The adaptive significance of local variations in the bill and jaw anatomy of North European Red-necked Grebes *Podiceps grisegena*

JON FJELDSÅ

FJELDSÅ, J. 1982: *The adaptive significance of local variations in the bill and jaw anatomy of North European Red-necked Grebes* Podiceps grisegena. — Ornis Fennica 59:84—98.

Red-necked Grebes from the northernmost breeding populations in Finland and Russia develop a long and slender bill. This trend, and also the large size of East Siberian and Nearctic Red-necked Grebes, might be associated with a change in the diet from invertebrates to fish in areas where the piscivorous Great Crested Grebe is missing. A sample of 87 Red-necked Grebes from a Danish wintering area comprised both South Scandinavian and slender-billed northern types. These were studied in order to discover to what extent the morphological and anatomical variation affects the diet.

The slender-billed Red-necked Grebes converge with Great Crested Grebes in the ability to open the bill rapidly and keep a strong grip on the prey without sliding of the mandible. Both adaptations may be valuable for catching fish. Study of the stomach contents showed that the Red-necked Grebes of South Scandinavian type fed mainly on annelids, gleaned from plants and picked up from the bottom, while individuals of the northern type specialized on squids and fish.

Although this does not prove anything, it provides support for the assumption that the morphological variation was caused by selection due to the presence or absence of Great Crested Grebes.

Jon Fjeldså, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.

The Red-necked Grebe *Podiceps grisegena* has two distinct subspecies (Storer 1979), the West Palaearctic *grisegena* and the Nearctic and East Siberian *holboellii*, the latter being rather pale and similar in size to the Great Crested Grebe *Podiceps cristatus*. Birds from Balchash (*"balchaschensis"*) are described as rather long-winged. All the specimens I have seen from this area are, however, within the *grisegena* range, and hardly qualify for taxonomic recognition. Similarly, the name *schiøleri*, proposed by Hortling (1929) for the rather big Finnish birds, was later synonymized. However, although there is considerable overlap with the other European birds, my data (Fjeldså 1982) confirm that there is a clinical change in this part of the range. As we move from southwestern Scandinavia to near the northern distribution limit of the species (inland areas from Kuopio to Finnish Lapland, Kola, Archangelsk, Dvina) the mean wing length increases by 1.5 % and the tarsus by 2.5 %, while the bill increases in length by as much as 11 % (Fig. 1) and becomes more slender, its shape approaching that of the Great Crested Grebe.

The interpretation of this trend will be the objective of this study.

A possible interpretation and how to test it

The morphological change in northern Red-necked Grebes may reflect adaptations to climate or to habitat gradients. However, according to general ecogeographical rule, adaptations to a colder climate should give smaller relative change in bill length than in wing length as we move north. Further, the summer temperatures of inland areas change little with latitude, and the wintering areas of the different Red-necked Grebe populations (Danish waters and according to Folkestad 1978 northwest Norway) have similar temperatures. Finally, *holboellii* shows no variation from the subarctic zone, with its bleak lakes, to the warm climate and rich lakes of the Canadian forest/prairie ecotones. Thus, considering the species as a whole, the geographical variation does not follow the climate or lake type zones.

It might be that the large size of the Red-necked Grebes in North America is due to the lack of Great Crested Grebes (compare the diet of *cristatus*, e.g. in Cramp & Simmons 1977, and *holboellii*, e.g. in Palmer et al. 1962). The smaller bill dimensions in the East Siberian than in the Nearctic *holboellii* (Fig. 1) agrees with the fact that the former has some contact with Great Crested Grebes on migration and in winter. The size variation of Finnish Red-necked Grebes could also be explained by the very sparse breeding of Great Crested Grebes outside the southern and western coastal zone. Population fluctuations (Thomasson 1953), gene flow contact through the European populations and some interspecific contact in all European winter quarters might explain the moderate amplitude of the geographical variation of the European Red-necked Grebes. Altogether, the variation in the species coincides well with what we could expect, if the variation was due to interspecific competition. More distribution and biometric data from North Russia would be desirable to reinforce the

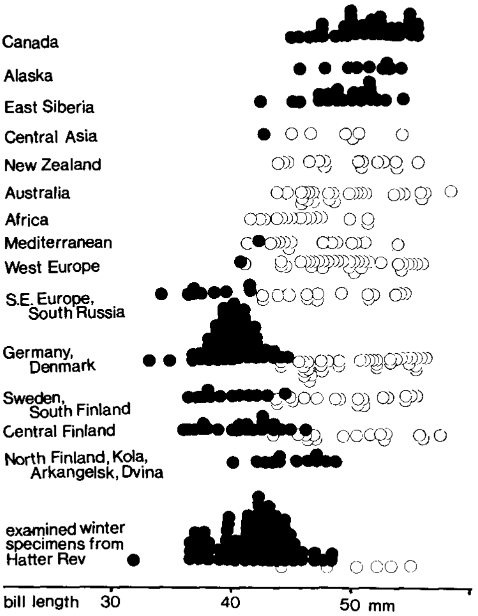


FIG. 1. Bill lengths of Red-necked (dots) and Great Crested Grebes (open circles) from different populations, measured on specimens in breeding plumage in the Zoological Museums of the Universities of Copenhagen, Oslo and Helsinki; the Swedish Museum of Natural History, Stockholm; the American Museum of Natural History, New York; the Australian Museum, Sidney, and the museum of CSIRO's Wildlife Research, Canberra. Bottom: bill lengths of the grebes collected in Danish winter quarters and used in this study.

documentation. Nevertheless, it appears to be a reasonable working hypothesis that Red-necked Grebes evolve morphological adaptations which permit them to live like Great Crested Grebes in areas where this species is missing. Alternatively, we may suppose that the two were originally allopatric ecological counterparts, and that the Red-necked Grebe managed to invade the range of the Great Crested Grebe by means of "character displacement", evolving a smaller size and smaller bill suited for taking invertebrate prey (for diet in the breeding areas, see Madsen 1957, Onno 1958, Markuze 1965).

It is pertinent to test whether the morphological changes affect the birds' ecology. This could be established by studying whether Red-necked Grebes change their ecology as we pass north through Finland. Unfortunately, though, a documented ecotope change would be insufficient as evidence, as it could have three or more causes: It could be due to the change in morphology, but it could as well reflect changes in the habitat and food resources, or changes in resource accessibility due to the lack, in the north, of interference competition from Great Crested Grebes (cf. Berndt & Drenckhahn 1974). The data might consequently be hard to interpret.

It may be safer to make the study in a common wintering area, where the interference competition is slight, and where all the birds use the same food supply.

The opportunity to make such a study arose in January 1979, when 400—500 Red-necked Grebes were killed by an oil-spill on Hatter Rev (55°55′N, 08°50′E) in Danish coastal waters (Larsen 1979). These birds can all be assumed to have fed in the same macrohabitat. What makes the study of the birds from these important winter quarters for Red-necked Grebes particularly interesting is the fact that they have very variable bills (Fig. 1), which suggests that birds of both North Finnish/North Russian and South Scandinavian provenience are represented. Altogether 87 Red-necked and six Great Crested Grebes were collected after the oil-spill by the Danish Game Research Station, Kalø, and sent to the Zoological Museum, University of Copenhagen.

Anatomical studies

Methods. In methods and terminology, the anatomical study follows that of Fjeldså (1981) on Peruvian Grebes.

The jaws and jaw muscles of one Great Crested and six Red-necked Grebes (including two of the most slender-billed) from Hatter Rev were dissected under a 10.5—67.5 × zoom Kyowa dissecting microscope. In addition an examination was made on the sculls of 26 Great Crested and 19 Red-necked Grebes (including *holboellii*). Distances from articulations to insertion points of muscles were measured with caliper rulers, and the "power arms" calculated by the appropriate trigonometric functions. The potential muscle force is determined from the number of fibres rather than the muscle mass (Bock 1974). To obtain an index of fibre number, I calculated the physiological cross section of the muscles as insertion area times the sine of the insertion angle. Since various parts of the muscle may have different insertion angles, the total cross section was calculated, section by section. This was done at either end of each muscle, and the mean of the two values was used. For pennate fibre arrangements, the cross section value. The potential speed of contraction pinnation angle to give a functionally relevant value. The potential speed of contraction is judged from the fibre lengths. Some cardboard models, in 4 × scale, were used to determine the effects of coupling ligaments and changes in action angles of muscles as the bones change position. Lever calculation was used to determine muscle torques, while the interaction of muscles was studied by constructing freebody diagrams (Bock 1974), elaborated for non-gravity and static situations, and disregarding the load against which the muscles act.

Due to the complexity of the superficial and deep muscles and space considerations, few aspects can be properly depicted. Fig. 2a shows superficial aspects, Fig. 2b areas of fleshy attachments of muscles, Fig. 2c the narrow (aponeurotic) attachments. Other aspects are shown in numerous illustrations in Bams (1956), Zusi & Storer (1969) and Fjeldså (1981) for *Podilymbus podiceps, Rollandia rolland* and *microptera, Podiceps occipitalis, taczanowskii* and *cristatus.*

Table 1 shows some of the functionally most important parameters and their correlation with bill size parameters. The largeness of the bill is expressed by the index LBI: bill length × π × bill depth × bill width. The best way to tell northern Red-necked Grebes in the Hatter Rev data apart from southern is to record how long and relatively thin the bill is. This is expressed as a "slender bill index" (SBI), viz. bill length times the ratio of bill length to the sum of bill depth and bill width.

TABLE 1. Some important distances (mm) and physiological cross section values (Ø, mm²) of jaw muscles of one Great Crested and six Red-necked Grebes. For the latter species, Spearman's rank correlation coefficients (r_S) are given in respect of the length, largeness (LBI) and slenderness (SBI) of the individual bills. For explanation of the bill indices, see the text p. 87.

	Range	*P. grisegena* (6)			*P. cristatus* (1)
		r_s with culmen	r_s with LBI	r_s with SBI	
Culmen	35.5—45.5	—	0.74	0.56	50.5
Distal symphysis of mandibular rami	7.8—11.3	0.72	0.74	0.52	10.5
M. depressor mand. Ø	20.9—30.8	0.86	0.86	*0.89*	32
power arm	5—6.3	0.86	0.83	*1.00*	7.1
M. add. mand. ext. III Ø	84—109	0.89	0.81	0.73	120
power arm	6.3—7.2	0.83	0.83	0.73	7.6
M. pseudo-temp. superfic. Ø	42—50	0.72	0.86	0.70	60
power arm	6—7	0.77	0.52	0.57	7.6
M. pseudo-temp. prof. Ø	8.5—10	0.73	0.76	0.52	11
power arm	7.4—8.2	0.81	0.70	0.43	9.8
M. protract. quadr. Ø	17—28	0.70	0.74	*0.94*	25
power arm	5.6—5.9	0.43	0.46	0.52	6.1

Opening of the bill. Opening of the bill is due to depression of the lower mandible, which may be speeded up by an increase in the fibre lengths and power arm of the involved muscle and by supplementary lifting of the upper mandible.

Musculus depressor mandibulae runs from the deltoid fossa of the skull with the surrounding crests (with apo. I), its long (rapid) fibres narrowly inserted on the posterior fossa of the lower mandible via apo. II and one small unnamed aponeurosis. Spanning two joints, it has a complicated effect. If the action line is steeper than the quadrate axis, it swings the quadrate forward, which causes a coupling between mandibular depression and protrusion of the palate bones and upper mandible. This effect is reinforced by the coupling action of the postorbital ligament.

There is a slight general increase with increasing bill size (Table 1). More important, though, is the relative increase in power arm due to a longer, more backwards directed, retroarticular process in specimens with high SBI (Table 1). These birds hereby approach *cristatus.* The change in action angle gives a basis for the protrusion and lifting of the upper mandible mentioned above, and acceleration of the gaping.

Adduction of the bill. Adduction is due to several muscles. Some are "two-joint" adductors, spanning both the cranio-quadratic and quadrato-mandibular joints, which complicates the calculation of their effects. Others are attached directly to the quadrate, and are "one-joint" muscles, which may control the movements of this bone. Sliding of the quadrate will be transferred through the palate bones to the upper mandible.

Musculus adductor mandibulae externus forms a powerful, multipennate complex, which may be divided into three main parts.

Part 1 is a superficial fan of long (rapid) fibres arising from the membrane which passes in front of the ear, with some fibres also arising from apo. III and the top of apo. VIII and XII. It is inserted narrowly via the big apo. IX on the surangular/dentary junction of the mandible edge. The mean vector at the insertion point parallels the jaw when the bill is slightly open. Thus, its main effect must be pulling the mandible back and rotating the quadrate backwards, which indirectly means that the upper mandible is depressed. This suggests that the muscle is most efficient in moving big prey items back into the throat by quick backward jerks.

The muscle was strongest in the largest-billed birds, but this involves no drastic functional variation.

Part 2 originates via apo. VIII and XII on the zygomatic process, with some fleshy attachments from the rostral demarcation of the temporal fossa. It is attached with a wide, fleshy attachment on the outside of the surangular bone and via apo. VII along its upper edge. It has a slightly more adductive effect than part 1, although with backward sliding of the quadrate. The long fibres give high speed in the final phase of adduction, when the action angle is optimal.

Some increase, particularly of the part attached in the temporal fossa, was recorded in long-billed individuals.

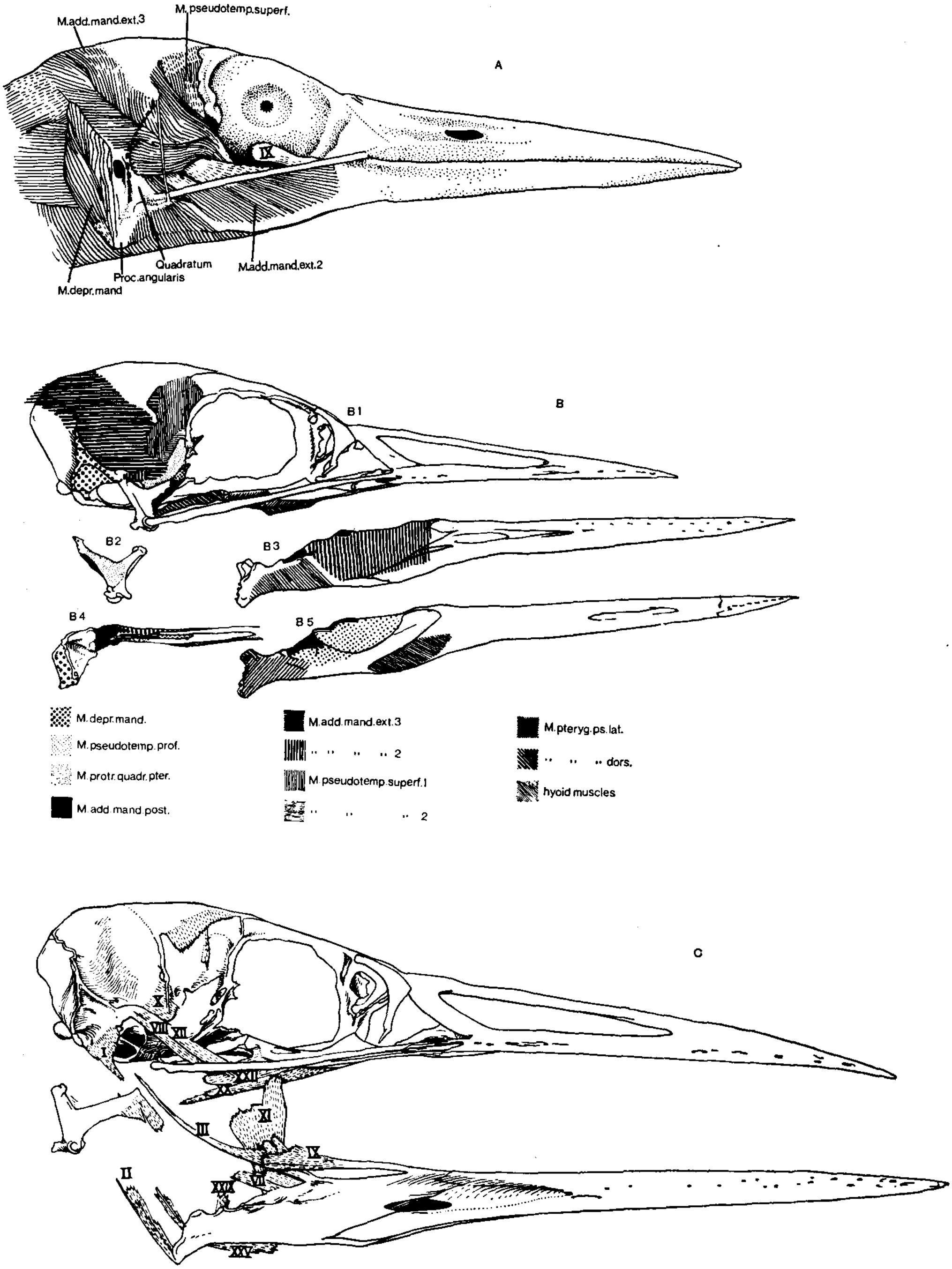
Part 3 is the main adductor, a big, pennate muscle whose fleshy origin occupies the whole temporal fossa of the skull with the surrounding crests. Many fibres originate from the outside of the complexus muscle, via apo. X from the rostral demarcation of the temporal fossa and from the posterior part of the orbit, above the fleshy origin of *M. pseudotemp. superfic.* A few fibres also arise from apo. VIII and XII and are inserted on apo. VIII. The central apo. VII is inserted as a strong tendon on the coroid process of the surangular edge.

The muscle gives more efficient adduction than part 2, although with backward sliding of the quadrate. The high number of short fibres suggests that force production rather than angular acceleration is the main function.

The variation in size is modest (Table 1).

Musculus pseudotemporalis superficialis, part 1, has a fleshy origin on the posterior wall of the orbit and is narrowly inserted via the big, superficial apo. XI and a stout tendon inside the previous muscle on the medial face of the mandible. The smaller part 2 lies still deeper and is inserted anterior to part 1. The high number of short fibres suggests maintenance of isotonic grip as the main function,

FIG. 2. Jaw muscles of grebes. — A. Red-necked Grebe, superficial jaw muscles; *M. add. mand. ext.* 1, which runs from the dashed line to the aponeurosis IX, is removed. — B. Red-necked Grebe, fleshy attachment areas of the jaw muscles on the skull (B 1), inside of quadrate (B 2), and outside (B 3), upper edge (B 4) and inside (B 5) of lower mandible. — C. Great Crested Grebe, narrow (aponeurotic) muscle attachments.


M.add.mand.ext.3
M. pseudotemp.superf.
A
IX
Quadratum
M.add.mand.ext.2
Proc.angularis
M.depr.mand
B1
B
B2
B3
B4
B5
M.depr.mand.
M.pseudotemp.prof.
M.protr.quadr.pter.
M.add.mand.post.
M.add.mand.ext.3
" " " " 2
M.pseudotemp.superf.1
" " " 2
M.pteryg.ps.lat.
" " " dors.
hyoid muscles
C
X
VIII
XII
I
XXII
XX
XI
III
IX
II
XXIX
VII
XXV

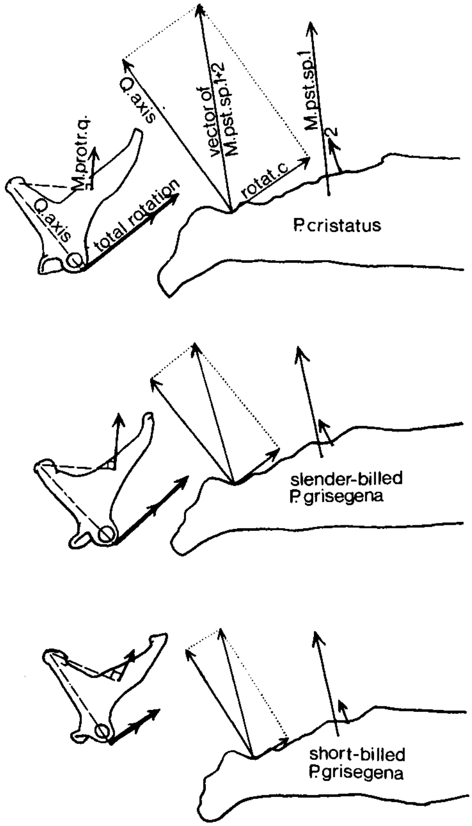


FIG. 3. The combined effect of two muscles which may counteract backward sliding of the lower mandible caused by the main adductor, *Musculus adductor mandibulae externus* part 3, in three dissected grebes. In the free-body diagrams of the rear end of the lower mandible are shown the forces exerted by *Musculus pseudotemporalis superficialis* parts 1 and 2 *(M. pst. sp.* 1, 2) and their combined vector at the quadrato-mandibular joint. This vector may be separated into a component which follows the quadrate axis *(Q axis)* and, perpendicular to this, a rotating component *(rotat c.)*. In the vector diagrams of the quadrate bone is shown the force exerted by *Musculus protractor quadrati (m. protr. q.)* and the calculated total forward-rotation force due to this muscle and *M. pst. sp.* 1, 2.

although the muscle may, with its short power arm, also give high angular acceleration. The vector at the quadrato-mandibular joint is steeper than the quadrate axis (Fig. 3), which means that this two-joint muscle rotates the quadrate forwards, giving slight protrusion of the upper mandible in the early adduction, or counteracting some backwards sliding due to the external adductors.

The Great Crested Grebe shows elongation of the skull due to an increase of the area serving as attachment for the pseudotemporalis muscles. The central aponeurosis of the muscle, from a ridge on the skull, also increases, and the power arm as well. This means considerable acceleration of the initial phase of adduction and stabilizing of the final phase, since the effect on the quadrate, according to a free-body diagram, balances that of *M. add. mand. ext. 3.*

The variation in this muscle in the Red-necked Grebes was very slight. *Holboellii* also showed only slight convergence towards the Great Crested Grebe state.

Muscles stabilizing the quadrate. Musculus adductor mandibulae posterior has a fleshy attachment on the inner two thirds of the orbital process of the quadrate, and its short fibres are inserted on the dorsomedial surface of the lower mandible, right ahead of the quadrato-mandibular joint. A one-joint muscle, it may oppose backward sliding of the quadrate due to the action of the external adductors, thus both stabilizing and reinforcing an isotonic grip. There was no obvious variation.

Musculus pseudotemporalis profundus runs with a central apo. XVIII from the distal part of the orbital process of the quadrate to a wide fleshy attachment on the medial fossa of the mandible. Being a long-fibred one-joint muscle, it secures stable and quick adduction about the quadrato-mandibular joint, even in the early phase of the adduction, and counteracts, due to its action angle, some protrusion of the quadrate caused by *M. pseudotemp. superfic.* The bulk and power arm (length of orbital process) did not vary clearly with the bill parameters in European Red-necked Grebes, but *holboellii* and above all Great Crested Grebes showed an increased power arm.

Musculus protractor quadrati & pterygoidei has a wide, fleshy attachment to the skull and fleshy and aponeurotic attachments (apo.'s XIII, XV, XVII) to the medial surface of the quadrate and posterior end of the pterygoid. The main function may be to counteract sliding of the quadrate due to *M. add. mand. ext.* 3. In addition it may protract the quadrate, which has a kinetic effect, and by an inward pull on the quadrate it may inhibit the quadrato-mandibular articulation and permit independent movements of the mandibles.

In Red-necked Grebes, the attachment area expands upwards and forwards as SBI increases (Table 1). In *holboellii* it reaches an extreme development along the entire anterior demarcation of *M. pseudotemp. superfic.* This is not seen in any Great Crested Grebes.

Kinesis. Kinesis involves the movement of the upper mandible about the frontonasal hinge, due both to some of the muscles mentioned above and to the palate muscles.

Musculus pterygoideus, pars lateralis, dorsolateral branch, has a wide, fleshy attachment to the dorsolateral surface of the palatines and further uses the big apo. XXII along the posterolateral edge of the bone. It is inserted via the medial and posteromedial faces of the articular. *Musculus pterygoideus pars dorsalis,* lateral branch, has a fleshy origin on the lateral surface and adjacent ventral edge of the pterygoid, and via apo. XXIX is inserted on the crest just ahead of the articulation of the mandible. These two muscles are the most efficient in retracting the palate, thereby rotating the upper mandible about the frontonasal hinge, so that it is lowered. This supplements the big *M. add. mand. ext.* 3 in exerting a strong grip, and may give a backward push to a big prey item during swallowing.

The power arm (height of upper mandible at frontonasal hinge) is long in relation to the bill length in most Red-necked Grebes, but is reduced in slender-billed birds (including Great Crested Grebes). This variation appears to be compensated for, in slender-billed *grisegena,* by variation in muscle size.

Inframandibular bending. Musculus pterygoideus, pars lateralis, ventromedial branch, originates in the ventral cavity of the palatine and via the big apo. XX and XXII. *Musculus pterygoideus, pars dorsalis,* median branch, originates from the ventral and ventromedian surface of the pterygoid. Both are inserted via the complex apo. XXV on the medial crest of the articular. The muscles supplement those mentioned above in depressing the upper mandible. In addition they pull the medial crest of the articular forwards, thereby rotating the bone about the quadrato-mandibular articulation, so that the mandibles bulge in the middle, at the pliable inframandibular "hinge". This allows a big prey item to pass between the mandibular rami, and pushes down its mass by pressure from the upper mandible.

There appears to be some increase in fibre numbers in the muscles in long-billed Red-necked Grebes, although the estimate of the physiological cross section was too inaccurate to determine whether this is more closely associated with SBI than with the general bill size. The power arm (inward bend of medial articular crest) showed no correlation with bill length or SBI, while a change in the shape of the bill tip and a relative shortening of the symphysis in slender-billed birds may imply a reduced resistance to bending (Table 1). In Great Crested Grebes, on the other hand, the elongation of the skull involves a relative increase of the part of the jaw which lies behind the hinge. This increases the potential maximum spread of the mandibular rami. Expansion of the foramina on the inframandibular hinge and a shortening of the symphysis at the bill tip reduce the resistance to bending. On the other hand, the long "arm" from the mandible joint to the tip of the prearticular wing (the hinge) in Great Crested Grebes means that torques given by the pterygoid muscles at the medial articular crest result in reduced torques at the hinge. Further, the short power arm for kinesis (low height of the upper mandible at the base) in relation to bill length means that the bill tip cannot exert strong pressure on the prey. Since reliable measurements of the resistance to bending of the bones can be obtained only on fresh birds, there are too many points of uncertainty for calculating whether species or populations differ regarding the ability to swallow large-sized animals.

Possible functional significance of the variation. Red-necked Grebes have strong jaw muscles, which in many respects resemble the unspecialized and probably primitive states shown by Golden Grebes *Rollandia* spp. (Fjeldså 1981). However, they approach their congeners *Podiceps occipitalis* and *taczanowskii* (also described in Fjeldså 1981) by showing some adaptations for foliage-gleaning, viz. moderate divergence of the insertion angles of the adductors and a relatively small pseudotemporal muscle with a short power arm. This means that the bird cannot fully contract the mandibular adductors without backward sliding of the mandible. Although Red-necked Grebes are certainly not so specialized as the two abovementioned congeners, the conditional phrases are certainly narrower than in *Rollandia.*

Most of the individual variation in Jaws and muscles may represent direct adjustments of the potential force production to variation in general size. This does not involve true functional changes.

Two trends were associated with SBI rather than the overall size, and may involve a change in mechanical properties. Slender-billed birds converge with Great Crested Grebes in showing an increase in the mandibular depressor and its power arm, which may speed up the depression of the lower mandible and couple this movement with a lifting of the upper mandible. This specialization in relation to what we see in most grebes may be important during rapid pursuit of fish, as the bird can maintain its streamlining, keeping the bill closed, till immediately before it can grasp its prey. Secondly, the quadrate protractor expands, which means increased ability to control the position of the quadrate. In normal (stout-billed) Red-necked Grebes, the forward rotation of the quadrate by the joint action of the superficial pseudotemporalis muscle and the quadrate protractor can do little to counteract the backward rotation due to full contraction of the powerful *M. add. mand. ext.* 3.

Great Crested Grebes show an adaptation for maintaining a stable grip even when this muscle is fully contracted, since they have a greater superficial pseudotemporal muscle. This is not the case in slender-billed Red-necked Grebes, but these instead show apparent paradaptation, an increase in the quadrate protractor. Fig. 3 shows that the combined forward torque of the superficial pseudotemporal muscle and quadrate protractor on the quadrate bone is about equally strong in Great Crested and slender-billed Red-necked Grebes. What is really important is that this combined torque vector approximately equals the component of *M. add. mand. ext.* 3 which rotates the quadrate backwards. The net effects is, then, that the short-fibred adductors, involved in exerting an isometric grip, can exert maximum torques without sliding of the quadrate. Thus Great Crested and slender-billed Red-necked Grebes both manage, by different mechanisms, to maintain a stable and very strong grip.

This may be important when grasping a slippery fish. That this adaptation is associated with fish-eating is further indicated by the fact that a similar functional state has evolved, probably independently, in other grebes which take fairly big fish *(Rollandia, Aechmophorus occidentalis;* unfortunately I lack anatomical material on *Podiceps major).*

There are no obvious convergent adaptations between slender-billed Red-necked Grebes and Great Crested Grebes for swallowing big prey animals, apart from the fact that a long bill gives a potential increase in the spreading of the mandibular rami.

Food selection

Method. The stomach contents of the 87 Red-necked and the six Great Crested Grebes were examined under the microscope to identify the remains of the prey. The number of prey items was counted from resistant and characteristic parts, such as cleithra and otoliths of fish, eye-lenses of squids, and the mandibles of most annelids and arthropods. The state of decomposition of most of the prey items was unfortunately too far advanced to allow safe determination of their size, or the mass composition of the diet.

The numbers of prey items in the stomachs showed hyperboloid variation, because most of the stomachs of the oil-killed birds were strongly decomposed. For this reason, logarithmic values (log. $(N+1)$) should be used in the analysis.

Stomach contents of Red-necked Grebes. The prey comprised:

— Hydrozoa: 1 *Dynamena pumila* colony.

— Annelida: 381 *Nereis* spp., mainly small *N. diversicolor* and *pelagica,* but also 16 big *N. virens* with estimated total lengths of 25—40 cm, masses 25—60 g; 685 *Nephthys* sp., 10 *Glycera* sp.; 2510 polynoids, mostly *Lepidonotus squamatus;* 139 *Pectinaria koreni;* 2 *Hyaloecia* sp., 3 unidentified.

— Arthropoda: 139 *Idothea* sp.; 11 *Gammarus* sp.; 2 Mysidacea (undet.); 1 *Crangon* sp.; 1 *Mallophaga* (undet.); 4 *Coleoptera* (Scarabaeidae, Hydrophiliidae and Curculionidae undet.).

— Mollusca: 4 *Buccinum undatum;* 7 *Littorina littorea;* 1 *Gibbula* sp.; 105 of the rapid squid *Aloteuthis subulata* (mass about 5 g).

— Echinodermata: 1 *Holothuria apoda (Leptosynapta inhaerens?).*

— Pisces: 2 *Rutilus rutilus;* 39 *Gasterosteus aculeatus;* 2 *Spinachia spinachia;* 1 *Merlucius merlucius;* 3 *Pholis gunellus.*

Further, all the stomachs had a variable amount of complete and more or less disintegrated feathers and sand (probably ingested with annelids), and many stomachs also had some fragments of fresh or dead plants, pieces of plastic and other indigestible roughage.

As stated above, no attempt was made to calculate the mass composition of the diet, but squids probably predominated, followed by *Lepidonotus* and big *Nereis virens.*

This diet differs greatly from the winter diets described by Madsen (1957). This is possibly because he examined birds accidentally collected near coasts, and not birds from the typical Danish wintering habitats, which may be on distant offshore shallows, generally habitats with Scoters *Melanitta* sp. and Eider Ducks *Somateria mollissima.*

Habitat variation. Insofar as it is not due to differences in the stage of decomposition, great individual variation in stomach contents certainly reflects differences in habitat and individual habits. Before we analyse the significance of bill size, it is necessary to check whether morphologically different grebes systematically select different microhabitats.

Individuals of *Nereis pelagica* and *Nephthys* measuring 5—15 cm must seem very similar to a grebe in appearance, mode of swimming and the way in which they can be mandibulated. However, they select markedly different habitats. *Nereis pelagica* occurs in offshore areas with rocks, boulders and crevices, particularly places with *Fucus* or *Laminaria. Nephthys* inhabits offshore mud-bottoms. Some grebes had taken only *Nereis,* other numerous *Nephthys,* which suggests different feeding habitats. However, the ratio between the two prey types was not closely correlated with the grebe morphology (Spearman's rank correlation tests; ratio calculated for sub-samples of each six specimens in a series). If the birds were arranged according to the wing lengths, r_s was 0.02. Arrangement by bill length gave r_s 0.03; by bill depth r_s 0.20; by LBI r_s 0.18; by SBI r_s 0.28; all $P>0.10$). This does not indicate that morphologically different birds select different parts of the winter quarters.

Variation with grebe morphology. Rank correlation tests on the average log $(N+1)$ values for each six individuals in a series were done for all the regularly occurring prey species. Some grebes could not be used in the analysis because the head or bill was damaged.

Lightly armoured animals which mainly crawl on algae, rocks, etc. *(Idothea, Lepidonotus)* were negatively correlated with the bill length (r_s —0.62, $P<0.02$; r_s —0.69, $P<0.01$) and LBI (r_s —0.70; $P<0.01$; r_s —0.68, $P=0.01$) rather than with SBI (r_s —0.36, $P>0.05$; r_s —0.45, $P=0.05$). Still stronger negative correlations, with SBI as well were found for *Pectinaria,* whose sand tubes project only slightly above the bottom ooze (r_s —0.70, $P<0.01$; r_s —0.84, $P<0.01$; r_s —0.77, $P<0.01$). Annelids which often swim freely show slighter correlations with the morphology. However, *Nereis* with mandibles measuring less than 5 mm showed a slight negative correlation with the bill length (r_s —0.66, $P<$ 0.02). Maybe there is a tendency for large-billed grebes to eat a greater proportion of big *Nereis* (LBI r_s —0.52, $P<0.05$, but SBI r_s —0.40, $P>0.05$).

Rapid nekton was mainly taken by long-billed birds. In the case of *Alloteuthis,* there was a stronger correlation with the bill length (r_s —0.80, $P<0.01$) and LBI (r_s —0.84, $P<0.01$)

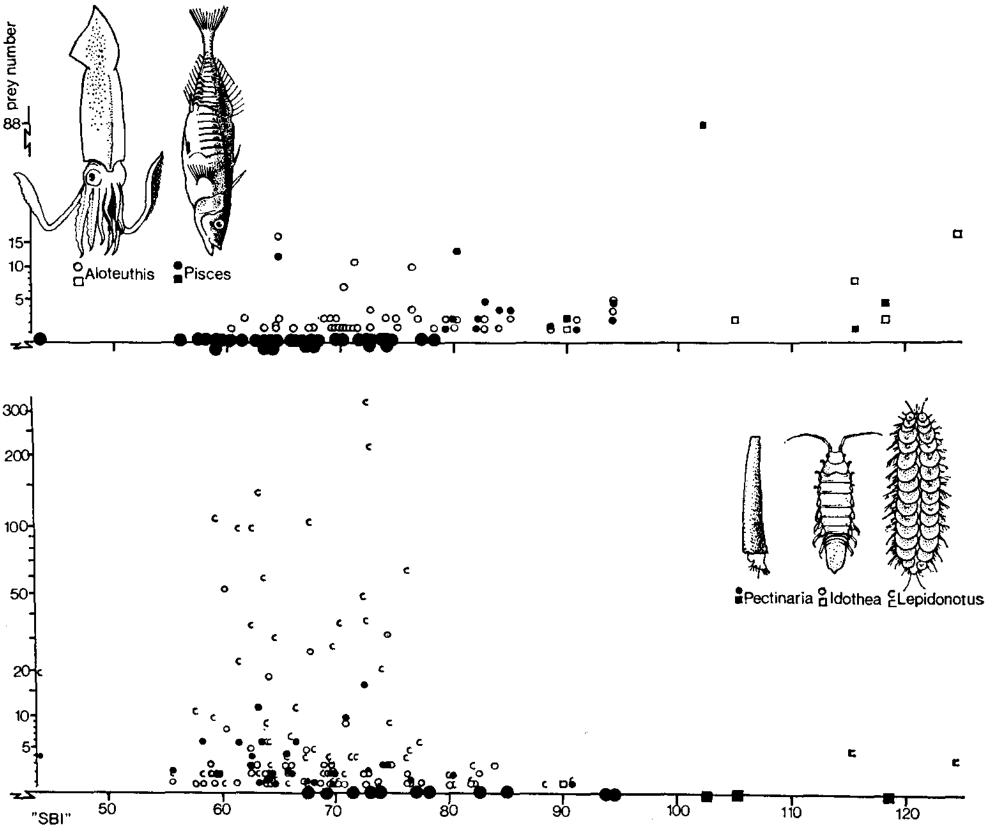


FIG. 4. Number of prey items (semilog. scale) in the grebe stomachs in relation to the "slender bill index" (SBI). The top diagram shows the numbers of the squid *Aloteuthis subulata* and fish, the bottom diagram the numbers of the worms *Pectinaria* and *Lepidonotus* and the crustacean *Idothea*. Large symbols mean that the stomach did not contain any of these prey types. Round symbols represent stomachs of Red-necked Grebes, square symbols stomachs of Great Crested Grebes.

than with SBI (r_s —0.68, $P=0.01$). Fishes were too poorly represented for a rank correlation test. One typical South Scandinavian bird had taken 11 *Gasterosteus*. If this bird is omitted, the 12 birds which had taken fish were among the 30 longest-billed birds or the 13 birds with the highest SBI (Fig. 4). According to one-sample runs tests, this gives $P=0.34$ and $P<0.02$, respectively, which suggests that fish-eating is associated with the long and slender bill type characteristic of North Finnish/North Russian birds.

No prey type showed significant correlations with the wing lengths or bill depths.

In conclusion, Red-necked Grebes of South Scandinavian types may mainly feed by foliage-gleaning and picking from the bottom, supplemented by capture of some squids and

TABLE 2. Similarity between diets of Red-necked and Great Crested Grebes from the Hatter Rev winter quarters (calculated from the percentage occurrence of *Idothea, Lepidonotus, Nereis, Nephthys, Glycera, Pectinaria,* Gastropoda, *Aloteuthis* and fish in series of six stomachs). The Red-necked Grebes are arranged in order of increasing wing-length, bill-length, LBI and SBI. The two samples with the highest SBI correspond to the North Finnish/Russian breeding population of Red-necked Grebes.

Red-necked Grebes arranged by	Indices of overlap with Great Crested Grebes												
wing-length	0.101	0.089	0.165	0.161	0.241	0.189	0.202	0.281	0.270	0.192	0.090	0.181	0.419
bill-length	0.092	0.127	0.096	0.109	0.135	0.408	0.102	0.100	0.181	0.096	0.190	0.227	0.492
LBI	0.091	0.097	0.122	0.120	0.197	0.085	0.297	0.166	0.231	0.119	0.291	0.102	0.203
SBI	0.005	0.098	0.101	0.105	0.098	0.126	0.184	0.167	0.091	0.135	0.165	0.596	0.630

maybe some large annelids by the largest-billed birds. The slender-billed northern birds specialize in eating squids and fish.

Stomach contents of Great Crested Grebes. The stomachs of the six Great Crested Grebes contained, besides the usual feather mush and some plant debris, remains of 1 *Idothea,* 9 *Lepidonotus,* 10 small and one large *Nereis,* 1 *Nephthys,* 2 *Glycera,* 29 *Aloteuthis,* 93 *Gasterosteus,* 1 *Spinachia,* 1 *Micromesistius poutassou.* Squids and fish clearly predominated by mass.

Diet similarity. The similarity of the diets of the Red-necked and Great Crested Grebes can be calculated as

$$C_2 = \frac{2 \sum_{i=1}^{s} x_1 \; y_1}{\sum_{i=1}^{s} x^2 + \sum_{i=1}^{s} y^2}$$

(Morisita 1959), where the two predators utilize each of the $i \ldots s$ resource states to the extents of x and y, respectively. Identical diets give the value 1.00.

Table 2 shows how the diet similarity between the grebe species increases with the wing length, bill length, LBI and SBI of the Red-necked Grebes. Since all the size parameters are partly connected, all the series show an increasing trend. However, the development of an extremely slender bill, evident in North Finnish/Russian Red-necked Grebes and 12—15 individuals in the present sample, is definitely the factor most clearly causing a shift in the diet of Red-necked Grebes towards that of the Great Crested Grebe.

Discussion

The anatomical approach suggests that the North Finnish/Russian Red-necked Grebe type converges with allopatric Great Crested Grebes in some functional properties of the feeding apparatus. The study of the feeding ecology shows that the morphological/anatomical characters characteristic of these northern Red-necked Grebes is just the kind of development which best secures a convergence in diet. The concordant results of the two approaches show that functional anatomy, largely neglected in contemporary European ornithology, may give a basis for ecological predictions, or at least be important for explaining ecological differences between species or populations.

Similarly, studies of the relation between the bill anatomy and the diet of Horned Grebes *Podiceps auritus* (Fjeldså 1973, reanalysed in Fjeldså 1982) provide evidence that what birds eat is, at least in part, determined by their anatomy/morphology. The presence of inherent "search images" for prey, or learning of the diet during feeding by the parents cannot be excluded as factors affecting the choice of food. The diet described here, in winter quarters with annelids and squids, can, however, hardly be due to learning during feeding by the parents. The individual variation in prey rather suggests that a substantial part of the development of food selection is steered by the anatomy, which excluded some prey animals, makes it inconvenient or uneconomic to feed on some and easy to feed on others. This might, by "trial and error", lead to specialization on those prey animals which give the highest yield/effort ratio (cf. theory of optimal feeding, see e.g. Krebs & Cowie 1976).

Morphology-related variations in diet could not be documented in grebes with an unpredictable food supply or a supply so sparse that the grebes need to eat every potential food type available (Fjeldså 1981, 1982 and unpublished results on Australian grebes). This is predicted by the theory of optimal feeding (Schoener 1971): Specialization on an optimal fraction of the food supply requires that it is easy to find enough food. If this is the case in the breeding habitats of the North Finnish/Russian Red-necked Grebes, we may postulate that these Red-necked Grebes will resemble Great Crested Grebes in their summer diet as well.

We cannot prove here that the geographical variation in Red-necked Grebes was caused by selection due to the presence or absence of Great Crested Grebes (character displacement/character release). However, previous writers (e.g., Onno 1958, Markuze 1965, Berndt & Drenkhahn 1974) have reported that the two species are well separated from each other ecologically, when breeding sympatrically. Our present results give reason to believe that they occur as ecological counterparts when allopatric, and further that the anatomical/morphological change shown in allopatry is precisely the change which best secures a switch to the diet of the Great Crested Grebe. Although this does not prove anything it certainly makes displacement a likely explanation of the variation.

There has been considerable scepticism recently regarding the validity of the theory of character displacement (see e.g. Grant 1972, Connell 1980). The evidence in favour of it may be discounted by arguing that if sufficiently many species are studied, some of the observations will happen to accord with the theory, even if the theory is wrong. This argument cannot, however, be used to reject the evidence found in grebes, since throughout the world, in every case of local contact between two closely allied grebe species, the variation is as predicted by the theory (Fjeldså 1982).

Acknowledgements. My best thanks are due to the Game Biology Station, Kalø, for providing the grebes on which this study was made. Mrs. Ursula Friis did the final typing of the manuscript, and Dr. Marc Ballan made the language corrections.

Selostus: Pohjois-Euroopan härkälintujen nokan ja leuan anatomian alueellisesta muuntelusta ja sen adaptiivisesta merkityksestä

Härkälinnun pohjoisimpien pesimäkantojen linnuilla Suomessa ja Venäjällä on pitkä ja kapea nokka. Tämä rakennepiirre, samoin kuin Itä-Siperian ja Etelä-Amerikan härkälintujen suuri koko, johtunee siitä, että laji on siirtynyt ruokavaliossaan selkärangattomista kaloihin niissä osissa asuinaluettaan, mistä silkkiuikku puuttuu. Kuvassa 1 on esitetty museonäytteistä härkälintujen (mustat ympyrät) ja silkkiuikkujen (avoimet ympyrät) nokan pituus eri osissa maapalloa. Tanskan talvehtimisalueilla tammikuussa 1979 öljytuhon uhreista kerätyt 87 härkälintua edustivat sekä Etelä-Skandinavian lyhytnokkaista että pohjoisempaa pitkänokkaista kantaa. Näistä yksilöistä tutkittiin, missä määrin rakenne-erot (ks. kuvia 2 ja 3) vaikuttavat ruokavalioon (kuva 4).

Anatomisten ominaisuuksiensa ansiosta pitkänokkaiset härkälinnut pystyvät silkkiuikun tavoin aukaisemaan nokkansa äkkiä ja pitämään saalista lujassa puristuksessa, mikä on epäilemättä eduksi kalanpyynnissä. Pitkänokkaiset yksilöt olivatkin mahanäytteiden perusteella erikoistuneet kalojen ja mustekalojen saalistukseen. Sen sijaan lyhytnokkaiset härkälinnut olivat syöneet etupäässä nivelmatoja pohjasta tai kasvillisuudesta. Tulokset osoittavat, että anatomiset ominaisuudet määräävät paljolti sen, mitä lintu käyttää ravinnokseen. Ne viittaavat myös siihen, että härkälintujen morfologian maantieteellinen muuntelu johtuisi luonnonvalinnan kautta silkkiuikun läsnäolosta tai puuttumisesta.

References

Bams, B. A. 1956: On the relation between the attachment of the jaw muscles and the surface of the skull in Podiceps cristatus L., with some notes on the properties of the head. — Proc. K. ned. Akad. Wet. Ser. C 59:82—101, 248—262.

Berndt, R. K. & D. Drenckhahn 1974: Vogelwelt Schleswig-Holsteins. Vol. 1. — Kiel.

Bock, W. J. 1974: The avian skeletomuscular system. — *In* D. S. Farner & W. B. King (eds.): Avian biology, Vol. IV: 119—257. New York.

Connell, J. H. 1980: Diversity and the coevolution of competitors, or the ghost of competition past. — Oikos 35:134—138.

Cramp, S. & K. E. L. Simmons 1977: Birds of the Western Palearctic. — Oxford.

Fjeldså, J. 1973: Feeding and habitat selection of the horned grebe, Podiceps auritus (Aves), in the breeding season. — Vidensk. Medd. Dansk Naturhist. Foren. 136: 57—95.

Fjeldså, J. 1981: Comparative ecology of Peruvian grebes. A study on the mechanisms of evolution of ecological isolation. — Vidensk. Medd. Dansk Naturhist. Foren. 144:125—246.

Fjeldså, J. 1982: Ecological character displacement and character release in grebes. — Ibis: in press.

Folkestad, A. O. 1978: Winter censuses and studies on the Red-necked Grebe Podiceps grisegena along the Norwegian coast. — Anser Suppl. No. 3:84—89.

Grant, P. R. 1972: Convergent and divergent character displacement. — Biol. J. Linn. Soc. 4:39—68.

Hortling, I. 1929: En ny geografisk ras av gråhakedopping: Podiceps griseigena schiøleri? — Ornis Fennica 6:11—14.

Krebs, J. R. & R. J. Cowie 1976: Foraging strategies in birds. — Ardea 64:98—116.

Larsen, A. H. 1979: Oliedøden. — Vågen 1979(2):23.

Madsen, F. J. 1957: On the food habits of some fish-eating birds in Denmark. — Dan. Rev. Game Biol. 3:19—83.

Markuze, K. 1965: K ekologii vidov pogonok v delte Volgi so svjazom s rybovodstvom. — Ornitologia 7:244—257.

Morisita, M. 1959: Measuring the interspecific associations and similarity between communities. — Mem. Fac. Sci., Kyushu Univ. Ser. E3:65—80.

Onno, S. 1958: Sravniteljnaja ekologija vidov pogonok Estonii. — Akad. Nauk. Estn. SSR. Inst. Zool. Bot. Tartu. Dissertation.

Palmer, R. S. (ed.) 1962: Handbook of North American birds. Vol. 1. — New Haven-London.

Siegel, S. 1956: Non-parametric statistics for the behavioural sciences. — Kogakusha.

Storer, R. R. 1979: Order Podicipediformes. — *In* E. Mayr & G. W. Cottrell (eds.): Check-list of birds of the world, Vol. 1. 2nd ed.: 140—155. Cambridge Mass.

Thomasson, K. 1953: Die Verbreitung des Rothalstauchers, Podiceps g. griseigena Bodd. in N.W.-Europa. — Zool. Bidrag Uppsala 30:157—166.

Zusi, R. L. & R. W. Storer 1969: Osteology and myology of the head and neck of the pied-billed grebes (Podilymbus). — Misc. Publ. Mus. Zool. Univ. Mich. 139:1—49.

Received March 1982