

The Functional Morphology of the Jaw Apparatus in the Black Guillemot (*Cepphus grylle*) and the Thick-Billed (*Uria lomvia*) and Common (*Uria aalge*) Murres

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Received September 9, 2013

Abstract—The jaw muscles of the thick-billed murre have been described in detail and depicted with comparative notes on the jaw muscles in the common murre and the black guillemot. Owing to adaptation to underwater hunting of mobile prey (first of all, small fish), the composition of the dorsal adductor muscles in the studied species has become simplified in part, compared with their ancestral form, and has become similar to that of another underwater fisher, the great crested grebe (*Podiceps cristatus*). The attachment of the superficial portion of the external adductor muscle to the postorbital projection was strengthened, especially in both murres. In the external layer of the medial portion of the adductor, the muscle fibers gained secondary insertion by the horizontal aponeurosis, similarly to those of the superficial portion, thus increasing the horizontal (retracting) force component, which lowers the long upper jaw. The caudal part of the deep portion of the external adductor became incorporated in the medial portion, but in the murres, especially in the thick-billed murre, part of it is similar to the posterior adductor, which enhances the retracting force as well. All three species show traces of a transfer of the muscle fascicle from the superficial pseudotemporal muscle to the deep pseudotemporal muscle, giving the same effect. Confirmation of the relatively separated position of the guillemot and of its generalized morphological state were found. The specific features of the murres' adaptation to fishing, including morphofunctional prerequisites for forage segregation of the two murre species, are understandable as the basis of their sympatric existence.

Keywords: murre, guillemot, trophic adaptations, jaw apparatus, jaw musculature

DOI: 10.1134/S1062359015080026

INTRODUCTION

Representatives of the family Alcidae exhibit an intriguing range of morphological features of the jaw apparatus, which, supposedly, reflects the variety of foods and techniques of procuring food. It is worthwhile to start analyzing this range with murres and guillemots, which possess a relatively long straight beak, similarly to grebes, loons, finfoots, and some other known hunters of mobile underwater prey. Although murres belong to the tribe Alcini in the subfamily Alcinae, while guillemots belong to the tribe Cepphini (Gaston and Jones, 1998; American Ornithologists' Union, 1983, 1998), their comparative study is expedient, as it will enhance our understanding of the morphofunctional similarity and genealogical differences of these genera.

The diet and certain traits of the nutritional biology of guillemots have been described in a wide range of literature sources summarized by Nettleship (Nettleship, 1996) and, more recently, by Weir and Murseleen (Weir and Murseleen, 2013). Murres and guillemots are fish-eating species, to some extent. The main prey

of the common murre are the capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes*), sprat (*Sprattus*), and, to a lesser degree, invertebrates (*crustaceans*, *mollusks*, and *polychaetes*) and fish roe (Nettleship, 1996). The thick-billed murre also consumes fish, in particular, cottids (Cottidae, genus *Triglops*), sticklebacks (Gasterosteidae), capelins, Atlantic herring, and sand lance. Its diet includes a greater proportion of invertebrates (amphipods, squids, polychaetes; Nettleship, 1996). The black guillemot feeds on benthic fish and invertebrates (polychaetes, sponges, and various crustaceans) and, more rarely, on alipeds, jellyfish, ctenophores, and pelagic fish. The fish diet of the guillemots consists of blennioids (*Blennioidei*), gobies (*Gobiidae*), cottids, Atlantic cod *Gadus morhua*, sand lance, sea perch *Sebastes*, flatfish (order Pleuronectiformes), and wrasses (family Labridae).

The way these birds find food has not been studied in detail owing to the difficulties of direct observation. This hindrance increases the significance of information on the trophic adaptations of guillemots, which

are determined by the construction of the jaw apparatus and can be studied by its biomechanical analysis (Dzerzhinsky, 1972).

The closest group to the ancestors of auks are primitive gulls, i.e., skuas (family Stercorariidae), which received this determination by both morphological (Yudin, 1965) and molecular works (Paton et al., 2003; Ericson et al., 2003; Baker et al., 2007; Mayr, 2011). The nonsibling position of murre and guillemots within the family was established through the results of both morphological (Hudson et al., 1969; Strauch, 1985) and molecular studies (Bedard, 1985; Moum et al., 1994; Friesen et al., 1993; Friesen et al., 1996; Baker et al., 2007). The sibling position of the murre has been noted by many authors (Friesen et al., 1996; Watada et al., 1987); the greater closeness of the thick-billed murre to the black guillemot than to the common murre was not confirmed (Moum et al., 1994; Watada et al., 1987). The greatest problem still consists in determining the relative position of the guillemot (Strauch, 1985; Moum et al., 1994; Friesen et al., 1996) although the monophylicity of its union with the murre is not denied (Friesen et al., 1996).

EXPERIMENTAL

In our study we used heads of the thick-billed murre (*Uria lomvia*), common murre (*U. aalge*), black guillemot (*Cepphus grylle*), and, additionally, pomarine skua (*Stercorarius pomarinus*) fixed in alcohol or formalin. The jaw musculature was anatomized in detail and drawn layer by layer. The skulls of the selected species were also studied (5 specimens of the guillemot, 11 specimens of the thick-billed murre, and 23 specimens of the common murre) from the collections of the Department of Invertebrate Zoology of Moscow State University, the Paleontological Museum of the Russian Academy of Sciences, and the Scientific Research Zoological Museum of Moscow State University. Several measurements were made: the total length of the skull A (measured from the caudal surface of the cerebellar projection to the tip of the beak), the length of the upper jaw G (measured from the basis of the maxilla pipit (from its flexible zone) to the tip of the beak), the height of the maxilla at the basis K (from the palatine bone to the flexible zone), and, finally, the maximum width B of the cranium in the postorbital projections and its minimum width C in the temporal zone. On the basis of these measurements, three parameters were calculated: the relative length of the upper jaw (G/A), the relative palatal height (K/G), and the relative maximum width of the cranium (B/C) (relative depth of the temporal cavities). Owing to the limited number of samples, the nonparametric Mann–Whitney criterion was used.

Characterizations of skulls (mean, %)

Parameter	<i>Cepphus grylle</i> , <i>n</i> = 5	<i>Uria lomvia</i> , <i>n</i> = 11	<i>Uria aalge</i> , <i>n</i> = 23
K/G	24.61 ± 4.26	25.19 ± 2.07	21.77 ± 2.25
G/A	55.02 ± 1.21	57.03 ± 1.83	59.55 ± 1.65
B/C	17.37 ± 5.24	33.74 ± 13.26	36.20 ± 6.39

K/G is the relative palatal height, G/A is the relative length of the maxilla, and B/C is the depth of the temporal recess

RESULTS

The skull structure of guillemots has been described well in the literature (Kozlova, 1957; Dzerzhinsky, 1962; Yudin, 1965), which frees us from the necessity of a detailed description. It preserves the schizorhynia, which is characteristic of almost all Charadriiformes: slitlike rear ends of bony nostrils (Fig. 1a, *Nar*) but has neither the basispterygoid joint, which is widespread in the sandpiper, nor any noticeable deviation of the mouth section line downward from the plane of the zygomatic arch (the skull is orthocranial as in other underwater fishers). Owing to adaptation to diving, the skull is apneumatic and its outer relief associated with the location of the musculature and nasal glands (glandula nasalis) situated above the orbits is very pronounced. Due to the visual search for food, the eye-bulbs are large; hence, the orbits are large as well.

Comparison of Skulls

Using the measured parameters described above, the relative palatal height, relative length of the maxilla, and depth of the temporal recess were calculated (all in percent). Their average values and the standard deviations can be seen in the table.

The Mann–Whitney paired test showed that in the guillemot, the maxilla is relatively shorter than that in the murre, both the common ($p = 0.000806$) and the thick-billed ($p = 0.027167$), which is inferior to the common murre ($p = 0.000693$) in this respect. In terms of the relative palatal height of the base of the maxilla, which allows us to judge its lever properties (mechanical advantage), the common murre is significantly inferior to the thick-billed murre, in full compliance with their specific names ($p = 0.000611$). The range of these values for the black guillemot exceeds the values of both murre. Based on the ratio of the maximum width of the skull (in the postorbital projections) to the smallest width (in the area of the temporal narrowing), which can be considered an indicator of the relative depth of the temporal recesses, the

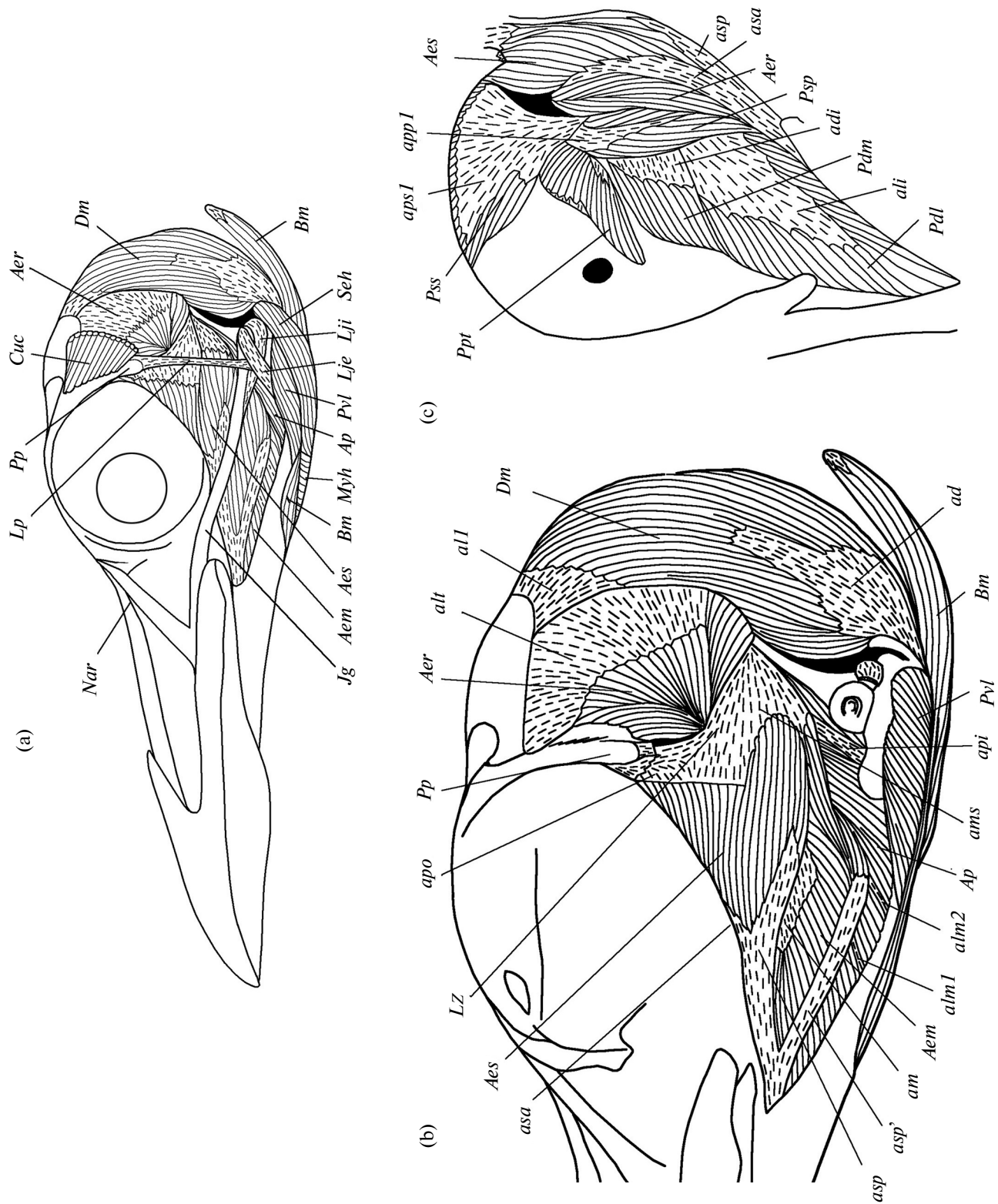


Fig. 1. The surface of head muscles of the thick-billed murre (*Uria lomvia*): (a) lateral view after the removal of the skin; (b) the same after the removal of the zygomatic arch; and (c) view from the orbit, half-turned, from above, and from one side.

guillemot is inferior to the thick-billed murre ($p = 0.027167$) and, even more clearly, to the common murre ($p = 0.001018$). This difference might be determined by the greater relative mass of the guillemot's brain due to its lower body weight. For guillemots, the figures overlap.

Such a component of the jaw apparatus of the guillemots as the jaw musculature has not been studied so fully (Yudin, 1965), and in this paper, as it is considered the main source of new information, it will be studied in detail. We selected the thick-billed murre as the main object. Comments on the differences between the common murre and guillemots are given in passing. In terms of the homology of the jaw muscles and their proportions, the authors followed Lakjer (Lakjer, 1926) and, in the nomenclature of the muscular aponeuroses, Dzerzhinsky and Potapova (Dzerzhinsky and Potapova, 1974).

Dorsal Adductors

(1) The outer adductor (m. adductor mandibulae externus), the largest among the dorsal adductors, is located behind and below the eye. The major surface portion of the muscle (m. add. md. ext. superficialis, Fig. 1, *Aes*) consists of two parts. The fibers of the zygomatic part begin at the zygomatic process of the skull (Fig. 2c, *Pz*) with aponeurosis *am*, *am* and at the zygomatic ligament (Fig. 1b, 2a, *Lz*), which connects the mentioned process with the postorbital projection (Fig. 1a, 1b, *Pp*). The fibers extending from this process with aponeurosis *apo* (Fig. 1b; in the black guillemot, only directly as the *apo* is missing) form the postorbital part of the portion. The superficial portion is attached by two aponeuroses that form a sort of crater with a greatly stretched common base (in the black guillemot and common murre their bases are widely separated) at the upper edge of the lower mandible (Fig. 1c, 2a, *asa*) and on its lateral side (Fig. 1b, 2a, *asp*). The portion is sandwiched between the eye and the zygomatic arch (Fig. 1a, *Jg*), ventrally to which another end aponeurosis lies, *asp'* (Fig. 1b, 2a), which has a common base with *asp*.

The slightly smaller medial portion of the external adductor (m. add. md. ext. medialis, Figs. 1a, 1b, *Aem*) begins with a fan-shaped aponeurosis *am* from the zygomatic process of the skull together with aponeurosis *ams* (Fig. 2a). This portion is two-layered in parts. In addition to the main layer of fibers, between the inner surface of the aponeurosis *am* and the lower mandible, there is a limited lateral layer of muscle fibers extending from the external side of *am* to the weak and fragmented superficial aponeurosis *alm*. The latter is represented by two ribbons (Fig. 1b, 2a, *alm1*, *alm2*) attached to the lateral surface of the lower mandible, each being fused by the apex with the mentioned aponeurosis *asp'*. The zygomatic arch (Fig. 1a, *Jg*) is strongly pushed into the muscle at the side, and thus affects its shape. In the common murre, both the apo-

neurosis *asp'* and the ribbons *alm* are noticeably wider. In the black guillemot, the aponeurosis *alm* is full, so the portion is entirely two-layered and reveals no connection with the zygomatic part *Aes*.

The deep portion of the external adductor (m. add. md. ext. profundus) consists of two parts: rostral and caudal. The rostral part of the deep portion (Fig. 1a, 1b, *Aer*) lies in the temporal recess and is covered externally with the initial aponeurosis *alt* (Fig. 1b, 2a), which is fixed at the edges of the recess. From it and from the wall of the skull, the fibers extend to the end aponeurosis *ar*, which is attached to the upper edge of the lower mandible (Fig. 2a, 2b). Its extensive apical lobe forms a crater with an internal ridge continuing the rear edge of the base. A small sheet *apr* is adjacent posteriorly to *ar* (Fig. 2b), which is the remainder of the initial end aponeurosis of the deep portion. The second initial aponeurosis of the rostral part is aponeurosis *amr* (Fig. 2c), which is forked in this species, but united in the black guillemot and common murre. It lines the muscle from the medial side, as though grafting the bone bottom of the temporal recess. In the black guillemot, the rostral part of the portion is spread more weakly over the surface of the skull, both dorsally and in the front, leaving open part of the superficial pseudotemporal muscle (see below).

The caudal part of the deep portion (*Aec*) is represented quite fully. The muscle fibers extend from the narrow aponeurosis (*amq*), which, in all three of our objects, does not start as usual at the aural process of the quadrate bone but is shifted to the zygomatic process of the squamosal bone (Fig. 2c, *Pz*) and is therefore referred to as *amq'*. This aponeurosis forms the core of the double muscle feather sending fibers to long aponeuroses *ace* and *aci*, which take fibers on their tops directly from the cranium and from the quadrate bone.

(2) The rear adductor (m. adductor mandibulae posterior, Figs. 1, 2, 3a, *Ap*), which belongs to the category of square adductors, is strongly developed and is noticeable after the removal of the skin between the medial portion of the external adductor and the jaw joint. Its front part, which is larger and is extended forward along the lateral side of the lower mandible, starts from the base of the orbital process of the quadrate bone with the aponeurosis *apq* (Fig. 3b). The rear part of the muscle, which is smaller and more typical, begins with the participation of the aponeurosis *aq* at the aural process of the quadrate bone and ends at the lower mandible near the joint, including the aponeurosis *api* (Fig. 2c, 3b). In the common murre, the hypertrophy of the posterior adductor is less pronounced; in the black guillemot and skua, it is entirely unnoticeable.

(3) The components of the internal adductor (m. adductor mandibulae internus) are the two, superficial and deep, pseudotemporal muscles and the pterygoid muscle. The large superficial pseudotemporal muscle (m. pseudotemporalis superficialis, Figs. 1b, 2b, 2c, 3,

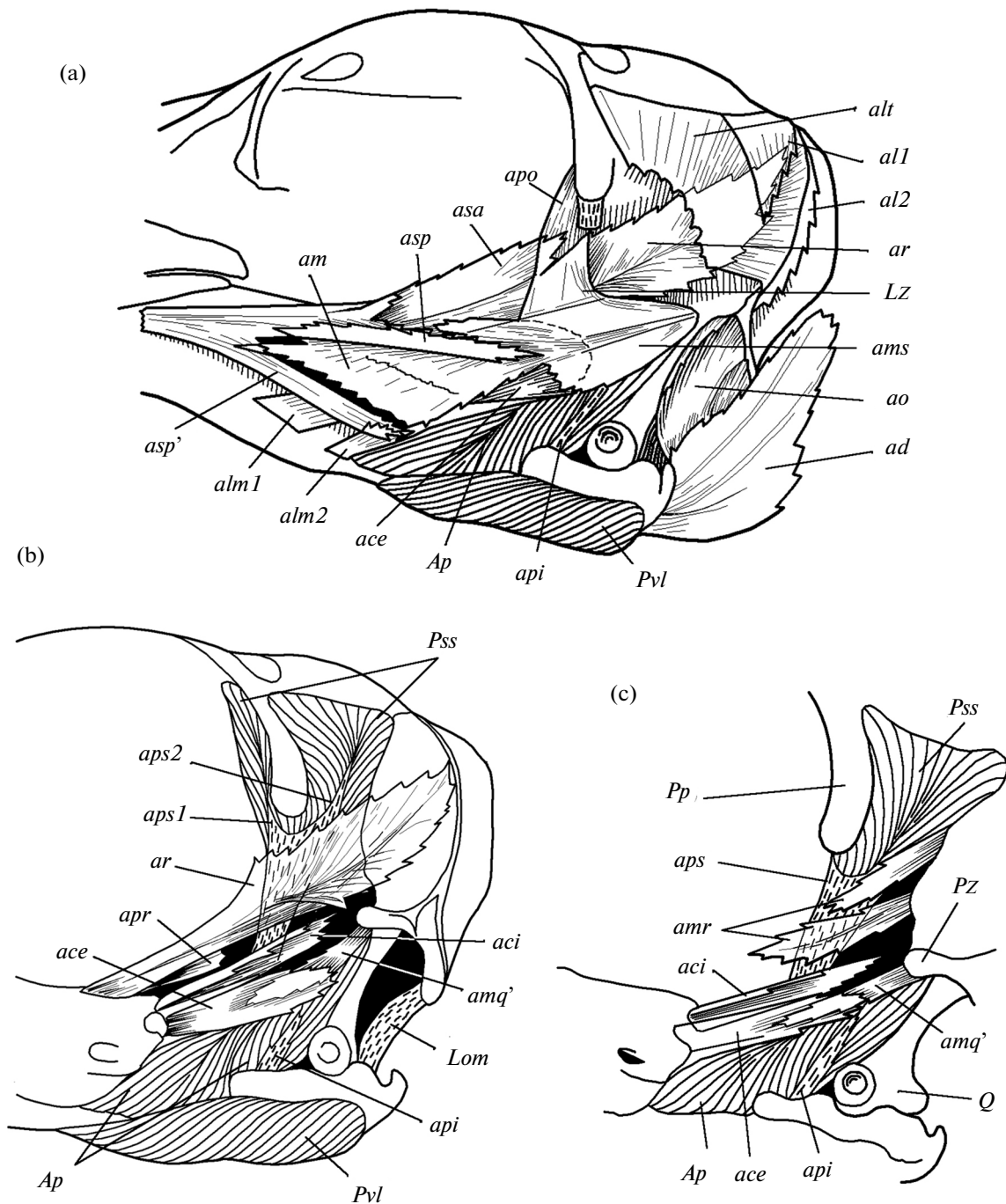


Fig. 2. Aponeurotic carcass of the external adductor of the thick-billed murre (*Uria lomvia*), lateral view: (a) the muscle fibers of the external adductor and depressor of the lower mandible are plucked; (b) the aponeuroses of the superficial and medial portions of the external adductor are removed, as well as the aponeuroses of the depressor; and (c) aponeurosis *ar* is additionally removed.

Pss) extends beyond the orbit, to the temporal surface of the skull (Figs. 2b, 2c). The single initial aponeurosis *ai* (Figs. 3b, 4a) is small and lies deep, while the vast majority of muscle fibers start immediately at the skull. The large and solid two-lobe end aponeurosis *aps* forms a half-glass open from the medial side, and is attached to a

special medial process of the articular bone with a core tendon. Its lobe *aps1* (Figs. 1b, 3) is located in front of the postorbital process (Fig. 1, *Pp*), while the lobe *aps2* (Figs. 2b, 3b) is situated behind it.

In the deep pseudotemporal muscle (m. pseudotemporalis profundus, Figs. 1b, 3a, *Psp*), the second

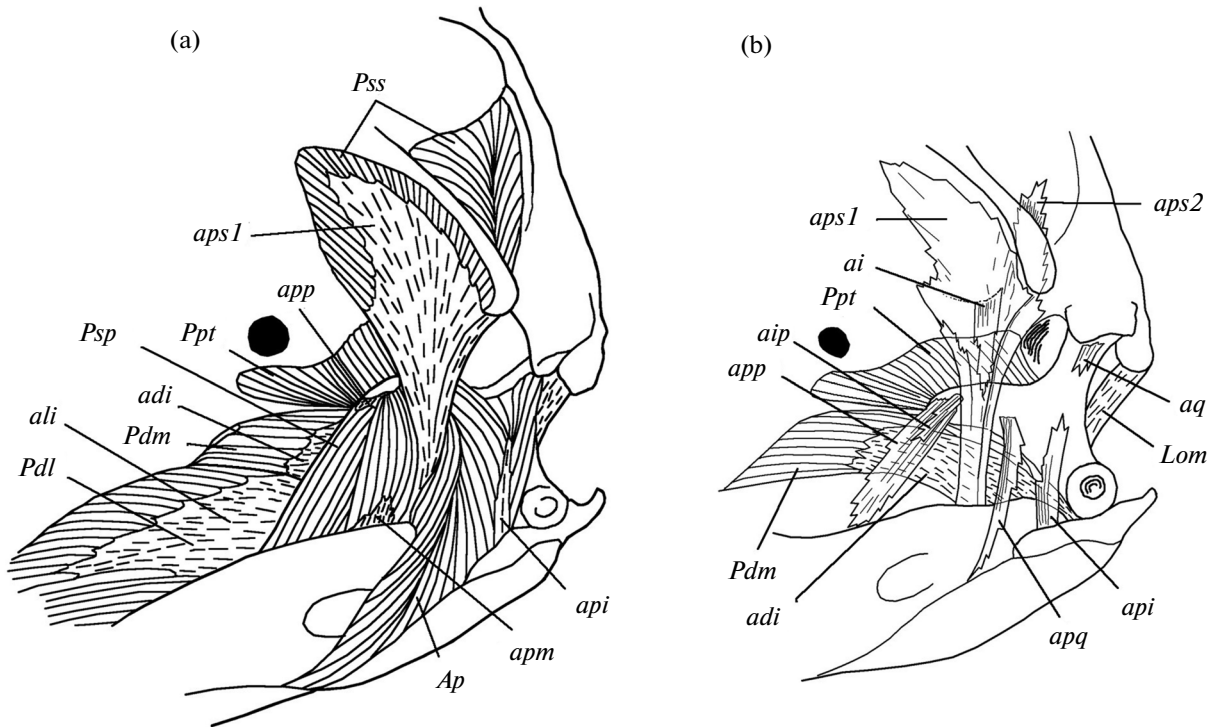


Fig. 3. Parts of the rear and inner adductors of the thick-billed murre (*Uria lomvia*), view half-turned and from the front: (a) muscle surface and (b) inner aponeuroses of muscles.

square adductor stretches from the top of the orbital process of the quadrate bone to the lower mandible and is noticeably forked. Its initial aponeurosis is completely divided into two sheets. The fibers from the tiny upper lobe *aip* (Fig. 3b; it is considerably larger in the black guillemot) extend to the end aponeurosis *apm* (Fig. 3a) attached to the top edge of the lower mandible. The fibers from the major lower lobe *app* (Fig. 3) extend directly to the medial surface of the lower mandible.

The Ventral Adductor, Pterygoid Muscle (*m. ptergoideus*)

The ventromedial portion of the pterygoid muscle (*m. pt. ventralis medialis*, Fig. 4b, *Pvm*) is externally fused with the ventrolateral portion, but is clearly distinguished by the specific features of the inner pinnate structure. The initial aponeurosis of the *avo* portion (Figs. 4b, 4c), which occupies more than half of the ventral surface of the muscle begins in two ways: at the ventrolateral crest of the palatine bone, where the aponeurosis of the ventrolateral portion *alo* also extends from, and at the medial crest of the bone, where it is connected with the longitudinal tendinous band *Tp* (Fig. 4b). The latter underlies the strip of skin at the

edge of the medial slot of the palate. The fibers from *avo* extend to the large deep aponeurosis *avi* (Fig. 4c, 4d) and directly to the lower mandible. The aponeurosis *avi* is attached with two small end aponeuroses, *avi'* and *avi''* (Fig. 4c), to the internal process of the lower mandible (Figs. 4a, 4d, *Pim*), which is raised above the level of the jaw joint.

The fibers of the ventrolateral portion of the muscle (*m. pt. ventralis lateralis*, Figs. 1a, 1b, 4b, *Pvl*) extend from the aponeurosis *alo* (Figs. 4b–4d), originating in the eponymous crest of the palatine bone, to the lower and lateral sides of the base of the mandible. From the medial edge of *alo*, a keel goes deep into the muscle forming the wrapper of the ventromedial portion with the blades *alo'* externally and *alo''* from above (Figs. 4c, 4d), giving rise to part of its fibers.

The dorsolateral portion of the pterygoid muscle (*m. pt. dorsalis lateralis*, Figs. 1c, 4a, *Pdl*) unites the top-lateral surfaces of the palatine bone and aponeurosis *alo'* (Fig. 4d) with the superficial dorsal aponeurosis *ali* (Figs. 1c, 4a) attached at the inner side of the lower mandible in front of the joint.

The dorsomedial portion (*m. pt. dorsalis medialis*, Figs. 1c, 4a, *Pdm*) is adjacent at the back to the previous portion and extends in almost the same way: from the dorsal side of the pterygoid (including the rear end

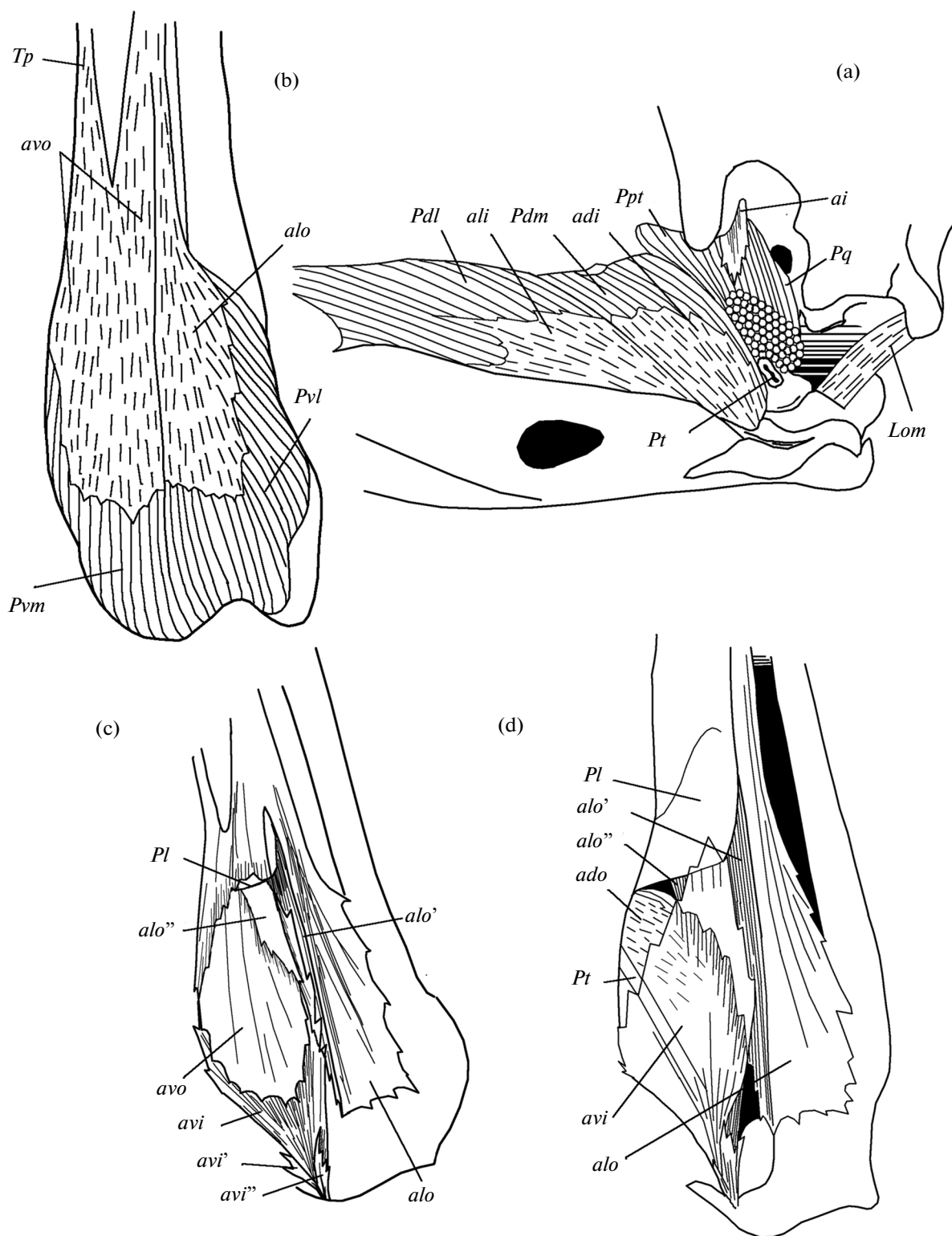


Fig. 4. Pterygoid muscle of the thick-billed murre (*Uria lomvia*): (a) lateral view and slightly above after the removal of the quadrate bone; (b)–(d) view from the bottom, successive stages of dissection.

of the palatine bone) and aponeurosis *ado* (Fig. 4d) to the ventral side of the aponeurosis *adi* (Figs. 1c, 4a), but it is oriented at a substantial angle (approximately 50°) to the longitudinal axis of the skull and is separated by a layer of loose connective tissue from the longitudinally oriented ventromedial portion.

(4) The protractors of the quadrate and pterygoid bones (m. protractor pterygoidei, m. pr. quadrati, Figs. 1b, 3, 4a, respectively, *Ppt* and *Pq*) are separated by a gap opposite the quadrate-ptyergoid joint. The protractor of the pterygoid bone extends from areas of the side surface of the main sphenoid, lateral sphenoid bones and the interorbital division formed by the mesetmoid, ending in a small internal aponeurosis, whereas the protractor of the quadrate bone passes to its medial surface from both sphenoids.

(5) The depressor of the lower mandible (m. depressor mandibulae, Figs. 1a, 1b, *Dm*) is subdivided into two portions: a long portion (m. depr. md. longus) and a triangular one (m. depr. md. triangularis). It is oriented almost vertically to the axis of the zygomatic arch and partly covers the external adductor with its upper part. The depressor is provided with large initial aponeuroses (Fig. 2a): medial aponeurosis *ao* and double *al* double as part of the lateral (*al1*) and medial (*al2*) sheets. The long portion extends from the lobes of *al* to the caudal edge of the lower mandible, where it ends with the superficial folded aponeurosis *ad* (Figs. 1a, 1b); the deep and shorter triangular portion begins at the lateral occipital bone with aponeurosis *ao*.

DISCUSSION

First of all, it should be noted that the long and thin beak of the murre and guillemots is well suited for underwater hunting of fish and large objects of zooplankton. At the same time, the elongated and narrow jaws allow these birds to grasp small objects under water unhindered (e.g., crustaceans), without pushing them out of the mouth with a jet of water. This effect had previously been discussed for loons (Korzun and Dzerzhinsky, 1975), which are not capable of active sucking of a suitable portion of water by spreading the lower mandible (Korzun, 1975).

In the early Charadriiformes, which collect small soft food, the inner feathery structure of the dorsal adductors (located behind the eye) was formed in the conditions of other motions and exertions, hence it formed completely differently and include more interspersed counter muscle "feathers," in particular, a developed caudal part of the deep portion, although it had no contact of the superficial portion with the postorbital projection of the skull (Yudin, 1965). As descendants of these collectors, the auks deftly grasp fast and small objects (that are not larger than the head of the hunter) in a more or less viscous medium. As a result, a significant transformation of the adductor layout occurred in the direction of their strengthening and a certain simplification. The proximity of the auks

with skuas (Yudin, 1965; Paton et al., 2003; Ericson et al., 2003; Baker et al., 2007; Mayr, 2011) is confirmed by the similarity of the structure of the jaw muscles. In particular, in the species studied, the caudal part of the deep portion of the external adductor is similar to the medial part, as its main initial aponeurosis *amq'* extends not from the quadrate bone but from the zygomatic skull process, i.e., farther from the jaw joint, which increases the efficiency of its efforts. This transition of the aponeurosis from the quadrate bone to the skull is characteristic of the skua.

The jaw musculature of the great crested grebe (*Podiceps cristatus*) described and depicted by Korzun (1980) can be considered as an example of an efficient structure of the external adductor in a similar underwater hunter. In this bird, the external adductor is divided very simply (Fig. 5). The two counter "feathers" located "head-to-toe" (*Aem* and *Aer*) are supplemented by the portion of *Aes* that covers the zone of meeting of their bases, whereas *Aec* is almost absent.

In the murre, some particular aspects of similarity with this scheme can be observed. First of all, there is the strengthening of the connection of *Aes* with the postorbital projection by aponeurosis *apo* (i), probably just for the sake of strengthening the dorsal adductors, but with the inevitable effect of a rise in the share of adduction in the muscular strength produced. Secondly, there is the functional connection of the external layer of *Aem* fibers to the zygomatic part of *Aes* (ii), which possibly strengthens the share of retraction. Finally, there is the growth of the share of *Aec*, which starts at the quadrate bone and simulates the rear adductor (iii).

(i) In our objects of study, the superficial portion is connected with the postorbital projection; in the murre, it is linked through the aponeurosis *apo*. In the skua, the superficial portion is not connected with the postorbital projection, it begins only at the zygomatic process of the skull with the aponeurosis *ams*.

(ii) After removing the skin, the medial portion of the external adductor appears to be relatively larger in the thick-billed murre. The skua lacks the end aponeurosis *alm*. Its superficial portion is extensive and is distinctly separated from the medial portion as in the black guillemot. The murre, on the contrary, have a tendency to merge these portions and exchange aponeuroses, namely, to reduce *alm* in favor of aponeurosis *asp'*, which runs parallel to the zygomatic arch, which functionally transfers the fibers of the second (lateral) layer from the medial portion to the superficial one. This can be seen as a means of strengthening the horizontal component of the force of contraction of *Aem*, which is necessary for retraction (pressing to the prey).

(iii) The hypertrophy of the rear adductor, as in the thick-billed murre, is typical of all gulls, the muscles of which are depicted in the paper by Yudin (1965), including the terns and skimmer *Rhynchops nigra*. But in the royal tern *Sterna maxima* and the skimmer, the

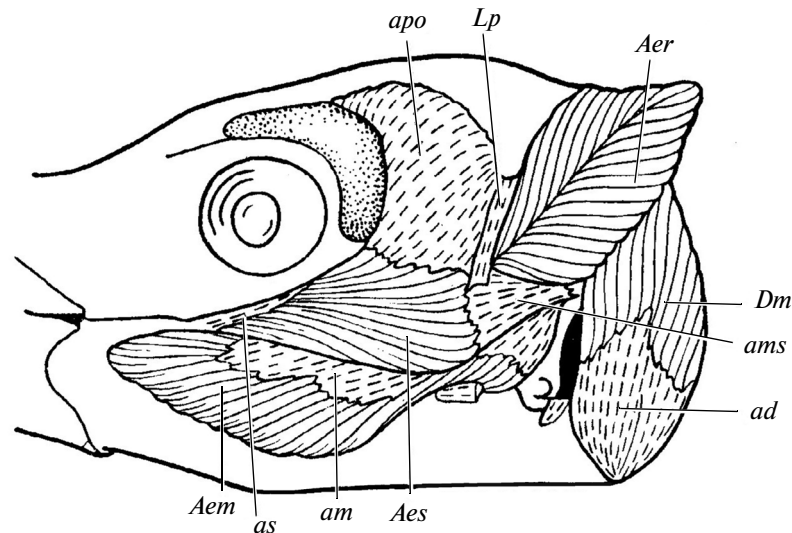


Fig. 5. Surface of the jaw muscles of the great crested grebe (*Podiceps cristatus*), lateral view (according to Korzun, 1980).

initial aponeurosis of the mysterious muscular portion, according Zusi (Zusi, 1962), is attached not near the upper edge of the orbital process of the quadrate bone, similarly to *apq* of the thick-billed murre, but on the ear projection, as a typical *amq*. It appears that in this place it is part of *Aec*. Based on the criterion of discontinuity proposed by Remane (Remane, 1952) for identification of a homology, we can see in the mysterious muscular feather of the thick-billed murre a product of differentiation of *Aec* likened to the rear adductor. Incidentally, in the black guillemot and the common murre, the aponeurosis *amq*' is much wider than in the thick-billed murre, as if it included a part that in the latter is represented in the form of *apq*.

As murre are so close to each other (Friesen et al., 1996; Watada et al., 1987), they are likely to be the result of a single "attempt" at occupying the niche of fish-eating birds, the natural capacity of which created for them bimodal conditions and thus provided a chance at food segregation for the two species. In the thick-billed murre, the strengthening of the jaws allows it to perform some processing of the catch, whereas in the common murre, the increased length of the beak is supposed to secure a tight grasp of the prey despite mechanical losses.

As for the idea of the isolated position of the guillemot, some of its generalized characteristics agree quite well with it.

(i) *Pss* extends in it to the lateral surface of the adductors between the interorbital projection and *Aer*, probably due to a certain weakness of *Aer*, its inclination, and the excessive size of the brain and the cranium, which is typical of smaller birds. Yudin (1965) considered these features observed by him in the sandpipers a primitive characteristic of Charadriiformes. In the skua, the superficial pseudotemporal muscle is attached at the back to the postorbital projection and

is located on the lateral surface of the skull, as in the guillemot, but it becomes apparent only after removing the rostral part of the deep portion, as in murre. A small skull in a relatively large bird (skua and murre) requires economical usage of space on the skull and leaves no place for *Pss*.

(ii) The connection of *Aes* with the postorbital projection is weakened, and the aponeurosis *apo* is not developed, which agrees well with the notion of the kin relation between the guillemots and the skua.

(iii) The medial portion of the external adductor has a typical two-layer structure without signs of the reorientation of the external layer. Convergence with the structure of the external adductor of the great crested grebe was manifested only in the transfer of the beginning of *amq* to the zygomatic process of the squamosal bone.

(iv) The lateral initial aponeurosis (*aip*) of the deep pseudotemporal muscle, which in the guillemot is significantly larger than in the murre, deserves attention. The lateral part *Psp*, which includes this aponeurosis, can belong to the superficial pseudotemporal muscle, for example, in Galliformes (Dzerzhinsky, 1980) and in Anseriformes (Dzerzhinsky, 1982). In the northern fulmar (*Fulmarus glacialis*), we observed variants with the intermediate position of the initial aponeurosis corresponding to *aip*, in which it was connected with the skull similarly to aponeurosis *ai*. The notion of the initial unity of the pseudotemporal muscle (Dzerzhinsky and Yudin, 1979) makes it possible for the starting point of this muscle strand to leap from the skull wall to the quadrate bone.

The functional effect of this leap is understandable: as the final effort of *Psp* always passes through the quadrate–skull joint (Dzerzhinsky, 1972), as a result of the leap, the degree of its inclination increases, like

the retraction component of its force, which presses the maxilla to the prey. The fundamental duality of *Psp* was found earlier by us in some storks (Ciconiidae). This allows us to consider the lateral part of *Psp* as a means of compensation of the mechanical loss of the maxilla, which appears when the jaws are extended. It must be taken into account that since the lever of the upper mandible is shorter than that of the lower, the stretching of the beak at a certain length elongates the maxilla more than it does the lower mandible.

Thus, the black guillemot demonstrates an intermediate state of transition between the portions. In the guillemot, the additional superficial strand *Psp*, which supposedly passed from *Pss*, is manifested more distinctly than in the murre, judging by the size of the aponeurosis *aip*, which is large, as in the skua.

CONCLUSIONS

The guillemot ancestors, primitive Charadriiformes, had a more complex composition of the external adductor, which in the guillemots and murre underwrote simplification in the course of evolution and became similar to the variant characteristic of the great crested grebe. Their closer predecessors were, undoubtedly, short-billed collectors of invertebrates; in the process of evolution, adaptation went on to the consumption of larger and more evasive prey. For the guillemot, a representative of an independent evolutionary line, these requirements were milder owing to the benthic lifestyle of its main food objects.

The long and thin beak of murre and guillemot suits well to the underwater hunting of fish and objects of large zooplankton. The elongated and narrow jaws allow these birds to capture small crustaceans without difficulty. The jaws of the murre and guillemots are adapted to catching fish, on the one hand (the external adductor and superficial pseudotemporal muscles are strongly developed, as is the depressor, which allows the bird to open the mouth abruptly), and to catching crustaceans, on the other (elongation of jaws and decrease in the water resistance). Higher specialization of the murre is associated with the greater proportion of fish in its diet, including relatively large fish, and with the preservation of the plankton component.

Independent development of adaptations to such a way of procuring food in the guillemot and murre and, at the same time, preservation of some similarities associated, first of all, with the mechanics of movement of the jaws is confirmed by the morphological analysis of the jaw musculature.

ACKNOWLEDGMENTS

The authors are deeply grateful to A.A. Lisovskii and Ya.A. Red'kin for help in obtaining the skeletal material and processing it, to S.V. Ogurtsov and V.V. Shakhparonov for help in processing the quanti-

tative data on the skull, and to K.B. Gerasimov for constructive discussion and important notes.

Lettering in the figures

(*Aec*) The Caudal part of the deep portion of the external adductor of the lower mandible; (*Aem*) the medial portion of the external adductor; (*Aer*) the rostral part of its deep portion; (*Aes*) the superficial portion of the external adductor; (*Ap*) rear adductor; (*Bm*) gill-maxillary muscle (branchiomandibularis); (*Cuc*) the head trapeziform muscle (m. cucullaris capitis); (*Dm*) depressor of the lower mandible; (*Lje*) external joint ligament (lig. jugomandibulare externum); (*Lji*) inner joint ligament (lig. jugomandibulare internum); (*Lom*) occipital-maxillary ligament (lig. occipitomandibulare); (*Lp*) postorbital ligament (lig. postorbitale); (*Lz*) zygomatic ligament (lig. zygomaticum); (*Myh*) sublingual maxillary muscle (m. mylohyoideus); (*Nar*) slitlike ending of the bony nostril; (*Pdl*) dorsolateral portion of the pterygoid muscle; (*Pdm*) its dorsomedial portion; (*Pl*) palatine bone; (*Ppt*) protractor muscle of the pterygoid bone; (*Pq*) protractor of the quadrate bone; (*Pvl*) ventrolateral portion of the pterygoid muscle; (*Pvm*) ventromedial portion of the pterygoid muscle; (*Pp*) postorbital projection of the skull; (*Psp*) deep pseudotemporal muscle; (*Pss*) superficial pseudotemporal muscle; (*Pt*) pterygoid bone; (*Q*) quadrate bone; (*Seh*) falcate sublingual muscle (m. serpihyoideus); (*ac, aca, ace, aci, ad, adi, ado, ae, ai, aip, al1, al2, ali, alm1, alm2, alo, alo', alo'', alt, am, amp, amq', amr, ams, ao, api, apm, apo, app1, app2, apr, apq, aps, aps1, aps2, aq, ar, asa, asp, asp', avi, avi', avi'', avo*) muscular aponeuroses.

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Translated by N. Smolina