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Cranial morphology of European passerine bird families (Aves, Passeriformes)

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Abstract The subject of this study focuses on the cranial morphology of 24 native European passerine bird families. In addition to the discussion of taxonomical questions regarding to the examination of beak, orbit, cranium and mandible, the author aims to provide guidance to the determination of raptors' prey remains. Most of the studied bird families are well-distinguishable using the knowledge on the mentioned osteological traits except some less-specialised families.

Keywords: taxonomy, determination, cranial morphology, songbirds

Összefoglalás A dolgozat az Európában honos 24 énekesmadár-család koponyamorfológiai jellemzésével foglalkozik. A csőr, a szemgödör, az agykoponya és az állkapocs vizsgálatával a szerző egyes taxonómiai kérdések megvitatása mellett a ragadozómadarak zsákmánymaradványainak meghatározásához kíván segítséget nyújtani. A vizsgált madárcsaládok többsége a felsorolt csonttani bélyegek ismeretében jól elkülöníthető, csupán néhány kevéssé specializált család meghatározása jelenthet gondot.

Kulcsszavak: Aves**,** Passeriformes, koponyamorfológia, határozás, taxonómia

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Introduction

Studying of avian osteo-morphology has a tradition dated back to the middle of the 19th century. Initially, the skeletal system was examined particularly in systematic perspectives: the structure of the palate (Huxley 1867, Hofer 1945, Witmer & Martin 1987, Zusi 1993), the sternum and humerus (Fürbringer 1888), the cranium, sternum, shoulder, pelvis and hindlimb (Suschkin 1905), number of the vertebra (Boas 1929, Zweers *et al.* 1987), and the morphology of carpometacarpus (Steiner 1922, Lambrecht 1933, Hinchliffe 1985) was considered in distinguishing the larger bird orders. In the past century, mainly palaeontologist used comparative osteo-morphological methods and studied less vulnerable skeletal compartments from excavations. Although, the examination of postcranial parts of the skeleton is dominant in paleontological researches, in some cases, the determination of cranial remains may also be necessary (Jánossy 1992). Whereas, fossils can confidently be classified among recent species, only with deep knowledge on bones (Lambrecht 1933), thus classical morphological researches – simultaneously with the emergence of molecular taxonomy – should be preserve their roles in systematics (Judin 1978). Several detailed osteological collections of different bird groups, which could also facilitate paleontological studies, have been made to date: Podicipediformes (Bochenski 1994), Ardeidae (Boev

1988), Anseriformes (Bacher 1964, Woelfle 1967), Galliformes (Ebersdobler 1968, Kraft 1972), Charadriiformes (Barbosa 1991), Columbidae (Fick 1974), Falconiformes (Otto 1981, Schmidt-Burger 1982, Solti 1980, 1981a, 1981b, 1994), Strigiformes (Winde 1970, Langer 1980), Picidae (Kessler 2016).

Despite passerines constitute most probably the prey of owls (März 1987), finches (Finckenstein 1937, Moreno 1985, Ujhelyi 1992) and corvids (Tomek & Bochenski 2000) are the most intensively studied groups within this order. The only detailed studies including more bird families are Jánossy's (1983) guide for humerus and the works of Moreno (1985, 1986, 1987), and Cuisin (1989) about the Spanish and French fauna. Numerous parts of the skeleton are also presented in Kessler (2015).

I assembled the craniomorphological characterization of 24 native European passerine families in this study. Besides the premaxilla and the cranium, I paid special attention to the morphology of mandible, because bone remains can be identified significantly easier with the knowledge on the structure of the *pars caudalis mandibulae*. Other authors did not attribute sufficient importance to it, however the complete *pars caudalis mandibulae* can often be found among food remains. Furthermore, my work contains the anatomy of the *vomer* since previous researches entirely omitted this. This study is based on the comparative osteological collection of the Hungarian Natural History Museum. Some specimens of a few groups were studied in the Paleontological Institute of the Russian Academy of Science (Moscow) and in the Museum of Natural History, Vienna (Naturhistorisches Museum, Vienna). I asked G. Csorba from the zoological collection of the Berlin's Museum of Natural History (Museum für Naturkunde, Berlin) to carry out some comparative examinations, particularly for this study. I would like to emphasize with the list of genera of each family that I mainly considered the European members of these families in the compilation of cranial morphology for this study. The original illustrations completed this text were also made in the above-mentioned collections. The delimitation of each bird families follows Voous (1977), however their order differs, because here I present sequentially the osteologically more related groups. Although, the linear listing could never perfectly reflect the complex system of songbirds, but it is remarkable that the osteological characteristics could be comparable with the biochemistry based systematics of Sibley and Ahlquist (1990) in many instances. Newertheless, the nomenclature of this study can partially be followed using the work of Baumel *et al.* (1979), I explain the terms on explanatory figures.

Corvidae

(*Perisoreus* Bonaparte, 1831; *Garrulus* Brisson, 1760; *Cyanopica* Bonaparte, 1850; *Pica* Brisson, 1760; *Corvus* Linnaeus, 1758; *Nucifraga* Brisson, 1760; *Pyrrhocorax* Tunstall, 1771)

Corvids are large songbirds which can already be distinguished by body size from other members of their order. Their upper beak is robust, the length of the *pars praenarialis* is often larger than the diameter of the nostril. The nostril is completely open in most of the species, but for example in *Pyrrhocorax pyrrhocorax* it is splitted by a horizontal bone plate. In some specimens of *Corvus corax* a well-developed *septum nasi* is located in the nasal

cavity, however this bone membrane is vestigial or absent in most of the species. In plan view the *brachium processi maxillopalatini* is visible through the nostril and the *foramen basale* forms its base. The *corpus processi maxillopalatini* is also well-developed and it is partialy hollow in some genera. The edges of the *vomer* are dorsally retracted on both sides, the *processus corniculatus vomeris* is well-developed. The *incisura interpalatina* is usually narrow and there is a bone crest on the ventral surface of the *lamella caudolateralis*. The *foramen orbitonasale* is a long gap in most of the cases but it can be devided by bone plates into more parts. The *septum interorbitale* is well-developed and thick. The *fenestra olfactoria* can be found in numerous genera *(Perisoreus, Garrulus, Pyrrhocorax, Pica, Cyanopica),* but this aperture is bony in *Nucifraga* and *Corvus* species. The *rostrum sphenoidale* is thickened in most of the species. The *processus orbitosphenoidalis lateralis* is particularly developed in *Nucifraga caryocatactes*. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* are moderately developed. The *symphysis mandibulae* is weak in the case of *Perisoreus infaustus* but in the species of other genera *(Nucifraga, Pyrrhocorax)* it is remarkably long. The *foramina postsymphysialia* are opened on the caudal edge of the *symphysis*, except for the *Nucifraga* genus, where these apertures are located on the ventral surface of the *symphysis*. Behind the *foramen laterale* the *impressio mandibularis* is moderately pronounced and the oval *fenestra mandibulae* is relatively small. On the ventral surface of the *pars caudalis mandibulae* between the peaks of the *processus externus* and the *processus internus* a V-shaped bone ridge streches.

Oriolidae
(*Oriolus* Linnaeus, 1766)

The upper beak is massive and the length of the bony palate approaches the half of the beak. The *pars praenarialis* is larger than the diameter of the nostril. The remnant of the *septum nasi* is located on the rostral end of the naval cavity. The wide *brachium processi maxillopalatini* and the *foramen basale* near its base are visible in plan view. At the end of its extension the lengtheneed *corpus* is hardly separated. The simply structured *vomer* is little pneumatized and the *processus corniculatus vomeris* is short. The *incisura interpalatina* ends at the base of the *processus spiniformis*. The remarkably spacious, single (not split) *foramen orbitonasale* opens close to the axis of the skull. The *fenestra olfactoria* is strongly lengthened in rostral direction, the *fenestra septi interorbitalis* is always located. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* is moderately developed, where extensions could not be found on the caudal bony wall near the eye socket. The *foramina venae occipitalis externae* opens far from each other and behind the *foramen magnum*. The slim mandible is slightly hooked in lateral view and there is no significant nook *(impressio mandibularis)* on the lateral surface of the mandible. The *foramen laterale* is also absent. The *symphysis* is well-developed, but the *fenestra mandibulae* is small. The bone ridge is vestigial on the ventral surface of the *pars caudalis mandibulae.* The *fossa caudalis mandibulae* is basically absent between the peak of the *processus externus* and the *processus internus*.

Laniidae
(*Lanius* Linnaeus, 1758)

The upper beak of *Lanius* species is relatively short and strength. The *septum nasi* is always located between the nostrils. The *foramen basale* opens at the base of the wide *brachium processi maxillopalatini* which is visible in plan view. The *corpus processi maxillopalatini* is barely separated from the *brachium* in their morphology. The structure of the pneumatized *vomer* is complex, the paired *processus corniculatus vomeris* is dorsally strongly curved. The *incisura interpalatina* is relatively wide, the *lamella caudolateralis* forms a long extension. In *Lanius* species the rostral part of the *pterygoideum* fusions to the *palatinum* differently to the majority of songbirds. The *foramen orbitonasale* is split: the *foramen orbitonasale laterale* is larger than the *f. o. mediale*. The *fenestra septi interorbitalis* is never completely bony. The *processus postorbitalis* is vestigial and the *processus zygomaticus ossis squamosi* is moderately developed. The *foramina venae occipitalis externae* open close to each other and these apertures are connected to the edge of the *foramen magnum* via the paired *sulcus occipitalis*. The *symphysis mandibulae* is moderately thick, the *impressio mandibularis* is varied by species. The *foramen laterale* is absent. The wide-based *tuberculum pseudotemporale* is moderately developed. A sharp bone ridges is located on the ventral surface of the *processus internus*. The *fossa caudalis mandibulae* is barely expressed.

Hirundinidae
(*Hirundo* Linnaeus, 1758; *Delichon* Horsfield et Moore, 1854; *Riparia* Forster, 1817; *Ptyonoprogne* Reichenbach, 1850)

The typically prolate beak of swallows and martins makes the members of this family to easily recognizable. The *brachium processi maxillopalatini* is not visible over the nostril, but it is located behind the *processus postnarialis*. The *foramen basale* exists. The *vomer* is flat, the contour of the *processus corniculatus* is angular. The basically wide *incisura interpalatina* ends at the peak of the *processus spiniformis*. The *pars interorbitalis* is narrow, the *septum interorbitale* is thin. The *foramen orbitonasale* is split: the *f. o. laterale* is smaller then the *f. o. mediale*. The *fenestra olfactoria* and the *fenestra septi interorbitalis* are spacious. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* weakly developed. A paired groove *(sulcus occipitalis)* extends between the *foramen magnum* and the *foramina venae occipitalis externae*. The *symphysis mandibulae* is weak, the *foramina postsymphysialia* open far from each other on its dorsal surface. The mandible branches are widely expanded. The *angulus mandibulae* is typical of the mandible with a peak in its middle. The *processus internus* is not visible in lateral view and bone ridge is never located on its ventral surface. The *fossa caudalis mandibulae* is deeply curved.

Comment: The swallows form a very special group of songbirds. Their anatomical specializations regarding to their lifestyle make it difficult to identify which families are closely related to them. Whereas the Corvidae-Oriolidae-Laniidae triplet is farther related to all other passerines than the swallows, thus I have listed them here right after the Laniidae.

It needs to be considered in the practice of the determination of families that the skull of the swallows remind to the skull of the swifts (Apodiformes: Apodidae), however these two groups differ in many morphological traits. The nook *(impressio supraorbitalis)* behind the *pars interorbitalis*, and the lateral position of the *foramina venae occipitalis externae* separate swifts from any other songbirds.

Bombycillidae
(*Bombycilla* Vieillot, 1808)

The upper beak with a significant widening at its base is relatively short. The bony palate is also shortened. The nostril is spacious and the *septum nasi* is always absent. The *corpus processi maxillopalatini* is short, wide and partially pneumatized. The *vomer* is flat and the contour of the *processus corniculatus* is angular. The wide *incisura interpalatina* is protractedly wedged forward. The orbital surface of the weakly pneumatized *ala mesethmoidei* is concave. The split-like *foramen orbitonasale* is single (not split). The *fenestra septi interorbitalis* is bony and absent in adults, whilst the *fenestra olfactoria* is remarkably spacious. The *processus postorbitalis* is almost melded into the cranium and the *processus zygomaticus ossis squamosi* is also vestigial. The *ala tympanica* hardly covers the *cavum tympani* in lateral view. The *foramina venae occipitalis externae* open at the end of one-one paired groove *(sulcus occipitalis)* behind the *foramen magnum*. The *symphysis mandibulae* is short, the mandible branches are widely expanded. The *impressio mandibularis* is always located and the *foramen laterale* opens in front of it. The ventral surface of the *pars caudalis mandibulae* is smooth, the *fossa caudalis mandibulae* is moderately notched. The axis of the lengthened *processus internus mandibulae* is approximately right angles to the mandible branch.

Sturnidae
(*Sturnus* Linnaeus, 1758; Pastor Temminck, 1815)

The upper beak is slim and pointed. The nostrils are spacious. The *septum nasi* is always absent. The *brachium processi maxillopalatini* is visible through the nostrils in plan view and the *foramen basale* is absent at the bottom of it. The strongly lengthened *corpus processi maxillopalatini* is partially pneumatized. A weak bone ridge is located at the midline of the *vomer*, the *processus corniculatus vomeris* is vestigial. The *incisura interpalatina* ends at the middle of the lengthened *collum vomeris*. The *foramen orbitonasale* is split: the larger *f. o. mediale* is in the interior eye cavity while the small *f. o. laterale* opens at the edge of the eye cavity. The *fenestra septi interorbitalis* can be found in both young and adult birds. The *processus postorbitalis* is barely appreciable, the *processus zygomaticus ossis squamosi* is also vestigial. A typical hump is located on the ventral surface of the *rostrum sphenoidale*. The *foramina venae occipitalis externae* open directly at the edge of the *foramen magnum*. In some species (*Sturnus* spp.), a sharp bone ridge *(crista nuchae)* extends at the edged of the *regio occipitalis*. A typical characteristic of the mandible is the mid-peaked *angulus mandibulae* in lateral view. The *foramen laterale* is absent near the *impressio mandibularis*. The *canalis mandibulae* opens just before the *fenestra mandibulae* at the lateral surface of

the mandible. The two European starling genera *(Sturnus, Pastor)* significantly differ in the structure of the *pars caudalis mandibulae*: the *processus externus* is already well-developed in the young of the *Sturnus* species, however in *Pastor roseus* this has standard size. A more or less developed hump is located at the rostral edge of the *processus internus*.

Comment: The differences in the morphology of the *pars caudalis mandibulae* absolutely justify the split of *Sturnus* and *Pastor* genera.

Cinclidae
(*Cinclus* Borkhausen, 1797)

The upper beak is slim and sharp and at its ridge, a weak concavity can be found before the *processus dorsonarialis*. The *septum nasi* is absent in the spacious and lengthened naval cavity. The *brachium processi maxillopalatini* is invisible in plan view. A sharp bone ridge extends at the midline of the lengthened *vomer*, which continues in a long bone mandrel at the front of the *vomer*. The *lamella caudolateralis* is significantly shortened. The *pars interorbitalis* is relatively narrow. The *ala mesethmoidei* is strongly pneumatized and it is markedly protuberant on its orbital surface. The *foramen orbitonasale* is split, the *f. o. laterale* opens at the edge of the eye cavity and it is also visible in plan view. The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both spacious. The *processus postorbitalis* is small and rounded, the *processus zygomaticus ossis squamosi* is vestigial. The *fenestra mandibulae* is a relatively small aperture on the rearer part of the mandible and the *canalis mandibulae* opens just before this at the lateral surface of the mandible. A sharp bone ridge is located on the ventral surface of the *pars caudalis mandibulae* which is split into two branches and extends to the rear extension of the mandible *(processus externus et processus internus)*.

Troglodytidae
(*Troglodytes* Vieillot, 1807)

The upper beak is slim, the diameter of the nostrils and the length of the *pars praenarialis* are equal. The *septum nasi* is absent in the naval cavity. The thin and hooked *brachium processi maxillopalatini* is invisible through the nostril in plan view. At the base of this extension, the *foramen basale* is absent and the *corpus processi maxillopalatini* is not pneumatized. The *vomer* is flat and the *processus corniculatus vomeris* is small. The *incisura interpalatina* is wide and the *processus spiniformis* is lengthened. The *foramen orbitonasale* is single (not split). The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both spacious. The *processus zygomaticus ossis squamosi* is vestigial and a relatively sharp bone ridge extends behind it, between the small *processus postorbitalis* and the tympanic cavity *(cavum tympani)*. The mandible is slim and slightly curved in lateral view. The *impressio mandibularis* is absent on its lateral surface. The lateral surface of the *processus externus mandibulae* is convex.

Certhiidae
(*Certhia* Linnaeus, 1758)

The upper beak is thin and slim and strongly curved in lateral view. The *septum nasi* is absent in the naval cavity. The *foramen basale* is absent, the hooked *brachium processi maxillopalatini* is behind the *processus postnarialis* in plan view. The *corpus processi maxillopalatini* is pneumatized. A tiny bone ridge is visible at the midline of the *vomer*, the *processus corniculatus vomeris* is vestigial. The wide *incisura interpalatina* is wedged in front of the short *processus spiniformis*. The *foramen orbitonasale* is single (not split). The *septum interorbitale* is relatively well-developed, the *fenestra olfactoria* and the *fenestra septi interorbitalis* is smaller than on the skull of the Troglodytidae and Regulidae families. The *processus postorbitalis* and the *prosessus zygomaticus ossis squamosi* are both vestigial. The moderately sharp *crista nuchae* separates well the occiput area *(regio occipitalis)*. The mandible is strongly curved in lateral view. The *foramina postsymphysialia* open at the end of the *symphysis* in a ventral groove. The little deviated, slim *processus externus mandibulae* is typical for the *pars caudalis mandibulae* which lateral surface is slightly concave.

Tichodromadidae
(*Tichodroma* Illiger, 1811)

The upper beak is long and thin, the length of the *pars praenarialis* and the nostril are equal. The *septum nasi* is absent in the naval cavity. The *brachium processi maxillopalatini* is invisible through the nostril in plan view. The *lamella caudolateralis* is short and rounded. The *foramen orbitonasale* is split. The *septum interorbitalis* is strongly perforated, the *fenestra olfactoria* is larger than the *fenestra septi interorbitalis*.The mandible is thin and curved and the *symphysis mandibulae* is well-developed. The *fenestra mandibulae* is vestigial and almost completely bony.

Sittidae
(*Sitta* Linnaeus, 1758)

The upper beak is long and slim, the diameter of the spacious nostril is slightly smaller than the length of the *pars praenarialis*. The *septum nasi* is absent in the naval cavity. The *brachium processi maxillopalatini* is invisible through the nostril in plan view. The very wide *incisura interpalatina* extends in front of the *processus spiniformis*. The *foramen orbitonasale* is a single (not split) aperture. The *septum interorbitalis* is highly developed, the *fenestra septi interorbitalis* is completely bony and the *fenestra olfactoria* is also significantly narrowed. The *processus zygomaticus ossis squamosi* and the *processus postorbitalis* are both developed. The hardly curved mandible is powerful and chisel-like. The *foramina postsymphysialia* open close to each other at the caudal edge of the *symphysis*. The *foramen laterale* is located in front of the *impressio mandibularis*. The *processus coronoideus* forms a sharp bone ridge above the relatively narrow *fenestra mandibulae*. Typical characteristics of the lateral edge of the *pars caudalis mandibulae* are the twin bone peaks and the rounded *processus externus*.

Paridae (s. str.)
(*Parus* Linnaeus, 1758)

The upper beak is short and massive, the diameter of the oval nostril is much smaller than the length of the *regio praenasalis*. The remnant of the bony bracing membrane *(septum nasi)* is always located at the caudal part of the naval cavity. The *processus dorsonarialis* is remarkably wide, the upper beak and the forehead is sharply separated by the *sulcus frontonasalis rectus* behind it. The *brachium processi maxillopalatini* is invisible through the nostril in plan view. The *corpus processi maxillopalatini* is short and partially pneumatized. The shape of the lengthened *vomer* differs by species. The *incisura interpalatina* is more wedged in front of the vestigial *processus spiniformis* often forwards to the *collum vomeris*. The *lamella caudolateralis* is barely developed, however the *lamella caudomedialis* is significantly wide. The *foramen orbitonasale* is split. The *septum interorbitale* is robust, the *fenestra olfactoria* is relatively narrow and the *fenestra septi interorbitalis* is ofthen completely bony. The *processus postorbitalis* is absent and the *processus zygomaticus ossis squamosi* is weakly developed. The mandible is relatively short and the *symphysis* is well-devleoped. The *foramina postsymphysialia* open close to each other in the groove on the dorsal surface of the symphysis. The *foramen laterale* is always located at the base of the sharply separated *impressio mandibularis*. The *fenestra mandibulae* is large and remarkably spacious in some species (e.g. *Parus caeruleus*). The ventral surface of the *pars caudalis mandibulae* is smooth and the *processus externus* is moderately developed and its contour is angular.

Remizidae
(*Remiz* Jarocki, 1819)

The upper beak is relatively short and triangular, the diameter of the nostril is much smaller than the length of the *pars praenarialis*. The *septum nasi* is well-developed in the naval cavity. The *processus dorsonarialis* is remarkably wide as in *Parus* species. The slightly curved *vomer* has multiple peaks and behind it, the *collum vomeris* significantly narrows. The *incisura interpalatina* is bony on a significant part, a slight notch can only be found on a short caudal part of the *palatinum*. The *processus spiniformis* is vestigial, but the *lamella caudolateralis* is spikwise lengthened. The *septum interorbitale* is relatively perforated: the *fenestra olfactoria* and the *fenestra septi interorbitalis* are both well-developed and behind the single (not split) *foramen orbitonasale,* an extra aperture breaks through the bone membrane. The *processus postorbitalis* is absent and the *processus zygomaticus ossis squamosi* is vestigial. The sharp edge of the *margo postorbitalis* merges into the cranium above the *processus zygomaticus*.The structure of the curved mandible is special and can be distinguished from any other songbirds: the lengthened *processus externus* is much longer than the *processus internus*. The latter extension contains a sharp bone peak at its rostral edge. The relatively narrow *fenestra mandibulae* is located on approximately equal distance between the caudal end of the *symphysis* and the peak of the *processus externus*. The position of the *foramina postsymphysialia* and the *foramen laterale* does not differ from the drescition in the Paridae family.

Comment: The Remizidae family is highly separated in the structure of the *pars caudalis mandibulae* from the Paridae and any other European passerine families.

Aegithalidae
(*Aegithalos* Hermann, 1804)

The typically shaped upper beak is short, the diameter of the spacious nostril sometimes exceeds the length of the *pars praenarialis*. Opposite to the Paridae and the Remizidae families, the *septum nasi* still could not be found in vestigial form too, the *processus dorsonarialis* is even narrower. The thin *brachium processi maxillopalatini* is invisible through the nostril in plan view. The two well-developed *processus corniculatus vomeris* at the beginning of the *vomer* contact to each other along the symmetry axis of the skull. The *incisura interpalatina* is wide and long, the *lamella caudolateralis* is short and rounded. The *foramen orbitonasale* is single (not split). The *septum interorbitale* is strongly perforated, the *fenestra olfactoria* and the *fenestra septi interorbitalis* are both well-developed. The *processus postorbitalis* is absent. The peak of the moderately developed *processus zygomaticus ossis squamosi* is widely rounded and the *margo postorbitalis* arches uninterruptedly to this peak. The *foramina postsymphysialia* open at the caudal edge of the moderately developed *symphysis*. The *fenestra mandibulae* is moderately spacious. The morphology of the *pars caudalis mandibulae* is mainly equal to *Parus* species, however the *processus externus* is slightly shifted outwards.

Paradoxornithidae
(*Panurus* Koch, 1816)

The upper beak is slim, the length of the *pars praenarialis* and the diameter of the nostril are equal. The *septum nasi* is always absent in the naval cavity and the *processus dorsonarialis* is relatively narrow. The *brachium processi maxillopalatini* is invisible in plan view and the *foramen basale* is absent at the base of this extension. The *corpus processi maxillopalatini* is lengthened and pneumatized. The *vomer* has multiple peaks. The wide *incisura interpalatina* extends in front of the short *processus spiniformis*. The *foramen orbitonasale* is single (not split). The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both well-developed. The tiny *processus postorbitalis* is melted in full length to the dorsal edge of the *processus zygomaticus ossis squamosi* in a specific way, but a negligible gap can be found between these two extensions in some young specimens. The mandible is slightly curved and the *symphysis* is weakly developed. The *foramen laterale* is located in front of the *impressio mandibularis*. A weak bone ridge extends at the ventral surface of the *pars caudalis mandibulae* and the *processus externus* is vestigial and widely rounded.

Comment: The *Panurus biarmicus* can be separated from any other European songbirds based on the rounded shape of the *processus externus mandibulae*.

Regulidae
(*Regulus* Cuvier, 1800)

The upper beak is slim and sharp, the *processus postnarialis* is particularly thin. A specific trait of *Regulus* species is the vestigial *septum nasi* in the caudal part of the nasal cavity. The *brachium processi maxillopalatini* is visible through the nostril in plan view too, at its end the *corpus* is relatively wide, lengthened and not pneumatized. The midline of the *vomer* is little peaked and the *processus corniculatus vomeris* is well-developed. The wide *incisura interpalatina* is wedged to the peak of the lengthened *processus spiniformis*. The *foramen orbitonasale* is single (not split). The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both remarkably spacious. The *processus postorbitalis* is vestigial and the *processus zygomaticus ossis squamosi* is moderately developed. The mandible is lengthened and thin and the *fenestra mandibulae* is relatively spacious. The *protuberantia caudolateralis* is ridge-like developed at the lateral surface of the *pars caudalis mandibulae,* a tiny aperture *(foramen pneumaticum)* can be found behind it. The peak of the *processus internus* is remarkably sharp.

Comment: Based on their measurement the *Regulus* species are recognizable and can easily be separated from the members of the Sylviidae family according to the existence of the *septum nasi* and the developmental level of the *protuberantia caudolateralis*.

Sylviidae
(*Sylvia* Scopoli, 1769; *Acrocephalus* J. A. et F. Naumann, 1811; *Lusciniola* Gray, 1841; *Locustella* Kaup, 1829; *Hippolais* Baldenstein, 1827; *Phylloscopus* Boie, 1826; *Cisticola* Kaup, 1829; *Cettia* Bonaparte, 1834)

The slightly curved upper beak is slim, aharp and the nostril is spacious. The *septum nasi* is always absent in the naval cavity. The *brachium processi maxillopalatini* is invisible through the nostirls in plan view and the spacious *foramen basale* is always located at its base. The structure of the *corpus processi maxillopalatini* and the *vomer* differ by genera. The *incisura interpalatina* is particularly wide in *Sylvia* species. In *Cettia* and *Sylvia* species, the *lamella caudolateralis* is rounded, but in the species of other genera, this bone plate is sword-like lengthened and sharp. The single (not split) *foramen orbitonasale* is usually spacious and little lengthened aperture. The *septum interorbitale* is strongly perforated, the *fenestra olfactoria* and the *fenestra septi interorbitalis* are equally spacious. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* are vestigial. The *foramina venae occipitalis externae* are a little far from each other and from the edge of the *foramen magnum*. The mandible is thin, lengthened, the *impressio mandibularis* is weakly expressed and the *fenestra mandibulae* is moderately spacious. The ventral surface of the *pars caudalis mandibulae* is smooth and the *fossa caudalis mandibulae* is barely notched.

Comment: This family contains osteo-morphologically little differentiated genera, thus the determination of species in practice is usually not feasible based on their cranial morphology.

However, the whole Sylviidae family can be well separated from the similar Muscicapidae family based on the structure of the *foramen orbitonasale*, the position of the *brachium processi maxillopalatini* and the *foramina venae occipitalis externae* and the notched *fossa caudalis mandibulae*.

Muscicapidae (s. l.)
(*Muscicapa* Brisson, 1760; *Ficedula* Brisson, 1760; *Cercotrichas* Boie, 1831; Saxicola Bechstein, 1803; *Phoenicurus* T. Forster, 1817; *Oenanthe* Vieillot, 1816; *Monticola* Boie, 1822; *Luscinia* T. Forster, 1817; *Turdus* Linnaeus, 1758; *Erithacus* Cuvier, 1800)

The upper beak is usually thin, lengthened, and in some genera (in the Muscicapinae subfamily), it is broadened at the base of the beak. The nostril is spacious and the lack of the *septum nasi* is typical in most of the genera. The *brachium processi maxillopalatini* is usually visible in plan view (through the nostrils) and the *foramen basale* opens at its base. The structure of the *vomer* is varied by genera and the *processus corniculatus vomeris* is usually vestigial. The *foramen orbitonasale* is split and the two apertures are sometimes located relatively far from each other. The *fenestra olfactoria* is flattened and the *fenestra septi interorbitalis* is a little more spacious. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* are both vestigial. The *foramina venae occipitalis externae* usually open close to each other at the end of the paired *sulcus occipitalis*. The mandible is slim, the *impressio mandibularis* is weakly expressed and the *fenestra mandibulae* is relatively narrow. The *tuberculum pseudotemporale* is relatively absent and the *processus coronoideus* is vestigial. The *fossa caudalis mandibulae* – opposite to the members of the Sylviidae family – is deeply notched.

Comment: Some genera within this family are distinguishable from other members based on some certain osteological traits. The concavity on the ridge of the upper beak is typical for the *Phoenicurus* and *Oenanthe* genera. The *foramen orbitonasale laterale* is remarkably shifted outwards in *Luscinia* species and it is also visible in plan view. The strongly protuberant *ala tympanica* is typical for *Turdus*. Furthermore, the *brachium processi maxillopalatini* and the position of the *foramina venae occipitalis externae* can be modified in these species. Among the European members of this family, the well-developed *septum nasi* can only be found in the nasal cavity of *Erithacus rubecula*.

Motacillidae
(*Motacilla* Linnaeus, 1758; *Anthus* Bechstein, 1805)

The upper beak is slim and sharp, the nostril is spacious and the *septum nasi* is always absent. A weak concavity can be found on the dorsal beak of *Anthus* species before the nostril. The *brachium processi maxillopalatini* is visible through the nostril in plan view and the *foramen basale* is absent at its base. The *incisura interpalatina* is wide, rostrally strongly lengthened and the *processus spiniformis* is particularly long and slim in *Motacilla* species. The *foramen orbitonasale* is usually single *(Motacilla* spp., *Anthus*

pratensis, A. spinoletta, A. cervinus), but in some *Anthus* species it is split *(A. trivialis, A. campestris)*. The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both spacious. The *processus postorbitalis* is vestigial, the larger *processus zygomaticus ossis squamosi* is sharply peaked. The *foramina venae occipitalis externae* open just behind the edge of the *foramen magnum*. The mandible is slim, the *fenestra mandibulae* is moderately spacious. The *processus externus* is short and angular, a weak bone ridge extends at the ventral surface of the *processus internus*.

Prunellidae
(*Prunella* Vieillot, 1816)

The upper beak is slim and sharp, a weak concavity can be found on its dorsal part. The nostril is spacious and the *septum nasi* is absent. The *brachium processi maxillopalatini* is invisible in plan view, the *foramen basale* is absent at its base. The *lamella caudolateralis palatina* is short and typically rounded. The *foramen orbitonasale* is a single (not split) aperture. The *fenestra olfactoria* and the *fenestra septi interorbitalis* are both spacious. The *processus postorbitalis* is vestigial, but the *processus zygomaticus ossis squamosi* is well-developed and its peak is widely rounded. The peak of the *lamina basiparasphenoidalis* is shortened. The mandible is slim, the *fenestra mandibulae* is moderately spacious. A weak bone ridge is located at the ventral surface of the *pars caudalis mandibulae*.

Comment: The developmental level of the *processus zygomaticus ossis squamosi* and the shape of the *lamella caudolateralis palatina* help in separating *Prunella* species from any other small, insectivorous songbirds.

Passeridae
(*Passer* Brisson, 1760; *Petronia* Kaup, 1829; *Montifringilla* C. L. Brehm, 1828)

The upper beak is relatively short and conical, the nostril is moderately spacious. The *septum nasi* is always located in the naval cavity. The split on the palate *(fenestra palatina)* wedges forward to approximately the half of the bony palate. The contour of the short and partially pneumatized *corpus processi maxillopalatini* is angular. The paired *processus corniculatus vomeris* at the peak of the vomer is particularly wide and dorsally hooked. The relatively wide *incisura interpalatina* is wedged toward the *collum vomeris*. The *foramen orbitonasale* is single (not split). The membrane which separates the eye sockets *(septum interorbitale)* is significantly bony and the *fenestra septi interorbitalis* is absent. The *processus postorbitalis* and the *processus zygomaticus ossis squamosi* are both well-developed and on the latter an extra lateral extension can be found. The *foramina venae occipitalis externae* are far from each other. The mandible is relatively short, the *symphysis* is moderately developed and the *foramina postsymphysialia* opens at the base of the mandible branches. The *tuberculum pseudotemporale* and the *processus coronoideus* are both well-developed. The *foramen laterale* opens at the beginning of the deep *impressio mandibularis*. The ventral surface of the *pars caudalis mandibulae* is smooth and its lateral edge is peaked. The

peak of the *processus externus mandibulae* points to the symmetry axis of the mandible and the *fossa caudalis* is deeply notched.

Comment: The developmental level of the *septum nasi* is typical for the whole Passeridae family among all European conical beaked passerine birds. Some similar bone membrane can exceptionally be found in some species of the Fringillidae, but never in the European members of the Emberizidae families.

Fringillidae (s. str.)
(*Fringilla* Linnaeus, 1758; *Serinus* Koch, 1816; *Chloris* Cuvier, 1800; *Carduelis* Brisson, 1760; *Acanthis* Borkhausen, 1797; *Carpodacus* Kaup, 1829; *Pinicola* Vieillot, 1807; *Pyrrhula* Brisson, 1760; *Loxia* Linnaeus, 1758; *Coccothraustes* Brisson, 1760)

The upper conical beak and the mandible are remarkably shortened and the nostril is relatively small. The *septum nasi* in well-development state can only be found in *C. coccothraustes* and it is vestigial in *Pinicola enucleator*, while it is absent in most of the species. The bony palate is particularly developed, the *fenestra palatina* is shifted backwards. The *corpus processi maxillopalatini* is lengthened, the *vomer* is partially pneumatized. The *incisura interpalatina* is completely bony in the Carduelinae subfamily, but it is narrow and forms a lengthened gap in *Fringilla* species (Fringillinae subfamily). A well-developed bone ridge usually extends at the ventral surface of the *lamella caudolateralis*. The *foramen orbitonasale* is a single (not split) aperture. The *septum interorbitale* which separates the eye sockets, is robust, the *fenestra septi interorbitalis* can only be found in *Fringilla* species but this aperture is bony in the member of the Carduelinae subfamily. The *fenestra olfactoria* is also reduced in proportion to specialization. The *processus postorbitalis* is usually small but the *processus zygomaticus ossis squamosi* is highly developed in specialized species. The *foramina venae occipitalis externae* open at the edge of the *foramen magnum*. The thickening of the *symphysis* and the existence of the *crista anterioventralis* at the ventral surface of the *pars caudalis mandibulae* are typical for the mandible. The *processus coronoideus* is markedly peaked and behind it, the well-developed *tuberculum pseudotemporale* is also visible in lateral view. The *foramen laterale* open at the beginning of the deep *impressio mandibularis*.

Comment: The existence of the *crista anterioventralis* is only typical in the Fringillidae family which distinguishes all members of this family from any other songbirds.

Emberizidae
(*Emberiza* Linnaeus, 1758; *Calcarius* Bechstein, 1803; *Plectrophenax* Stejneger, 1882)

The upper beak is thinner and slimmer than in the Passeridae and Fringillidae families and the contour line has a typical fracture at the midpoint in lateral view. The nostril is relatively spacious, the *processus postnarialis* is thin and the *septum nasi* is always absent in the naval cavity. The *corpus processi maxillopalatini* is lengthened and partially pneumatized.

The developed lateral extension of the twin peaked *processus corniculatus vomeris* is slim. The wide *incisura interpalatina* is rostrally lengthened towards the *collum vomeris*. The *pars interorbitalis* is markedly narrow. Differently to the seed-eater songbirds, the *septum interorbitale* which separates the eye sockets is strongly perforated. The *fenestra septi interorbitalis* is more spacious in *Emberiza* species than the *fenestra olfactoria*; in the *Calcarius* and the *Plectrophenax* this aperture is smaller or could be exceptionally bony. The *processus postorbitalis* is vestigial, however the *processus zygomaticus ossis squamosi* is wide and forms a rounded bone plate. The *ala tympanica* is some species *(Emberiza cia, E. citrinella)* is particularly developed. The *angulus mandibulae* is typically peaked and the curve of the mandible is refracted near the deep *impressio mandibularis* in lateral view. The *symphysis* is moderately thick and the *foramina postsymphysialia* are visible at the base of the mandible branches in bottom view. The *fenestra mandibulae* is spacious, the *processus coronoideus* and the *tuberculum pseudotemporale* are both well-developed. The ventral surface of the *pars caudalis mandibulae* is smooth and the *fossa caudalis mandibulae* is deeply notched.

Comment: The members of the Emberizidae family can easily be distinguished from the members of other bird families based on the refracted curve of the mandible.

Alaudidae
(*Galerida* Boie,1828; *Calandrella* Kaup, 1829; *Melanocorypha* Boie, 1828; *Eremophila* Boie, 1828; *Lullula* Kaup, 1829; *Alauda* Linnaeus, 1758)

The peak of the beak is relatively blunt, a lengthwise groove extends on the midline of the bony palate. A tiny aperture is located next to the rostral connection point of the *lamella craniolateralis* (this is absent in species of other families). The bone membrane *(septum nasi)* between the spaciour nostrils is vestigial but it can be found in all species. The *foramen basale* and the *brachium processi maxillopalatini* are both visible through the nostrils in plan view. The *corpus processi maxillopalatini* is lengthened and pneumatized. Particularly well-developed, paired *processus corniculatus vomeris* is located at the beginning of the relatively short *vomer*. The exceptionally wide *incisura interpalatina* is singnificantly lengthened to the front of the *processus spiniformis*. The *pars interorbitalis* is narrow. The *septum interorbitale* is robust and the *foramen septi interorbitalis* becomes completely bony by the age of the indicidual (usually at very young). The *fenestra olfactoria* can be found in every species. The single (not split) *foramen orbitonasale* opens close to the axis of the skull in the eye cavity. The *processus orbitosphenoidalis lateralis* is well-developed in some members of the family *(Eremophila, Melanocorypha, Calandrella)* but it is absent in others. The well-developed *processus postorbitalis* and the *processus zygomaticus ossis squamosi* are melted into a single extension on their peaked ends and a spacious aperture *(fenestra postorbitalis)* is located between the bases of the two extensions. The *rostrum sphenoidale* is remarkably thicker in comparison to the insectivorous passerine birds. The *foramina venae occipitalis externae* is located close next to the edge of the *foramen magnum*. The *symphysis mandibulae* is relatively short and a weak concavity can be found on

its dorsal surface. The *foramen postsymphysiale* which opens at the symmetry axis is typical at the caudal edge of the *symphysis*. The mandible is slim in most of the members of this family, however the mandible of the specialized *Melanocorypha* species is robust. The *fenestra mandibulae* is moderately spacious and the short *processus coronoideus* forms a sharp bone ridge above it. The *processus internus mandibulae* is also visible in lateral view and its peak bends in dorsorostrally.

Comment: The fusion of the peak of the *processus postorbitalis* and the *processus zygomaticus ossis squamosi* which typical for the larks is absent in any other European songbird families. These two extension could be ended very close to each other in some woodpecker species (Piciformes: Picidae), but this analogous trait similar to larks can only be found among the members of Tetraonidae, Phasianidae (Galliformes) and Pteroclidae (Columbiformes) of the European avifauna.

Many characteristics of the upper beak, the position of the *foramen postsymphysiale* and the shape of the *processus internus* may be helpful in the determination of the larks in practice.

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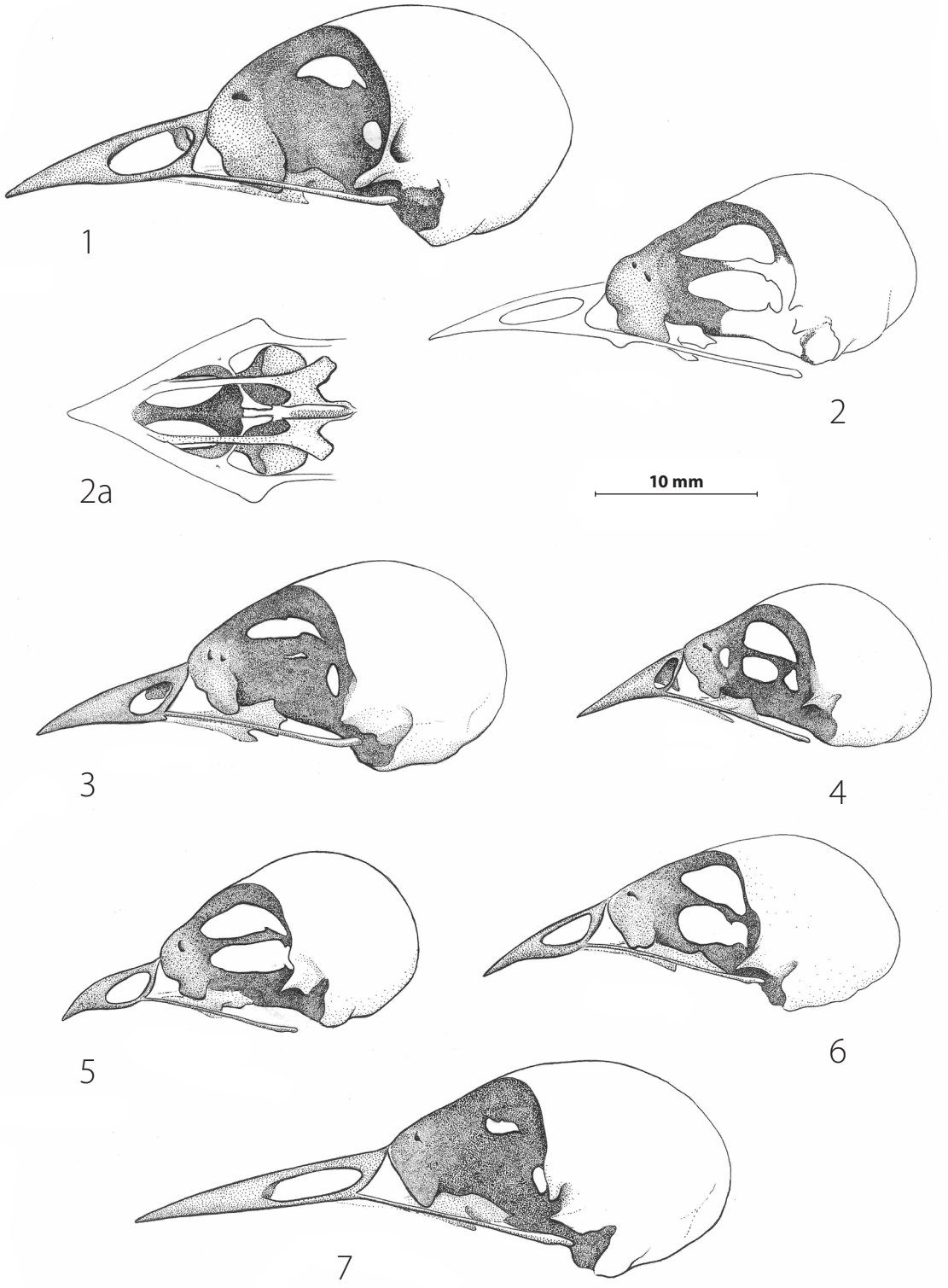

Plate 1. Skulls
1. táblakép Koponyák
1. Alauda, 2. Hirundo, 3. Parus, 4. Remiz, 5. Aegithalos, 6. Panurus, 7. Sitta

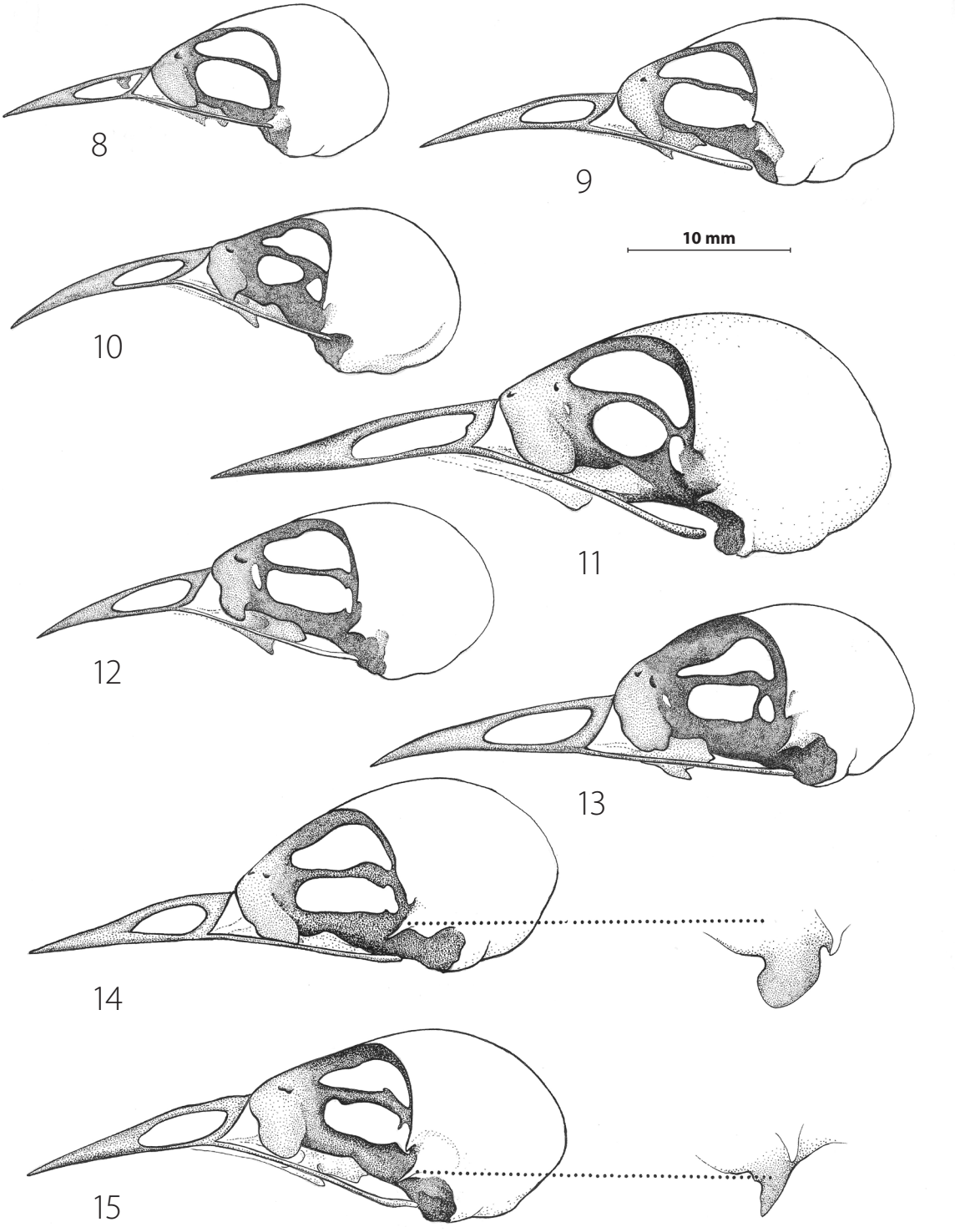

Plate 2. Skulls
2. táblakép Koponyák
8. Regulus, 9. Troglodytes, 10. Certhia, 11. Cinclus, 12. Sylvia, 13. Muscicapa, 14. Prunella, 15. Motacilla

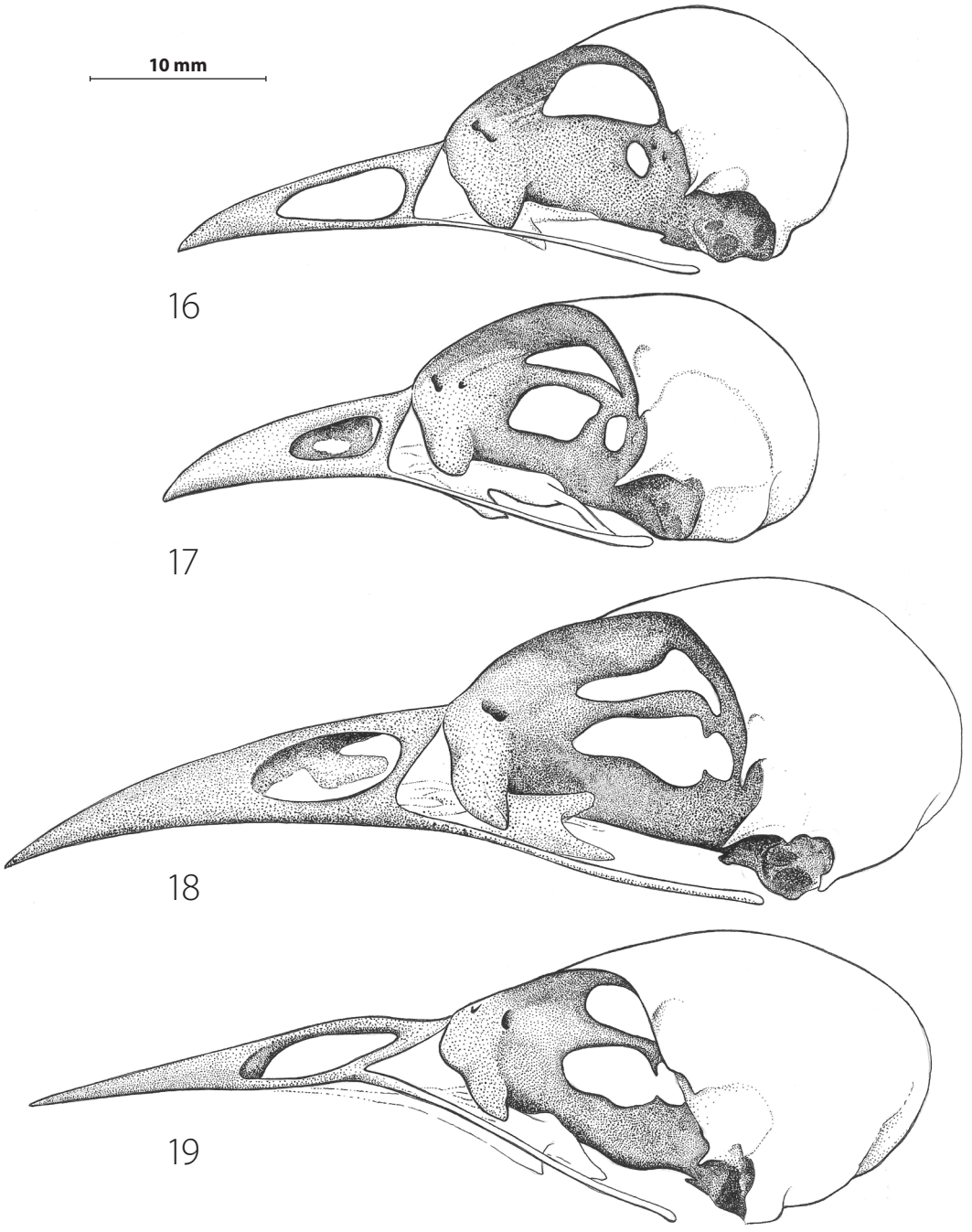

Plate 3. Skulls
3. táblakép Koponyák
16. Bombycilla, 17. Lanius, 18. Oriolus, 19. Sturnus

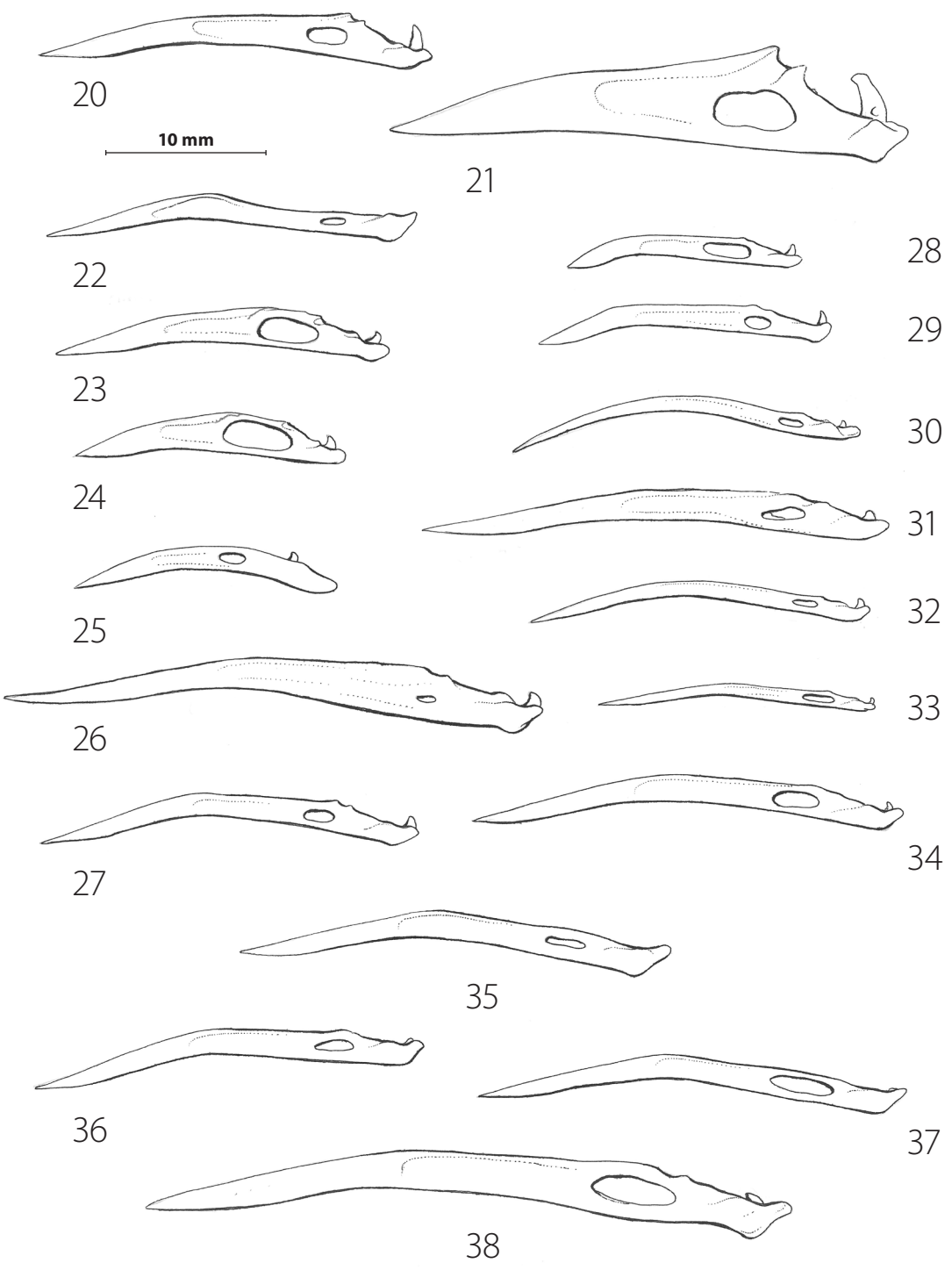

Plate 4. Lower jaws
4. táblakép Állkapcsok
20. Galerida, 21. Melanocorypha, 22. Hirundo, 23. Parus major, 24. P. caeruleus, 25. Remiz, 26. Cinclus, 27. Prunella, 28. Aegithalos, 29. Panurus, 30. Certhia, 31. Sitta, 32. Troglodytes, 33. Regulus, 34. Motacilla, 35. Muscicapa, 36. Sylvia, 37. Luscinia, 38. Turdus

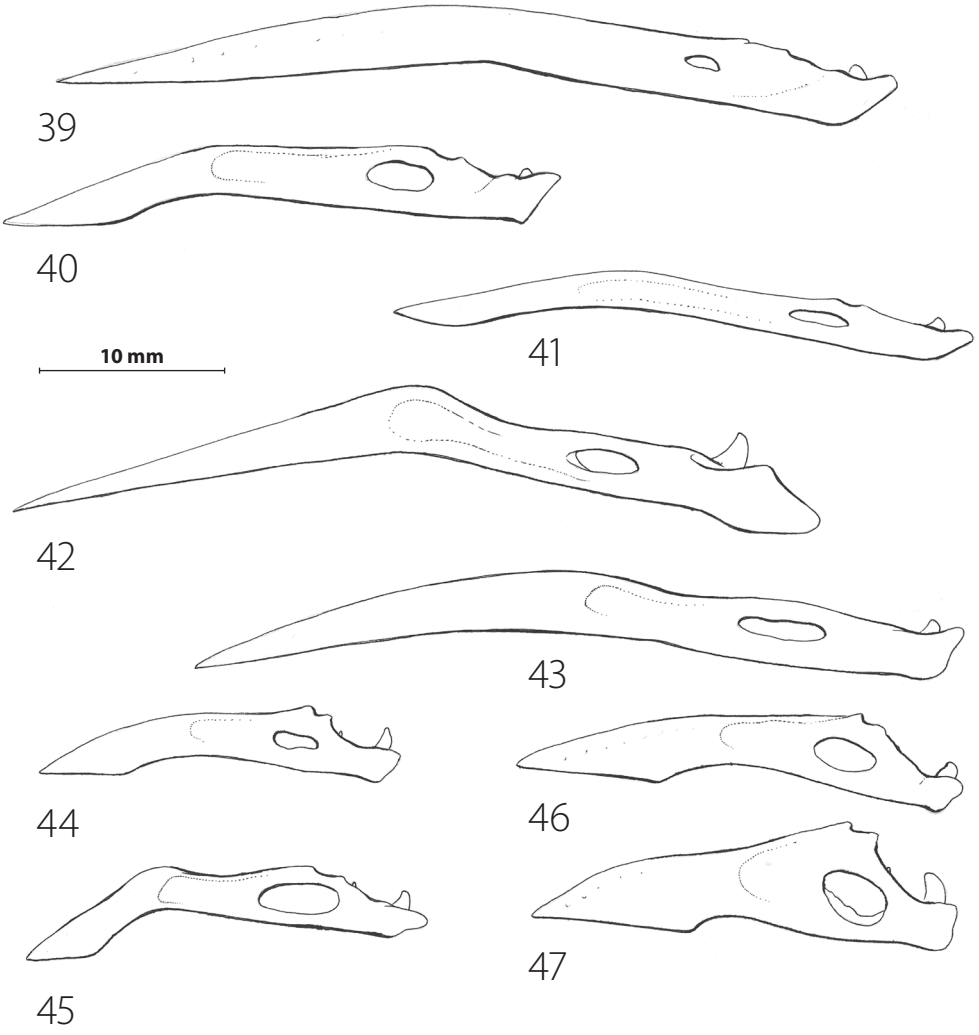

Plate 5. Lower jaws
5. táblakép Állkapcsok
39. Oriolus, 40. Lanius, 41. Bombycilla, 42. Sturnus, 43. Pastor, 44. Passer, 45. Emberiza, 46. Fringilla, 47. Chloris

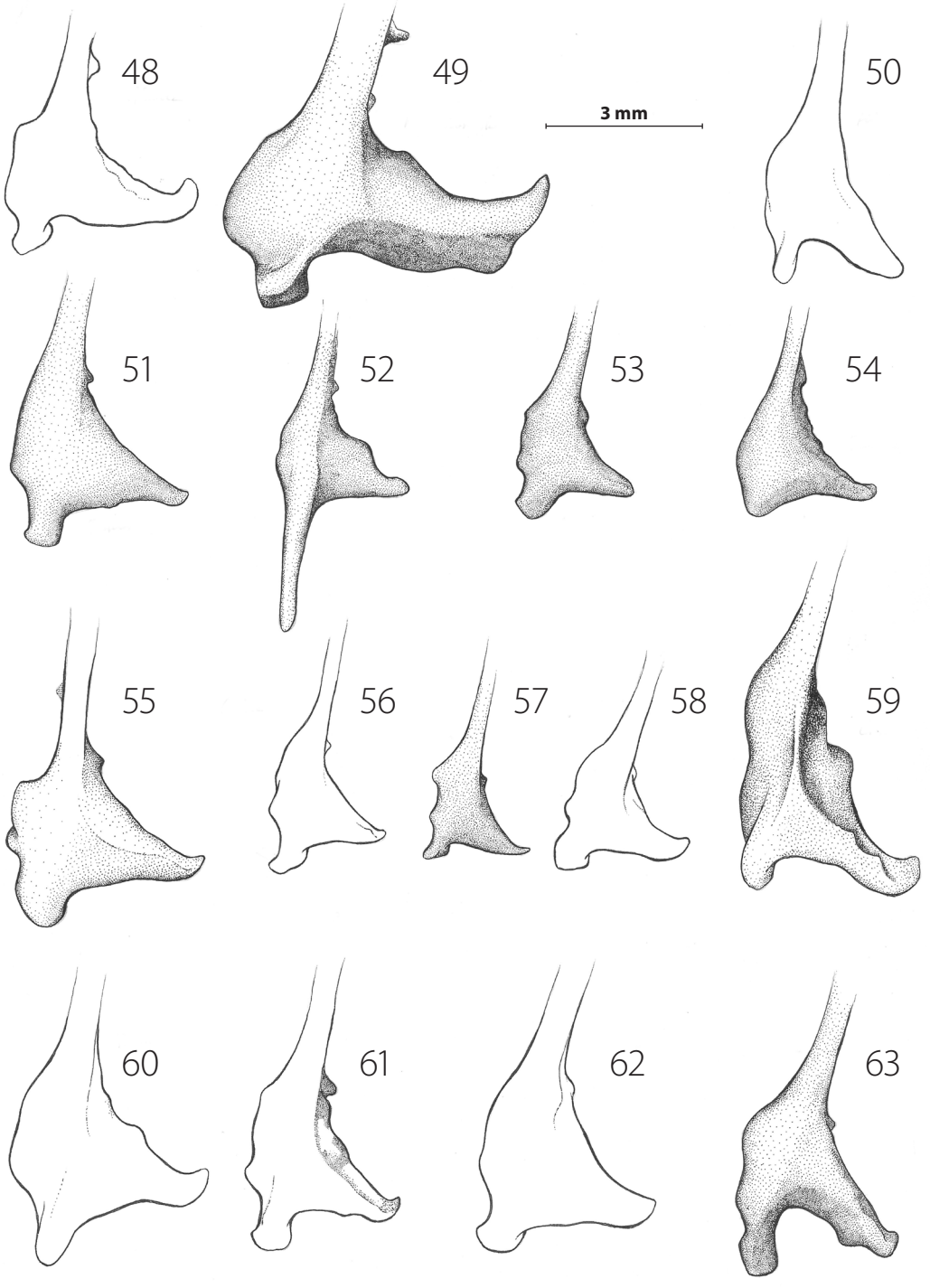

Plate 6. Caudal part of the lower jaws
6. táblakép Az állkapocs caudalis része
48. Alauda, 49. Melanocorypha, 50. Hirundo, 51. Parus, 52. Remiz, 53. Aegithalos, 54. Panurus, 55. Sitta, 56. Certhia, 57. Regulus, 58. Troglodytes, 59. Cinclus, 60. Prunella, 61. Motacilla, 62. Sylvia, 63. Muscicapa

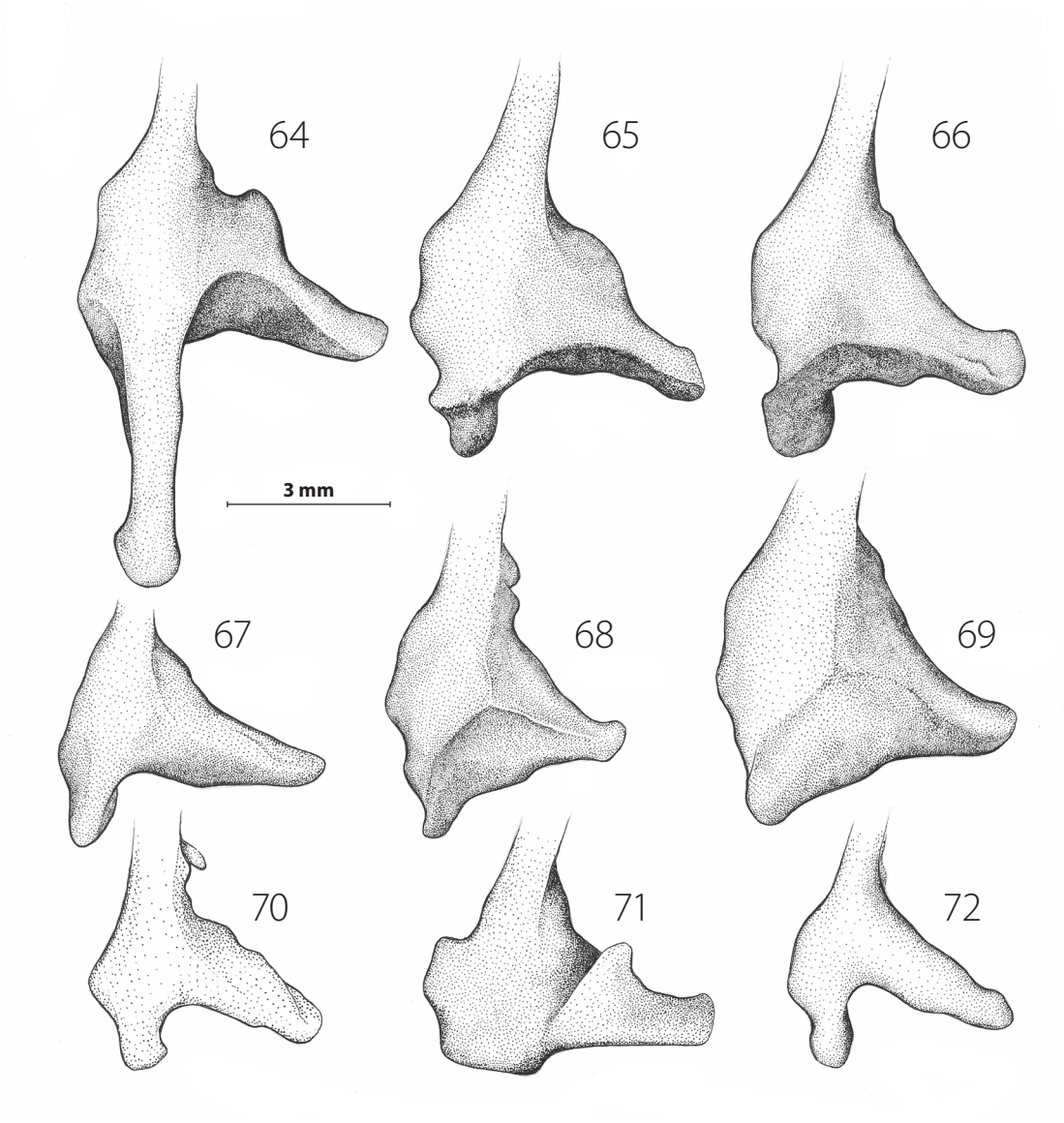

Plate 7. Caudal part of the lower jaws
7. táblakép Az állkapocs caudalis része
64. Sturnus, 65. Pastor, 66. Turdus, 67. Bombycilla, 68. Lanius, 69. Oriolus, 70. Passer, 71. Chloris, 72. Emberiza