin has an initial aponeurosis *app* attached to the orbital process of the quadrate bone

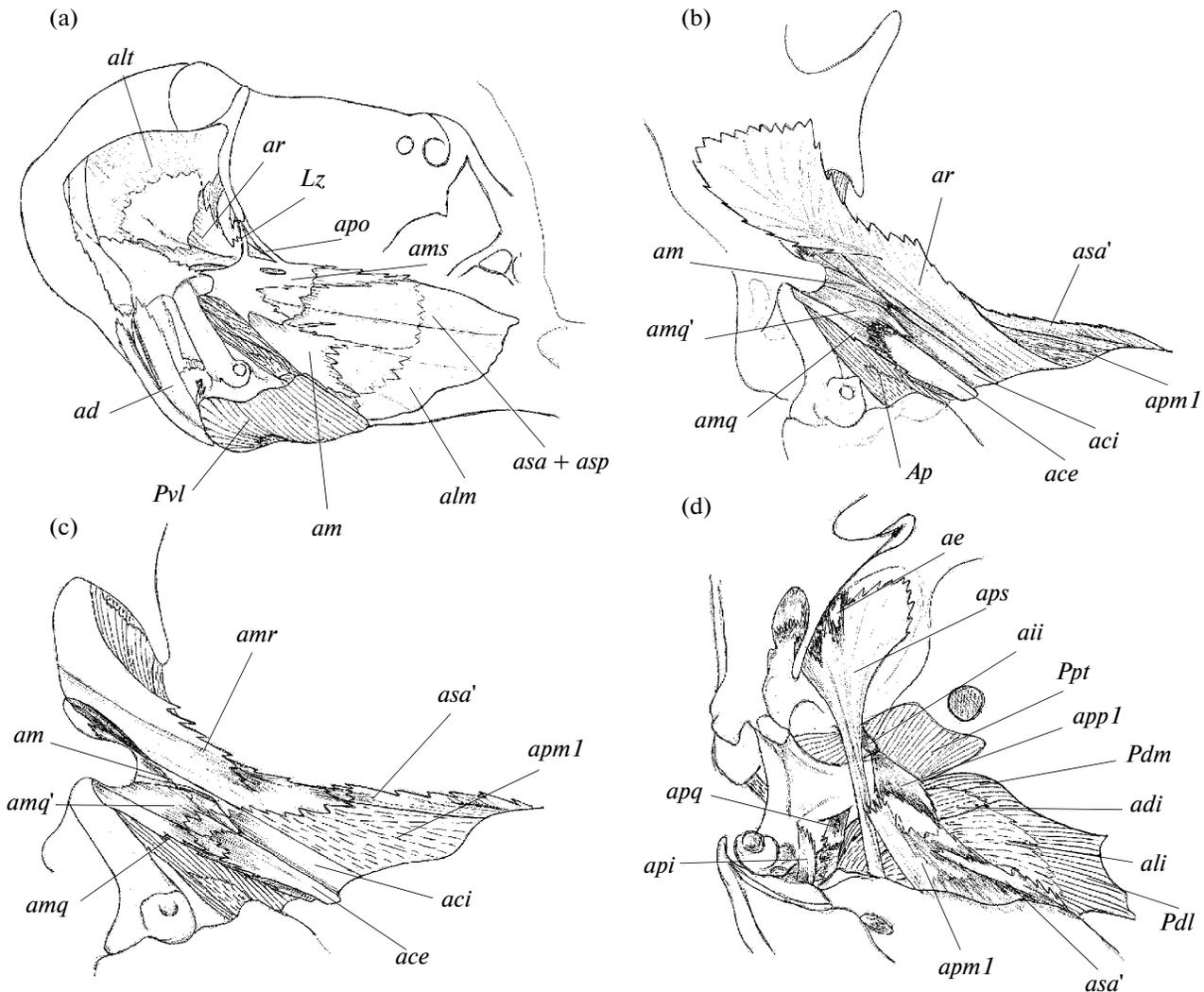


Fig. 3. The aponeurotic framework of jaw muscles of the tufted puffin (*Fratercula cirrhata*), lateral view: (a) muscles fibers of the external adductor and the depressor of the mandible were pulled out, (b) aponeuroses of the superficial and medial portions of the adductor and depressor were removed, (c) aponeurosis *ar* was additionally removed, (d) muscle fibers of the pseudotemporalis profundus were removed.

and the terminal superficial *apm* attached to the inner surface of the mandible. Some fibers from the *app* go directly to the lower jaw. In the horn billed puffin, this muscle has several initial aponeuroses (*app1* and *app2*) and one terminal aponeurosis.

The tufted puffin has an additional initial aponeurosis *aii* (*ap. interna intermedia*), which starts on the wall of the eye orbit (Fig. 3b). Fibers coming from this aponeurosis are not associated with the orbital process of the quadrate bone and do not use its articulation; therefore, in contrast to other muscle fibers, they do not give such a contribution to the retraction force. The typical part of the deep pseudotemporalis profundus muscle is an unusually complex pennate, indicating increased biting force and most importantly

the retraction effect (the force potential of the upper jaw, perhaps to tear objects), but also to reduced cranial kinetics. The increasing complexity of the internal structure of this muscle in the tufted puffin is manifested in that it has two *apm* (Figs. 3b, 4a), and fibers from *app2* partially terminate at the pterygoid muscle aponeurosis *ali*. The adaptive meaning from preservation of the intermediate fibers between the pseudotemporalis profundus muscles is incomprehensible; it is possible that delay of their separation was a side effect of complicating the pennate structure.

In addition, in the tufted puffin, a unique initial aponeurosis of the superficial pseudotemporalis profundus muscle *ae* is found (Fig. 3d). This aponeurosis

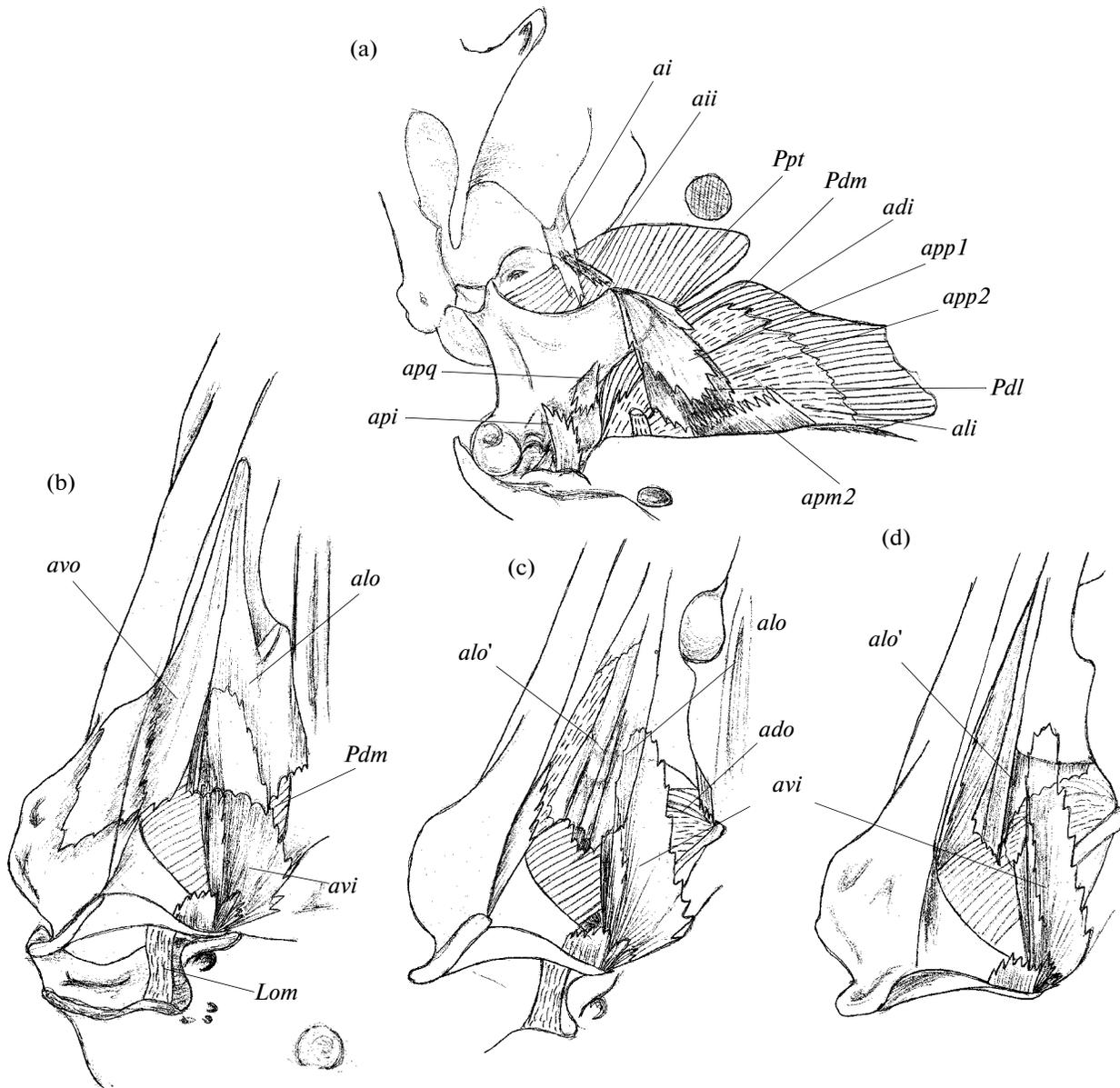


Fig. 4. The aponeurotic framework of jaw muscles of the tufted puffin (*F. cirrhata*): (a) pseudotemporalis profundus muscles, (b–d) subsequent steps of dissection of the pterygoid muscle.

was discovered by E.G. Potapova in wheatears (Potapova and Panov, 1977).

(9) In the horn billed puffin, as well as in auks (Badikova et al., 2014), the pseudotemporalis profundus superficial muscle goes far back behind the postorbital process of the skull, which is considered a primitive sign in charadriiformes (Yudin, 1965).

(10) Special remarks.

(i) Pterygoid muscle.

The aponeurosis *ali* of the dorsolateral portions in the horn billed puffin is attached to the lower jaw dorsal to the *adi* dorsomedial portion, and in the Atlantic

puffin, it is at the same level, while in the tufted puffin, it is located ventrally to *adi*, which may be due to the oblique orientation of the aponeurosis *ali*, which increases the proportion of its adducting effort. In the Atlantic puffin *adi* near the front edge of the dorsomedial portion, it is covered with muscle fibers from below. This may indicate a sign of a partially two-layered portion.

(ii) The rear adductor is small and typical, in contrast to that marked in murrets (Badikova et al., 2014).

(iii) The depressor consists of long fibers that allow the bill to open wide.

DISCUSSION

In the search for the relationship between the desired direction of muscle strength and the features of the overall layout of the skull, we have built a distribution scheme of muscular strength in thick-billed murre and the Atlantic puffin (Fig. 5) during immobile squeezing of catch by the most common way (Dzerzhinsky, 1972), i.e., under combined muscular control with both jaws.

(1) The lower jaw divides effort A of the external adductor between the object (F) and the area of its support (strength K).

(2) Upwards it has support on the skull through the quadrate bone (force M), and backwards the support is to the palatine bone through the tight pterygoid muscle (strength R).

(3) The palatine bone transmits the force on the upper jaw, where its fate is similar to the fate of force A on the lower jaw. Its component F presses on the subject, and the support strength on the skull (N) goes through a flexible zone at the base of the ridge of the maxilla (point b).

(4) Forces M and N pressing the skull up and down balance the tension applied by the external adductor (see below for when they cross with it at one point).

One can use a geometric criterion for assessing the performance of certain muscles. To achieve equality of useful forces F and F' the total force of the external adductor must pass through the point z , where the vector M and N intersect. Situations occur in which the balance should be broken in favor of one of the jaws to compensate for the weight of the item squeezed in the bill or the squeezing pressure during grasping.

In trying to unravel the adaptation of the jaw apparatus of puffins, one should search for a natural situation that is associated with the need to crack hard items.

(1) In the figures of the distribution of forces, one can see that the point z is located much further back in the puffin than in the murre; it determines the need for a more oblique orientation of the external adductor forces evidenced from its topography. However, infraorbital portions are oriented more obliquely than might have been expected, seemingly compensating for the additional loads (a decreased retraction force would let the item to slip out of the bill) during breaking of the grasped items, i.e., pieces of turf during digging burrows.

(2) The need to solve the problem of construction of nesting shelters by themselves (which is absolutely not available, for example, to murre) could create a high selection pressure and determine the formation of the corresponding adaptation of the jaw apparatus, which acquired the value of the key factors in the formation of a new morphofunctional appearance of these birds and, in particular, the method of fishing.

The adaptation of the jaw apparatus of puffins and tufted puffins permitted digging burrows and catching live prey.

As was mentioned the jaw apparatus was most likely influenced by sexual selection and adaptation to digging burrows, and the first has an impact on the size and color of the rhamphotheca, while the second influences the height of the premaxilla. It is possible to reconstruct the processes of change and to propose an evolutionary scenario. In the external adductor, the portion located under the eye and parallel to the mouth cut is large. The horizontal arrangement of the superficial portion, firstly, pushed the eye upwards necessitating elimination of bone supports for nasal glands, and, secondly, led to the secondary reduction of the postorbital part of the superficial portion, which became unnecessary. The effectiveness of this reorientation of muscles in the use of muscular strength by the jaws is markedly enhanced due to the relatively more ventral position of the jaw joint than in murre. This lowering of the joint is achieved by bending the lower jaw, orienting mouth cut relative to the skull arch, namely due to clinorhynch. The flat vertical bill of puffins is insensitive to the slope, while in murre clinorhynch is not available due to the hydrodynamic requirements. The second factor is an increased palatal maxilla base height compared to the generalized ancestral form, which, in turn, leads to increased biting strength and, as a consequence, to the ability to bite hard items and, obviously, to burrow. The palatal height in all puffins is greater than in murre, and this shows that it effectively influences their adaptation to the influence of force on the objects. In the case of the horn billed puffin, we see the result of secondary despecialization. Its return to typical fishing is limited by competition with murre. The lack of a high bill evidences that the height of the bill is not required for the ability to hold a few objects in its bill. It is possible it found some softer hunting and breeding habitats (in particular, it is characterized by a tendency to nocturnal habits). Under the conditions of a high maxilla, there were possibilities for unlimited (limited only by the size of the bird) and possible (but not necessarily) expansion of the rhamphotheca in the vertical plane, which is influenced by sexual selection. This explains the fundamental diversity of bill forms in puffins and tufted puffins. Widening of the bill upwards in different species is due to growth of different parts of the maxilla (Atlantic puffin and tufted puffin) or only due to rapid growth of the rhamphotheca (horn billed puffin). In fossils intermediate cases of dorsoventral expansion of the maxilla are known (*Fratercula dowi*, Guthrie, 1999), in which it is more pronounced than that of the horn billed puffin, but weaker than that of modern *Fratercula*.

It is typical to show surprise at puffins' ability to carry in its bill more than a dozen long, thin fishes grasped across the bill, which are hanging far out of its mouth. While another fish is being caught, they can be

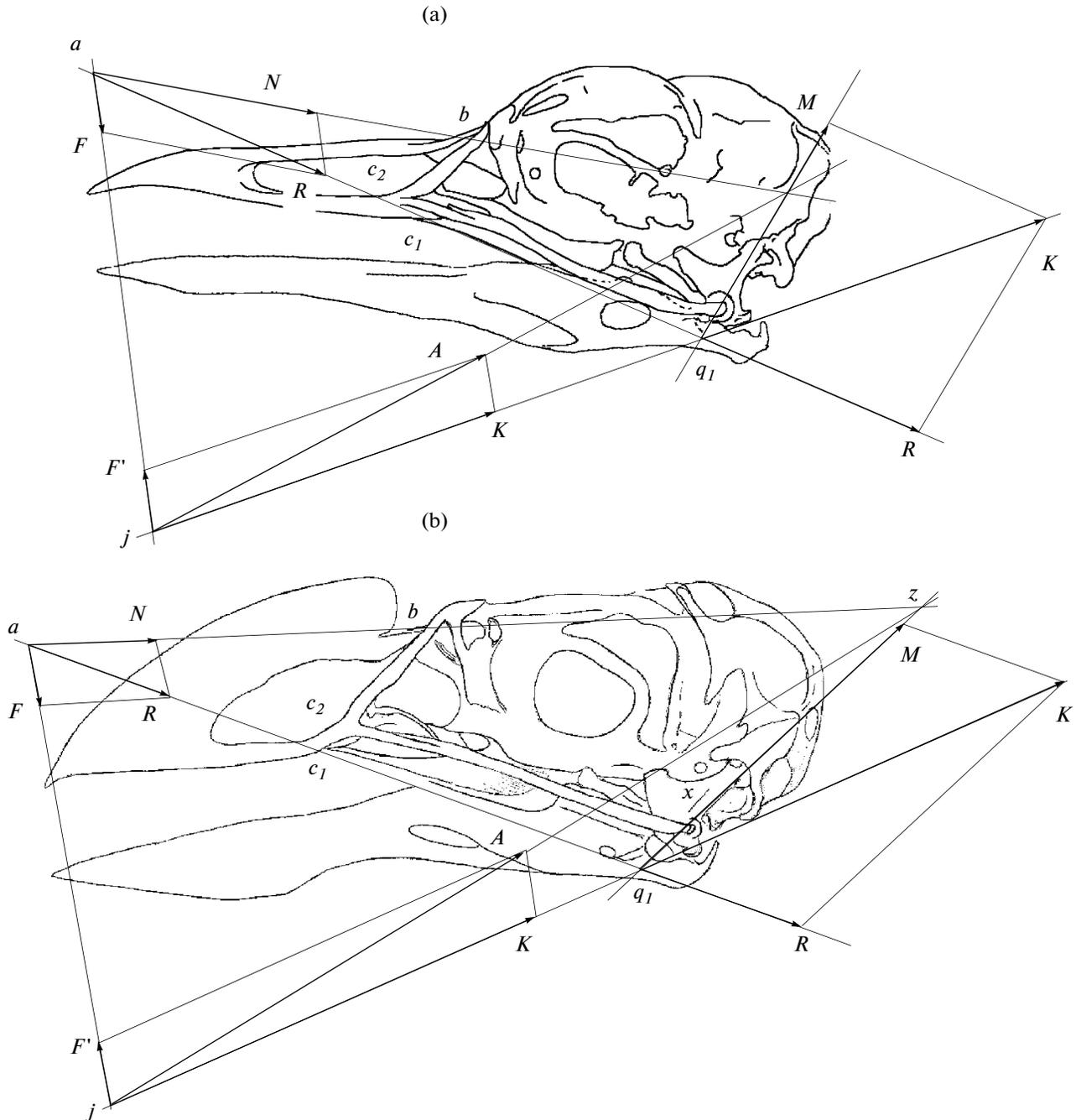


Fig. 5. The scheme of distribution of muscle forces in a stationary item that is squeezed during the combined muscle control of the jaws: (a) thick-billed murre (*Uria lomvia*), (b) Atlantic puffin (*Fratercula arctica*).

squeezed into the corners of the mouth due to water resistance. In addition, fish caught are badly damaged, crushed by powerful jaws, and therefore are likely to stick to it. It is possible that there are other mechanisms that allow the bird to hold a few items in its bill while catching the next. The tongue can also participate carrying spinelets at the base directed backwards; it probably presses the fish to the palate, like in many land birds (Korzun, 1978). Furthermore, in puffins, the sickle-shaped sublingual muscle has a dual attach-

ment to the mandible. Fibers of the second, medial attachment form a narrow semicircle more effectively raising the root of the tongue and limiting its lateral deviations.

CONCLUSIONS

Our conclusions about the adaptive traits of the organization of the jaw apparatus of puffins are the following.

(1) The state of the Atlantic puffin can be considered as fundamental for the genus. Its flat bill is a tool for the destruction of turf in constructing dense nesting shelters and forms a key adaptation of the genus. Furthermore, it plays an important role in intrapopulation communication as a visual signal. The flat and very strong bill for accidental reasons proved to be suitable for effective fishing with accumulation of the catch in its bill (preadapted). The horned puffin on the level of adaptation is similar to the Atlantic puffin, but it evolved in an independent way and, therefore, gained some morphological differences.

(2) The tufted puffin represents the top of transformation processes in the described direction. In particular, it has a maximum degree of reduction of the postorbital part of the superficial portion and it shows the maximum limited cranial kinetics in favor of the deep pseudotemporalis profundus force achieved by its complication, i.e., formation of shorter fibers from a larger number of fibers.

(3) The horn billed puffin is nocturnal, so the signaling role of the rhamphotheca is minimal, and the puffin shows the least specialized state, perhaps, secondary. Its bill is close to more typical for auks, and its "horn" probably represents the residue of signal rhamphotheca of ancestors close to typical puffins.

APPENDIX

Letter symbols in the figures: *Aem*—the medial external adductor; *Aer*—the rostral part of the deep portions; *Aes*—the superficial portion of the external adductor; *Ang*—angular bone; *Ap*—posterior adductor; *Bm*—branchial-mandible muscles; *Bs*—Basisphenoid; *Cnt*—occipital crest; *Den*—dental bone; *Dm*—depressor of the mandible; *Fr*—frontal bone; *Fs*—supraorbital cavity; *Fo*—occipital fontanelle; *inmd*—internal process of the mandible; *Jug*—jugal bone; *Lac*—lacrimal bone; *Lje*—external articular ligament; *Lom*—occipital-maxillary ligament; *Lp*—postorbital ligament; *Lz*—zygomatic ligament; *maxnas*—maxillary process of the nasal bone; *Md*—mandibular bone; *Myl*—sublingual-maxillary muscles; *Nas*—nasal bone; *or*—orbital process of the quadrate bone; *ot*—otic process of the quadrate bone; *Pal*—palatine bone; *palmax*—palatine process of the maxillary bone; *Pdl*—dorsolateral portion of the pterygoid muscle; *Pdm*—dorsomedial portion of the pterygoid muscle; *pmd*—posterior process of the mandible; *Pmx*—premaxilla; *Ppt*—protractor of the pterygoid muscle; *Pp*—postorbital process of the skull; *Ppoc*—paroccipital process; *Pt*—pterygoid bone; *Pz*—zygomatic process; *Q*—quadrate bone; *Ser*—sickle-shaped sublingual muscle; *Sio*—interorbital septum; *Socc*—supraoccipital bone; *ace*, *aci*, *ad*, *adi*, *ado*, *ae*, *ai*, *aii*, *al*, *alm*, *alo*, *alo'*, *alt*, *am*, *amp*, *amq'*, *amr*, *ams*, *api*, *apm*, *apo*, *app1*, *app2*, *apq*, *aps*, *ar*, *as*, *asa*, *asa'*, *asc*, *asp*, *avi*, *avo*—muscular aponeuroses.

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