Adaptation of seedsnipes (Aves, Charadriiformes, Thinocoridae) to browsing: a study of their feeding apparatus

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ABSTRACT

The present study describes in detail for the first time the skeleto-muscular system of the jaw and hyoid apparatus (i.e. feeding apparatus) of seedsnipes (Thinocoridae), a small (two genera, four species) South-American bird family the biology and particularly the diet of which are still barely known. Morpho-functional analyses interpreted in the light of presently available behavioural and diet data show a strongly developed adaptation to the removal of attached plant items based on the acquisition of the separate control of jaws. In order to acquire this mechanism and because they are separated in two very different size-classes, large *Attagis* and small *Thinocorus* species did not modify the same osteo-muscular structures. *Attagis* species expanded *m. pseudotemporalis superficialis* of which they increased the intricacy of the internal aponeurotic system. *Thinocorus* species evolved a specific orbito-zygomatic process (mainly by expansion and fusion of postorbital and zygomatic processes by ossification of aponeuroses), expanded the medial portion of the external adductor of the mandible and increased the complexity of the aponeuroses of this medial portion. Seedsnipes appear to be well specialized in the continuous removal of small plant fragments thanks to a tongue raising mechanism joint to enlarged salivary glands and crenate areas in the buccal cavity. Thinocoridae seem to have followed a morpho-functional evolutionary pathway similar to that followed by sandgrouse (Pteroclididae) in the course of the adaptation of their bill and hyoid apparatus to a vegetarian diet essentially based on the removal of small attached plant fragments in rather similar habitat conditions.

KEY WORDS
Aves,
Charadriiformes,
Thinocoridae,
Thinocorus,
Attagis,
functional morphology,
feeding adaptations,
jaw and hyoid apparatus,
birds,
seedsnipes,
sandgrouse.

RÉSUMÉ

L'adaptation des attagis et thinocores (Aves, Charadriiformes, Thinocoridae) au broutage : une étude de leurs appareils du bec et hyoïdien.

Dans la présente étude sont décrits en détail pour la première fois le squelette et la musculature des appareils du bec et hyoïdien des Thinocoridae, petite famille (deux genres, quatre espèces) d'oiseaux sud-américains dont la biologie demeure plutôt mal connue. Les analyses morpho-fonctionnelles, interprétées à la lumière des données actuellement disponibles sur le comportement et le régime alimentaire, montrent une profonde adaptation au détachement d'items végétaux fixés fondée sur l'acquisition du mécanisme de contrôle séparé du mouvement des mâchoires. Pour acquérir ce mécanisme et en raison de leur séparation en deux classes de taille fort différentes les attagis (grandes espèces) et les thinocores (petites espèces) n'ont pas modifié les mêmes structures ostéo-musculaires. Les premiers ont développé le *m. pseudotemporalis superficialis* dont ils ont complexifié le système interne des aponévroses alors que les seconds ont à la fois constitué un processus orbito-zygomatique (essentiellement par développement et fusion des processus post-orbitaire et zygomatique par ossification des aponévroses) et développé la portion médiale de l'adducteur externe de la mandibule dont ils ont également complexifié la structure aponévrotique. Les Thinocoridae apparaissent bien spécialisés dans le détachement en continu de petits fragments végétaux grâce à un système de relèvement de la langue couplé à un système de glandes salivaires développées et à un dispositif de zones crénelées dans la cavité buccale. Les Thinocoridés semblent avoir suivi un cheminement évolutif morpho-fonctionnel similaire à celui des gangas (Pteroclididae) durant l'adaptation de leurs appareils du bec et hyoïdien à un régime alimentaire végétarien basé pour l'essentiel sur le prélèvement de petits fragments végétaux fixés, dans des conditions d'habitat relativement similaires.

MOTS CLÉS
Aves,
Charadriiformes,
Thinocoridae,
Thinocorus,
Attagis,
morphologie fonctionnelle,
adaptations trophiques,
bec et appareil hyoïdien,
oiseaux,
attagis et thinocores,
gangas.

INTRODUCTION

Endemic to Patagonia and the Andean zone of South America, the four species of seedsnipes (two in each of the genera *Thinocorus* Eschscholtz, 1829 and *Attagis* Geoffroy Saint-Hilaire & Lesson, 1831) represent a lineage of grass steppe, semi-desert and alpine habitats birds (Fjeldså 1996). Their taxonomic position is still discussed although molecular as well as anatomical data converge in placing them among the Charadriiformes; their closest relative appears to be the Plains-wanderer *Pedionomus torquatus* Gould, 1841, an endemic of the lowland native grasslands of eastern Australia (Sibley *et al.* 1968; Strauch 1978; Olson & Steadman 1981; Sibley & Ahlquist 1990; Paton *et al.* 2003; Paton & Baker 2006).

These birds are particularly interesting because in their shape, morphology, behaviour and habitat (see MacLean 1969; Fjeldså 1996): 1) they resemble buttonquails (Turnicidae, a family of birds usually placed in the Gruiformes but which is most probably the sister group of the Lari among the Charadriiformes [Paton *et al.* 2003; Paton & Baker 2006]); 2) particularly *Thinocorus* species, they also resemble sandgrouse (Pteroclididae, a family closely allied to Columbiformes but that some authors place among the Charadriiformes or close to them in a separate order, see Sibley & Ahlquist 1990); and 3) particularly *Attagis* species, they also look like ptarmigans (Galliformes). The four species (which quite exceptionally for Charadriiformes have a crop, a gizzard and long intestinal caeca) are almost certainly strictly vegetarian, feeding on tiny bits of plants, e.g., buds, leaf tips, small green leaves and seeds. Many not to say most food items come from succulent plants: nobody ever observed them drinking in the wild although they may do that in captivity (see MacLean 1969; Fjeldså 1996, and references therein).

Although there exist some general descriptions of the skull (e.g., Olson & Steadman 1981), the anatomy of the jaw apparatus of the Thinocoridae had not been previously studied in details. Only Fjeldså (1996) mentions in *Thinocorus* the strong tendon, ossified along much of its length, originating from the postorbital and zygomatic processes and connecting the mandible with the postorbital region of the skull. He suggests that the bill might be primarily adapted for high-precision browsing. He also insists on the fact that the skull of *Attagis* differs in many respects from that of *Thinocorus* but that the functional implications of this are still unknown.

As we have already agreed (see e.g., Korzun *et al.* 2003, 2004a, b, 2008), descriptive morphology is the source of functional information and a mean to propose hypotheses. Our objective is to obtain new data on the adaptations of the studied species, these adaptations being considered as a state and as content of evolutionary transformations. We interpret observed osteo-muscular characters in terms of functional units. In the present study we describe the jaw and hyoid apparatus of the Thinocoridae, based on the dissection of heads of specimens of both *Thinocorus* and *Attagis*. We examine whether the observed characters support the hypothesis that Thinocoridae are mechanically adapted to browse, bite off, attached succulent plant food items from which they also extract the water they require.

MATERIAL AND METHODS

MATERIAL EXAMINED

We dissected specimens of *Thinocorus orbignyianus* Geofroy Saint-Hilaire & Lesson, 1831 (one adult, in the Muséum national d'Histoire naturelle, Paris), *T. rumicivorus* Eschscholtz, 1829 (a young, from the Zoologisk Museum, Copenhagen) and *Attagis gayi* Geoffroy Saint-Hilaire & Lesson, 1831 (one adult from the American Museum of Natural History, New York, AMNH 11213).

The ornithological nomenclature used is that of the classical *Checklist of the Birds of the World* (see Dickinson 2003).

For all species we examined the skull as well as the cranial muscles and the hyoid skeleton and musculature.

Working procedure

We conducted a biomechanical analysis of the skull and dissected the musculature associated with the functioning of the jaw apparatus. Specimens were examined under magnifying binocular glasses Leica WILDM3Z and Zeiss SV11; drawings were done with a drawing tube Zeiss S. Syndesmological preparations were handled to simulate all possible movements and allowed better analyses.

We follow here the nomenclature of muscles and aponeuroses (Dzerzhinsky & Potapova 1974) which we used elsewhere (e.g., Korzun *et al.* 2004a, 2008). Muscles and aponeuroses originate on the braincase and insert on the mandible and other moving parts.

The general morpho-functional approach to the bill and hyoid apparatus that we follow here has already been applied to various groups of birds (cf. Korzun *et al.* 2004b). It rests on methods that use anatomically-based working drawings to conduct graphical analyses of the static balance of the forces during gripping and manipulation of items (Dzerzhinsky 1972; a method elaborated in the continuity of von Kripp 1933 and Kummer 1959). Contrasted with available biological, ecological and behavioural data, results bring precision on the mechanical functions of the jaw and hyoid apparatus considered as a single functional unit. These functions can be interpreted in terms of feeding adaptations and generate new hypotheses testable through direct observation of living animals.

Morpho-functional analyses have been interpreted in the light of the relatively few behavioural and diet data on the species existing in the literature (see MacLean 1969; Fjeldså 1996 and references therein).

Abbreviations

Muscle aponeuroses

ace	*aponeurosis caudalis externa*;
aci	*ap. caudalis interna*;
acg	*ap. ceratoglossis*;
ad	*ap. depressoris*;
ado	*ap. dorsalis originalis*;
ai	*ap. interna*;
ali	*ap. lateralis insertionis*;
alm	*ap. lateralis mandibularis*;
alo	*ap. lateralis originalis*;
am	*ap. medialis*;
am1-3	aponeuroses of origin of the medial portion of the external adductor;
ami1-3	aponeuroses of insertion of the medial portion of the external adductor;
amq	*ap. medioquadrata*;
amr	*ap. mediorostralis*;
ams	*ap. mediosuperficialis*;
ao	*ap. occipitalis*;
apm	*ap. pseudotemporalis mandibularis*;
app	*ap. pseudotemporalis profunda*;
apo	*ap. postorbitalis*;
apq	*ap. posterior quadrata*;
aps	*ap. pseudotemporalis superficialis*;
ar	*ap. rostralis*;
as	*ap. superficialis*;
avi	*ap. ventralis insertionis*;
avo	*ap. ventralis originalis*.

Other abbreviations

Aec	*m. adductor mandibulae externus profundus caudalis*;
Aem	*m. add. md. ext. medialis*;
Aer	*m. add. md. ext. profundus rostralis*;
Aes	*m. add. md. ext. superficialis*;
Ap	*m. add. md. posterior*;
Bas	*basihyale*;
Bm	*m. branchiomandibularis*;
Bmc	*m. branchiomandibularis caudalis*;
Bmr	*m. branchiomandibularis rostralis*;
Bpt	vestigial basipterygoidal joint;
Cb	*ceratobranchiale*;
Cga	*m. ceratoglossus anterior*;
Cgp	*m. ceratoglossus posterior*;
Ch	*m. ceratohyoideus*;
cl	lateral condyle of the quadrate in the mandibular joint;
cm	medial condyle of the quadrate in the mandibular joint;
Dm	*m. depressor mandibulae*;
Ent	*entoglossum*;
Fl	leaf fragment;
Gls	salivary gland;
Hp	*m. hypoglossus*;
Jg	*jugale* (*arcus jugalis*);
Lji	*lig. jugomandibulare internum*;
Lom	*lig. occipitomandibulare*;
Lp	*lig. postorbitale*;
Md	*mandibula*;
Mst	*mesethmoideum*;
Mstcr	rostral crest of the mesethmoid;
Mh	*m. mylohyoideus*;
Ns	(*os*) *nasale*;
NV	*nervus trigeminus*;
Oc	olfactory capsule;
Pdl	*m. pterygoideus dorsalis lateralis*;
Pdm	*m. pt. dorsalis medialis*;
Pl	*palatinum*;
Pim	*processus internus mandibulae*;
Ppm	*proc. palatinus* (*ossis*) *maxillaries*;
Po	*proc. orbitalis* (*ossis*) *quadrati*;
Poz	*processus occipito-zygomaticus*;
Ppo	*proc. postorbitalis*;
Pr	*m. protractor pterygoidei et quadrati*;
Pra	*proc. retroarticularis*;
Psp	*m. pseudotemporalis profundus*;
Pss	*m. pseudotemporalis superficialis*;
Pt	(*os*) *pterygoideum*;
Pvl	*m. pt. ventralis lateralis*;
Pvm	*m. pt. ventralis medialis*;
Pz	*proc. zygomaticus*;
rc	row of crenellation;
Sf	serrated fold;
Sn	*septum nasale*;
So	*septum orbitale*;
Tng	tongue;
Ur	*urohyale*;
Q	(*os*) *quadratum*;

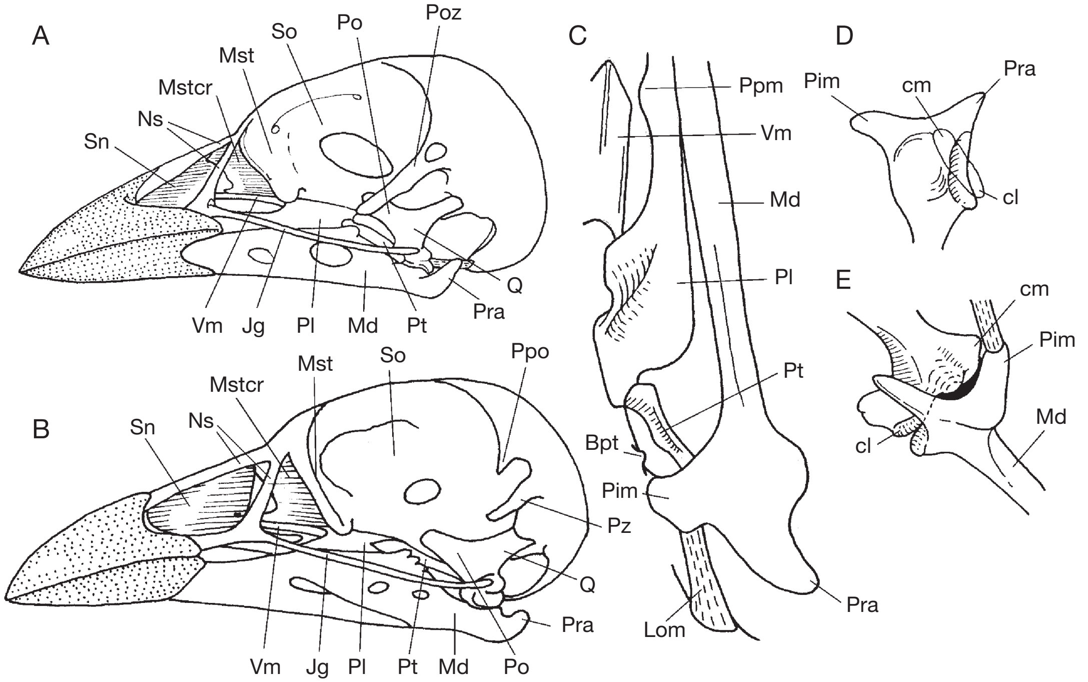

FIG. 1. — Particularities of seedsnipe's skull: **A**, *Thinocorus orbignyianus* Geoffroy Saint-Hilaire & Lesson, 1831; **B**, *Attagis gayi* Geoffroy Saint-Hilaire & Lesson, 1831; **C**-**E**, *Thinocorus* Eschscholtz, 1829; **C**, ventral view of the mandible and palate; **D**, surface of the mandibular joint with location of the contact area of the lateral and caudal condyles of the quadrate; **E**, caudal view of the mandibular joint. Abbreviations: see text.

Sh	*m. serpihyoideus*;
Sth	*m. stylohyoideus*;
Vm	(*os*) *vomer*.

RESULTS

ANATOMICAL CHARACTERISTICS OF THE BILL OF THE THINOCORIDAE

All the following descriptions apply to the genus *Thinocorus* as well as to the genus *Attagis*. When they exist, differences between these genera are clearly indicated.

Skull

The skull of Thinocoridae (Fig. 1A, B) is clinorhynchic, i.e. the base of the upper jaw and that of the neurocranium make an obtuse angle. Bill is relatively thick. Culmen is curved but the extremity of the upper jaw, with the rhamphotheca, is not hooked and overhangs only very slightly the rounded tip of the mandible. The rims of the rhamphotheca of the upper jaw overlap those of the mandible, making a kind of scissors.

The rounded external nares are covered with a keratinized fold of skin which leaves open just a narrow horizontal slit. Each bony naris extends almost over half the length of the upper jaw and dorso-caudad ends in an acute angle the vertex of which inserts just slightly between the maxillary and pre-maxillary processes of the nasal bone.

The pliable area of the upper jaw (a hinge between the upper jaw and the neurocranium) is clearly indicated by a very narrow slot between the caudal edge of the nasal septum and the rostral crest of the mesethmoid. It is located a little frontal relatively to the vertex of the dorso-caudal extremity of the bony naris. The pliable area of the maxillary process of the nasal is more caudal, located at the level of the vertex of the bony naris. Such an arrangement of the pliable areas explains well the unavoidable warping of the upper jaw during protraction. This is clearly visible when one manipulates syndesmological preparations.

The palate is of the schizognathous type, i.e. the contralateral halves of the upper jaw are separated by a wide slot. In *Thinocorus* the palatine processes of the maxillars slightly overlap the lateral edge of the palatines. On the other hand they are larger in *Attagis* where they extend caudad along the surface of the palatines and more clearly overlap the medial edge of the palatines but nevertheless leave a wide slot between them. The enlarged blade-like caudal part of the palatines is not oriented in the frontal plane, i.e. the lateral edges of these blades are more ventral than the medial edges which are applied to the base of the interorbital wall. This latter separates the palatines along most of their length; these bones join only by their caudal extremity near the contact zone with the pterygoids. Sympalatiny exists but is not very well marked. The vomer is wide and flattened, and its caudal processes attach to the palatines (diastasy *fide* Hofer 1945). In its medial half the enlarged part of the palatines bears a ventrally oriented blade. In *Attagis* the medial edge of the ventral wing of the palatines is fixed to the palatine process of the maxillar by a very narrow bridge; this link is absent in *Thinocorus*.

The pterygoids are straight. There is no basipterygoidal joint in adults: there is no contact between pterygoids and skull base. In adult *Thinocorus*, on the basisphenoid there is however a small bump oriented towards the pterygoids which them too possess a small bump oriented towards cranium base (Fig. 1C) whereas in the young (here a *pullus* of *T. rumicivorus*) there is a true basipterygoidal joint. We failed to find any such bumps in adult *Attagis*.

The quadrate has an enlarged orbital process and three condyles in the quadrato-mandibular joint. The lateral and caudal condyles make a saddle, with convexity oriented downwards and connected to the concave lateral edge of the mandible in the joint area (Fig. 1D, E). In the posterior part of the latter there is a groove in which the caudal condyle of the quadrate goes down when the mandible lowers. It must be noted here that this caudal condyle does not come into direct contact with the mandible. The medial condyle is medially well apart of the other two. The longitudinal axis of this medial condyle is almost perpendicular to the longitudinal axis of the skull. There are two condyles in the quadrato-cranial joint. The axis passing through these two condyles is oriented almost perpendicular to the longitudinal axis of the pterygoid.

In the braincase the interorbital septum shows two windows rather small in *Attagis* but rather large in *Thinocorus*. The anterior wall of the orbit is constituted by the large lateral wing of the mesethmoid. The olfactory capsules fill a great volume in the upper jaw and even give the impression that they push the mesethmoids backwards. We did not find any trace of lacrymal, even in the *pullus* of *T. rumicivorus* we examined as this bone could have been visible before an eventual fusion with the wing of the mesethmoid.

The greatest cranial difference between *Attagis* and *Thinocorus* lies on the relation between the postorbital and zygomatic processes (Fig. 1A, B). In *Attagis*, these processes are typical of those found in most birds whereas in *Thinocorus* a part of the large superficial aponeurosis of the head that attaches to the postorbital process is ossified and fuses with the equally ossified aponeurosis of the medial portion of the external adductor. These two ossified aponeuroses build a very long process (a fact also pointed out by Fjeldså 1996 and illustrated in Olson & Steadman 1981) that for convenience we call thereafter “orbito-zygomatic process”. This process extends down almost to the dorsal edge of the mandible and its transversal section is shaped as a V pointing towards the orbit (see below, Fig. 5A, a, B, b). At the base of this process there is a small window through which pass muscular fibres of the rostral part of the deep portion of the external adductor of the mandible. The parts of the aponeuroses which contribute to form the orbito-zygomatic process of the adult are not yet ossified in the *pullus* of *T. rumicivorus*.

The mandible shows two windows the most caudal one being smaller in *Attagis* than in *Thinocorus*. The mandible has a rather particular shape in that its height increases gradually and caudad along the first three quarters of its length, and then decreases

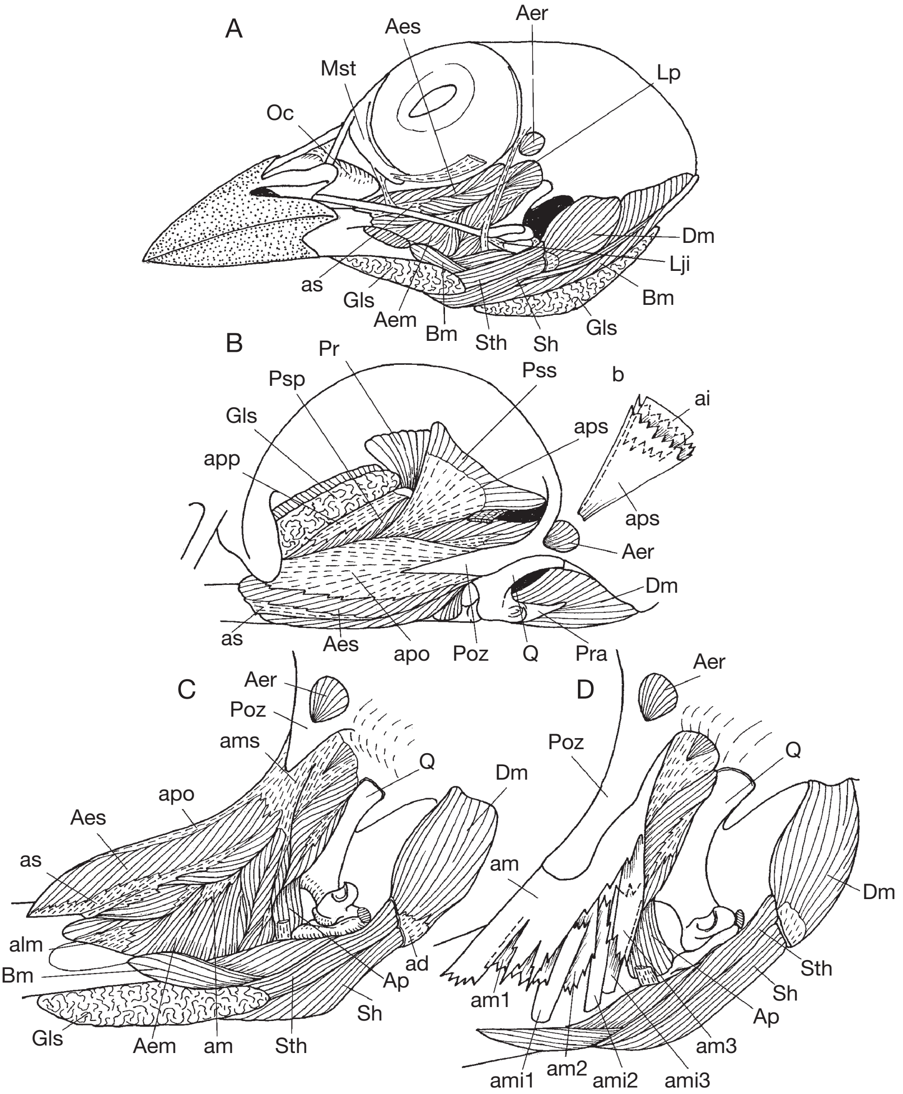

FIG. 2. — Cranial musculature of *Thinocorus* Eschscholtz, 1829, successive planes of the dissection: **A**, general view; **B**, lateral view through the orbit; **b** aponeuroses of *m. pseudotemporalis superficialis*; **C**, **D**, lateral views of the superficial and medial portions of the external adductor. Abbreviations: see text.

along the last quarter. The maximal height (marked by bumps corresponding to the attachments of the aponeuroses of insertion of the external adductor) is plumb with the rostral end of the orbito-zygomatic process. The mandible also shows an upward-hooked retro-articular process as well as a well-marked internal process (Fig. 1A-C).

Cranial musculature (Figs 2-6)

According to the classical morphological opinion (Lakjer 1926), cranial muscles may be divided into adductors and protractors. The adductors of the mandible are divided into an external adductor (*m. adductor mandibulae externus*), a posterior adductor (*m. adductor mandibulae posterior*) and three internal

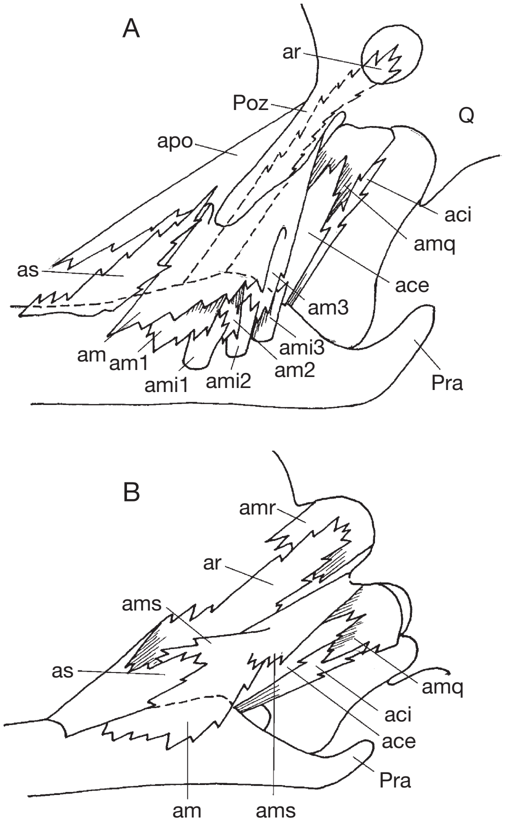

FIG. 3. — Schema of the arrangement of the internal aponeuroses of external adductor in *Thinocorus* Eschscholtz, 1829 (**A**) and *Attagis* Geoffroy Saint-Hilaire & Lesson, 1831 (**B**). Abbreviations: see text.

adductors (*m. pseudotemporalis superficialis*, *m. pseudotemporalis profundus* and *m. pterygoideus*). However, from a functional viewpoint the external and posterior adductors, together with the two *mm. pseudotemporales*, are generally seen as constituting the group of the dorsal adductors whereas *m. pterygoideus* is considered as the ventral adductor.

Among the cranial muscles we find also the protractor of the quadrate (*m. protractor quadrati*), the protractor of the pterygoid (*m. protractor pterygoidei*) and the depressor of the mandible (*m. depressor mandibulae*).

M. adductor mandibulae externus. The external adductor of the mandible includes three portions: one superficial, one medial and one deep. The latter is composed of two parts: one rostral and one caudal. It is useful to point out that in Thinocoridae the superficial portion attaches to the dorsal edge of the mandible very far forwards, passing below the eye and under the mesethmoid, almost reaching the level of the olfactory capsule. This superficial portion has a rather complex internal structure.

In *Thinocorus* (Figs 2A-C; 3A) the aponeuroses of origin and of insertion of this superficial portion are much enlarged. The aponeurosis of insertion **as** attaches along the dorsal edge of the mandible. Its central part is very thick and very elongated dorsocaudad. At the surface of this aponeurosis attach muscular fibres originating from the lateral surface of the aponeurosis of origin **am** of the medial portion and from the surfaces of the two aponeuroses of origin of the superficial portion, **apo** and **ams**. Aponeurosis **apo** seems to be a continuation of the orbital branch of the orbito-zygomatic process, and **ams** to represent a short lateral lobe of **am**, lateral to its base. The aponeurosis of origin **apo** is also very long (like **as**) and wide, and it even wraps up **as** a little and then extends parallel to it. Aponeurosis **apo** is fused at its origin with the aponeurosis **ams.** It is important to underline here that muscular fibres from **apo** also insert more medially than **as** on the particularly enlarged surface of the dorsal border of the mandible.

In *Attagis* (Figs 3B; 4B, C), the superficial portion differs from that in *Thinocorus*. Although extending as far forwards as in *Thinocorus*, in *Attagis* the aponeurosis of insertion **as** shows a shorter and more localized attachment. The rostral part of this aponeurosis **as** folds medially, giving rise to an extension which, attaching farther caudad to the dorsal edge of the mandible, makes a long aponeurosis **ar** which belongs to the rostral part of the deep portion of the external adductor of the mandible. The aponeurosis of origin **ams** is in two parts: one originates from the surface of the aponeurosis **am**, the other is formed by the laterally folded rostral edge of **am**. There are no signs of the aponeurosis of origin **apo**.

Differences also exist between the two genera of Thinocoridae in the medial portion of the external adductor of the mandible. In *Thinocorus* (Figs 2C, D; 3A) the internal structure is very particular and

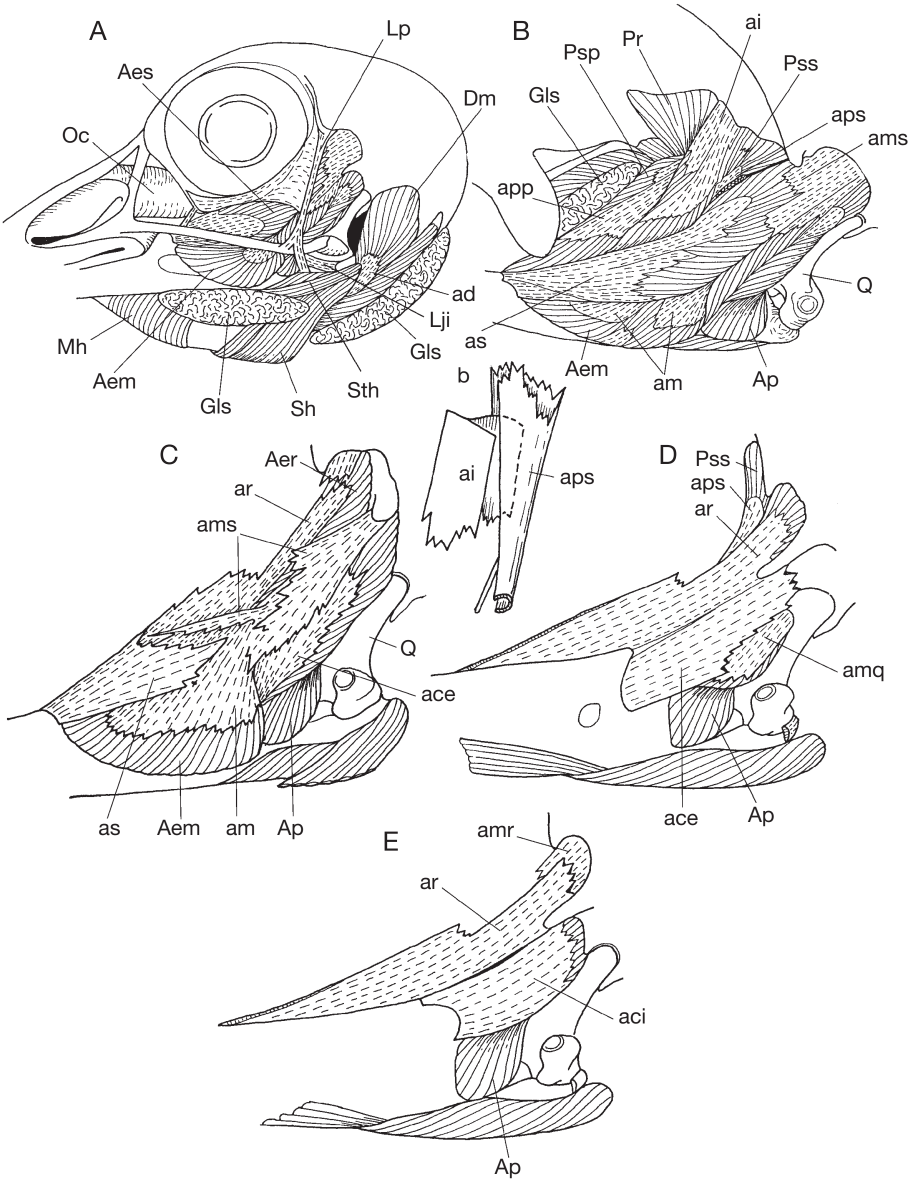

FIG. 4. — Cranial musculature of *Attagis* Geoffroy Saint-Hilaire & Lesson, 1831, successive planes of the dissection: **A**, general view; **B**, lateral view through the orbit; **b**, internal aponeuroses of *m. pseudotemporalis superficialis*; **C**-**E**, lateral views of portions of the external adductor. Abbreviations: see text.

complicated. In most studied avian groups there is only a single aponeurosis of origin **am** and sometimes a small aponeurosis of insertion (**alm**) attached to the lateral surface of the mandible. In *Thinocorus* there exists in the medial portion of the external adductor a system of aponeuroses of origin (**am1**, **am2**, **am3**) in which the aponeurosis **am** is separated into four aponeurotic blades attached to the orbito-zygomatic process, and a system of three aponeuroses of insertion (**ami1**, **ami2**, **ami3**) which attach to the lateral surface of the mandible. The number of aponeuroses in this portion increases caudad: the closest is the mandibular joint the most numerous they are. In general extension and shape (superficial view) the medial portion in *Attagis* looks like that in *Thinocorus* however the dissection shows that the aponeurosis **am** is not internally divided (Figs 3A; 4C).

In both genera the most enlarged part of the deep portion of the adductor is the caudal one. The rostral part is smaller in *Thinocorus* than in *Attagis*.

In *Thinocorus* (Fig. 5D) this rostral part of the deep portion extends below the orbito-zygomatic process, a small part coming from the surface of the braincase after passing through the window located at the base of this process. The aponeurosis of insertion **ar**, bifid at its top (one external blade and one internal) is rather thick and independent, i.e. without link with the aponeurosis of insertion **as** as in *Attagis* (Fig. 4C, D). The internal blade receives muscular fibres coming from the aponeurosis of origin **amr** and from the deep niche between **amr** and the quadrate. The external blade receives muscular fibres coming from the internal surface of the orbito-zygomatic process and from the surface of the braincase from where these fibres pass through the window located at the base of the orbito-zygomatic process.

As described above, there is in *Attagis* a relation between **ar** (which is not bifid) and **as**. The aponeurosis of origin **amr** attaches to the skull in front of the zygomatic process.

In Thinocoridae, there are one aponeurosis of origin and two of insertion in the caudal part of the deep portion of the adductor. The aponeurosis of insertion **ace** attaches near the highest point of the mandible; its rostral edge is very thick. In *Thinocorus* (Fig. 5C) the non-ossified part of **am** that fringes the ossified part gives rise to the aponeurosis of origin **amq** of the caudal part of the deep portion of the external adductor. This aponeurosis **amq** attaches to the skull, caudal to the orbito-zygomatic process, and to the quadrate. In *Attagis* too (Fig. 3D, E), **amq** is the caudal extension of the aponeurosis **am** but here **am** passes through the narrow slot between **ace** and **ar** before forming **amq**. The deepest aponeurosis of this caudal part is the aponeurosis of insertion **aci**. This aponeurosis keeps the link with the aponeurosis **ar** in *Attagis* but not in *Thinocorus*.

M. pseudotemporalis superficialis. It is quite large in both genera between which differences exist. It is more typical in *Thinocorus* (Fig. 2B, b). Its aponeurosis of insertion **aps** makes a kind of funnel which attaches to the internal side and at the highest part of the mandible. Into this funnel enters the aponeurosis of origin **ai** which is attached to the crest of the posterior wall of the orbit. More medial to this crest there is a niche filled by muscular fibres directed to the internal surface of **aps**. In *Attagis* (Fig. 4B, b) this muscle is larger and more complex. Its aponeurosis of insertion makes also a medially-open funnel and its point of insertion is marked by a bump on the dorsal edge of the mandible. The aponeurosis of origin **ai** begins more medially on the skull than in *Thinocorus*. It forms two blades. An internal one gets into the funnel and the muscular fibres of its surface go to the internal surface of the aponeurosis **aps**. An external blade is located outside the funnel and the muscular fibres which attach to its surface extend down to the internal surface of the mandible, giving rise to a voluminous additional portion of the muscle. It is important to note here the presence of a very narrow aponeurosis which originates from the lower part of the aponeurosis **aps** and vanishes into the additional portion (Fig. 4, b). It is very interesting that this tendinous tail resembles closely the aponeurosis of origin of the intramandibular portion in the Fulmar (Dzerzhinsky & Yudin 1979).

M. pseudotemporalis profundus. It is enlarged in both genera. It originates from the orbital process of the quadrate (its aponeurosis of origin **app** is attached to the rostral extremity of the process) and inserts on the internal surface of the mandible (aponeurosis of insertion **apm**). In *Thinocorus* (Fig. 5E, e) the aponeurosis **app** is particularly enlarged so that its inferior edge is located much lower than the dorsal edge of the mandible whereas in *Attagis* this inferior edge does not reach the mandible.

M. pterygoideus. Usually four portions are distinguished: two ventral and two dorsal. We did not find

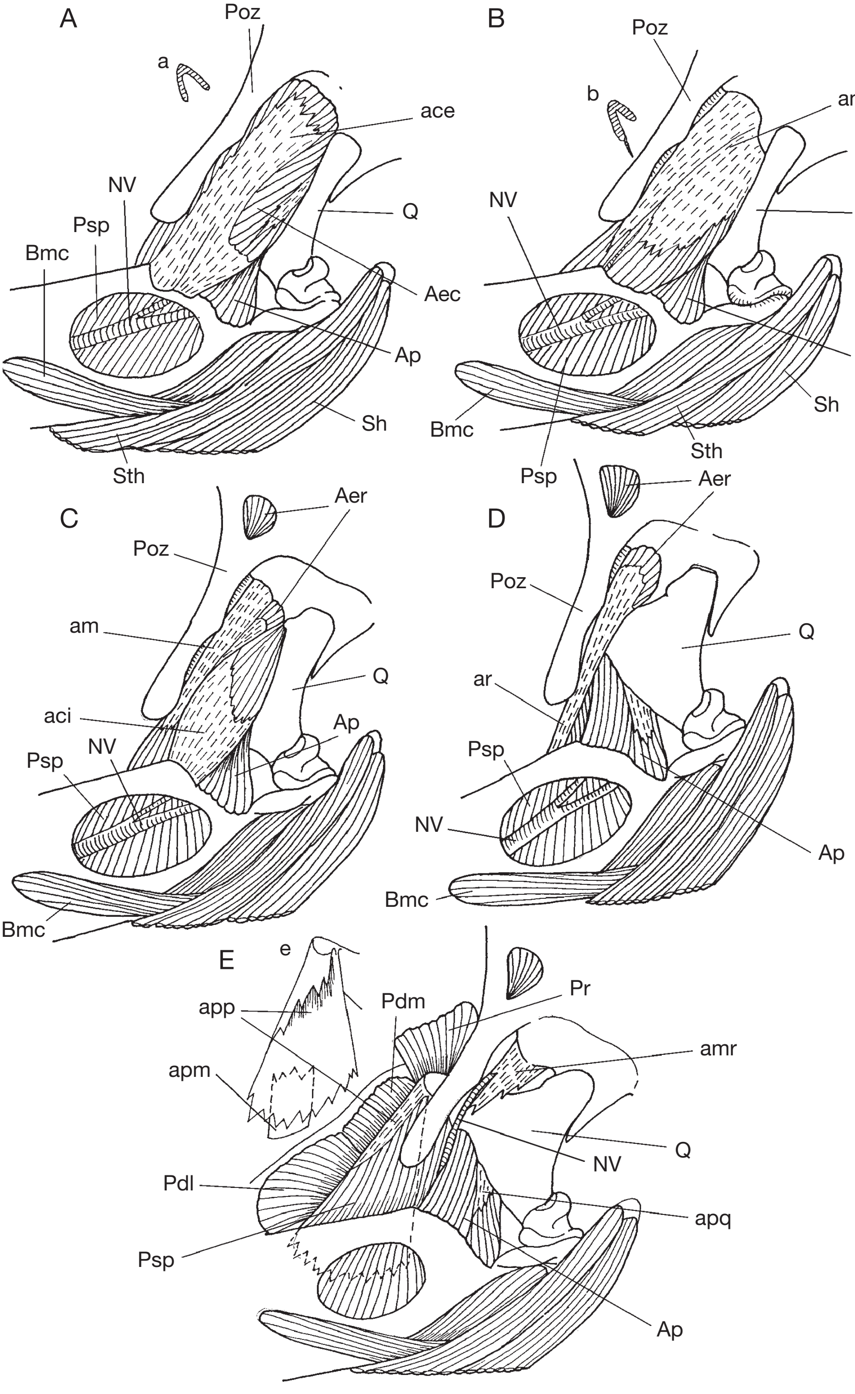

FIG. 5. — Lateral views of the successive planes of the dissection of the dorsal adductors in *Thinocorus* Eschscholtz, 1829: **A**-**D**, deep portion of the external adductor; **E**, *m. pseudotemporalis profundus,* posterior adductor and protractors; **a**, **b**, transversal sections of the orbito-zygomatic process; **e**, aponeuroses of *m. pseudotemporalis profundus.* Abbreviations: see text.

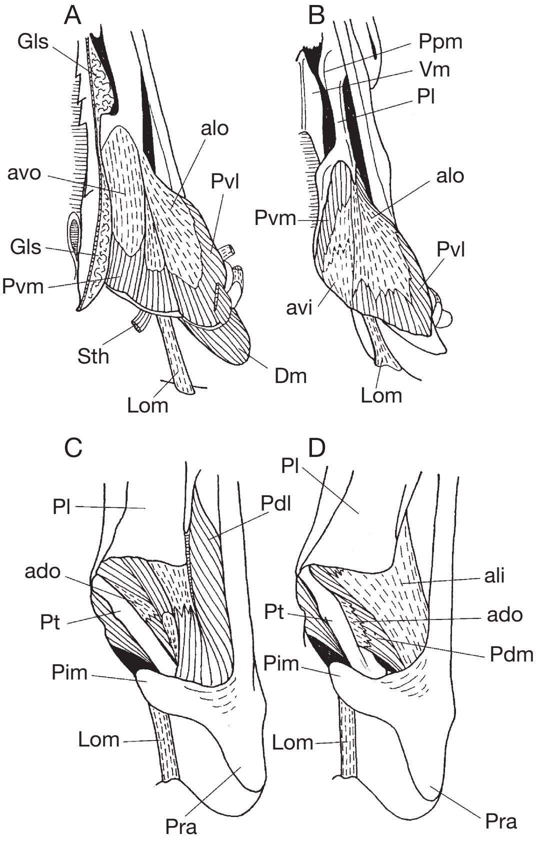

FIG. 6. — **A**-**D**, ventral views of the successive planes of the dissection of *m. pterygoideus* in *Thinocorus* Eschscholtz, 1829. Abbreviations: see text.

any significant difference between the two genera. The ventral portions (Fig. 6A, B) originate from the surface of the palatine and from the rostral part of the pterygoid. The ventro-lateral portion possesses a large aponeurosis of origin **alo** the superficial part of which attaches along the lateral edge of the palatine but which, after folding, attaches farther to the caudal edge. From its surface the muscular fibres extend to the ventral and lateral surface of the caudal part of the mandible. The ventro-medial portion contains two aponeuroses: one of origin **avo** which attaches transversely to the palatine and one of insertion **avi** which attaches at the top of the internal process of the mandible. The medial edge of the aponeurosis **avi** folds up dorsally, forming an additional blade.

The muscular fibres of the dorsal portions originate from the dorsal surface of the palatine and pterygoid, and from the dorsal surface of the aponeurosis **alo** (Fig. 6C, D). It must be noted that the origin of these fibres, particularly that of the most caudal ones, is more dorsal than their insertion. The muscular fibres of the dorso-lateral portion attach to the surface of the aponeurosis of insertion **ali** which itself attaches to the mandible, a little in front of the base of the internal process. The dorso-medial portion is separated from the other portions by its more transverse orientation of fibres. Most of its muscular fibres originate from the pterygoid. The aponeurosis of origin **ado** of this portion attaches to the specific crest of the lateral surface of the pterygoid. The muscular fibres of this portion insert on the surface of the aponeurosis of insertion **adi** and on the mandible at the base of its internal process.

Medial to the pterygoid are muscular fibres which make up a portion sometimes called caudal portion but which, in Thinocoridae, has no aponeurosis.

M. adductor posterior. It originates from the orbital process of the quadrate more basally than the *m. pseudotemporalis profundus* behind which it is located (Figs 2C, D; 4; 5). Its aponeurosis of origin **apq** attaches along the inferior part of the process. We did not find any significant difference between the two genera.

M. protractor quadrati **and** *m. protractor pterygoidei.* They are of the generalized type usually found in birds (Figs 2B; 4B). They are difficult to distinguish and separate in their area of origin which is located in the lower part of the posterior wall of the orbit. The muscular fibres of *m. protractor quadrati* insert on the quadrate near the mandibular joint whereas those of *m. protractor pterygoidei* attach to the caudal part of the pterygoid.

M. depressor mandibulae. It originates from the lateral surface of the occipital part of the skull and inserts on the retro-articular process of the mandible (Figs 2; 4A). Its aponeurosis of origin **ao** attaches along the paroccipital process. The external edge of this aponeurosis constitutes a ligament which links the paroccipital process to the top of the retro-articular process, and the internal edge fuses with the occipito-mandibular ligament. There is also a small aponeurosis of insertion **ad**.

Ligaments

Like *Attagis*, *Thinocorus* has an entirely non-ossified postorbital ligament (Figs 2A; 4A). Its origin remains free above the ossified orbito-zygomatic process which *Attagis* lacks (see above). This implies that the orbito-zygomatic process may result from the coalescence and ossification of two aponeuroses. One is the aponeurosis of origin **apo** of the postorbital part of the superficial portion of the *m. adductor mandibulae externus*. The other is the aponeurosis **am** of the medial portion of the *m. adductor mandibulae externus*. In both genera, the postorbital ligament is bifid at its insertion: one part attaches to the jugal bar, the other to the mandible.

In the mandibular joint there is no external jugo-mandibular ligament.

The internal jugo-mandibular ligament (Figs 2A; 4A) originates from the caudal extremity of the jugal bar, warps behind the mandibular joint and inserts on the base of the internal process of the mandible near the occipito-mandibular ligament. The internal jugo-mandibular ligament has a sesamoid ossicle behind the joint.

There is also a particular ligament which joins the lateral wing of the mesethmoid and the jugal bar (Figs 2A; 4A).

The occipito-mandibular ligament (Fig. 6) links the internal process of the mandible to the base of the skull. Its principal peculiarity is its very slanting, almost horizontal orientation: it is almost in the same plane as the mandible.

As noted above, the lateral edge of the aponeurosis of origin of the depressor of the mandible constitutes a ligament which links the paroccipital process to the top of the retro-articular process of the mandible (Fig. 7A).

Buccal cavity

The roof of the buccal cavity bears a transversal row of crenellations in its medial part and a serrated fold at the entrance of the oesophagus. The tegument of the buccal roof is rather flexible, covering large and individualized salivary glands.

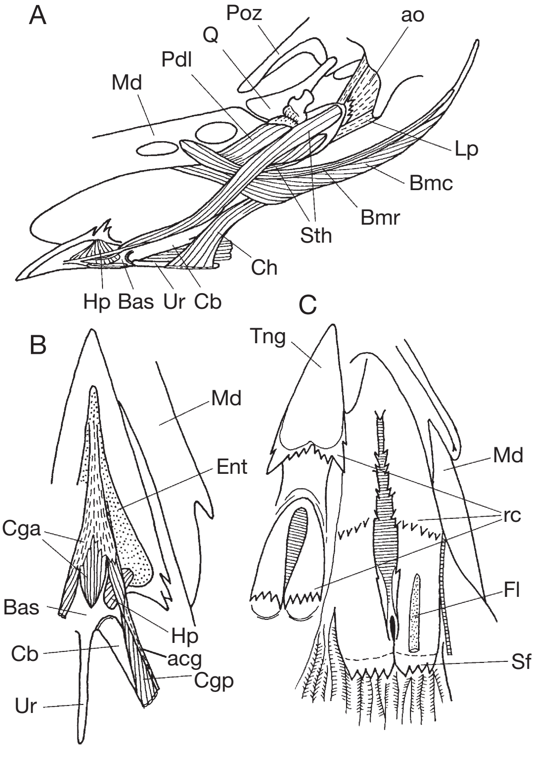

Fig. 7. — Hyoid apparatus and buccal cavity of seedsnipes (here *Thinocorus* Eschscholtz, 1829): **A**, lateral view of the hyoid apparatus displaced downward relative to the mandible; **B**, rostral part of the hyolingual apparatus; **C**, buccal cavity, the floor on the left, the roof on the right, a plant item present in the buccal cavity of the dissected specimen has been left in its place. Abbreviations: see text.

The tongue is relatively short and thick. It goes hardly beyond the mandibular symphysis. Its surface is rather flexible. Its posterior edge has on each side well-marked hard serrations. Behind the glottal slot there is also a row of serrations (Fig. 7).

Salivary glands

Without special dissection for their observation, four enlarged and individualized salivary glands were apparent during the study of the musculature (Figs 2A, B; 3A, B). One is located along the inferior part of the mandible (group of the *gl. mandibularis anterior* sensu Fahrenholtz 1937 and McLelland 1979), another one behind the hyoid horns (group of the *gl. mandibularis posterior*), a third one in the orbit along the palatines (*gl. palatinae*) and the fourth one in the buccal roof near the entrance of the oesophagus (*gl. sphenopterygoideae*).

Hyoid apparatus (Fig. 7)
M. mylohyoideus makes a kind of hammock caudally slung between the mandibular rami, from the symphysis to half the length of the rami (Fig. 3A). Between the two contralateral halves of the muscle there exists a longitudinal tendon: an aponeurotic band to which attach the muscular fibres of these contralateral halves.

M. serpihyoideus originates from the top of the retro-articular process of the mandible and, slantwise, attaches to the longitudinal tendon mentioned above.

M. stylohyoideus is bifid. One portion which includes most muscular fibres originates like *m. serpihyoideus* but a little more frontal, from the retro-articular process of the mandible. The other portion (a portion never observed before in any other Neognath) is smaller and originates from the base of the skull. Both portions fuse just underneath the ventral border of the mandible and then attach to the dorsal surface of the basihyal.

The muscular fibres of *m. ceratohyoideus* originate from the caudal half of the ceratobranchial and attach also to the longitudinal tendon which fuses at this level with the urohyal.

M. branchiomandibularis is composed of two portions: one caudal and one rostral. The caudal portion originates from the caudal part of the epibranchial, passes along the hyoid horn and inserts on the lateral surface of the mandible. The rostral portion originates also from the epibranchial, follows the hyoid horn wrapping it into a kind of case and attaches to the internal surface of the mandible.

M. ceratoglossus is double-bellied. The fibres of *m. ceratoglossus posterior* originate from the surface of the ceratobranchial. They end as a long tendon which inserts on the ventral surface of the entoglossal (*sensu* Engels 1938: internal skeleton of the tongue, i.e. paraglossal and its anterior and posterior processes, see also Tomlison 2000). *M. ceratoglossus anterior* (Fig. 7B) is relatively complicated. Its two contralateral parts originate from the surface of the tendons of insertion of *m. ceratoglossus posterior*. Together with the medial part which attaches to the basihyal, they end by a common aponeurosis which passes along and under the entoglossal and attaches near its rostral extremity.

M. hypoglossus is triangular in shape. Its base attaches to the ventral surface of the basihyal and its vertex inserts in the caudal corner of the entoglossal.

We did not find *m. genioglossus*.

DISCUSSION

There are still relatively few detailed biological data on the Thinocoridae. The most significant observations have been synthesized by MacLean (1969) and Fjeldså (1996). The four species appear to be strictly vegetarian (even their *pulli* which feed by themselves at birth) although the ingestion of mealworms has been mentioned for captive birds. They feed mainly on plant fragments such as buds, leaf tips and small leaves which they bite off green plants. But they also peck seeds on the ground, particularly during the seasons when climatic conditions reduce the availability of green vegetation. Fjeldså (1996) describes how these birds forage in a crouch position, walking slowly and taking items off the plants with rapid snapping movements. The fragments are torn off by moving the bill towards the breast with a quick movement and are swallowed whole. The birds may also stretch up a little to bite off the top of grasses or to browse on taller herbs. All observers underline that the consumed plants are usually succulent ones and that in natural conditions these birds have never been seen drinking, water being obtained from succulent and green plant items.

Although it is represented without comments in Olson & Steadman (1981: fig. 2C) who give a quite good drawing of the skull of *Thinocorus rumicivorus*, Fjeldså (1996) was the first to describe in *Thinocorus* the ossified tendon that we call here "orbito-zygomatic process" (see above) and which is missing in *Attagis* (this might be one of the differences in relation to *Thinocorus* to which Fjeldså alludes without clarifying them). He also rightly mentions that the upper jaw and the muscles of the palate play an important role in bill functioning but without explaining how the system works.

On the basis of our morpho-functional analyses and of the scanty available eco-ethological field data we can propose hypotheses on the potentialities of the bill of the Thinocoridae. These hypotheses will of course require further field and laboratory studies, particularly to measure the actual performances of the anatomical structures we have described.

WHAT DOES IMPLY BROWSING, I.E. REMOVING AN ATTACHED ITEM OR TEARING OFF A PIECE OF IT?

Usually, pecking (i.e. collecting of free items, e.g., seeds) proceeds from morpho-functional characters which are generalized among neognathous birds, and thence does not require particular adaptations (see Korzun *et al.* 2004b), contrary to when attached food items have to be bitten off as is the case here with the Thinocoridae. Pecking birds use the classical "catch and throw" movement (see e.g., Zweers 1982; Zweers *et al.* 1994; Gussekloo & Bout 2005) with or without a "slide and glue" oropharynx mechanism (Zweers 1982; Zweers *et al.* 1994). The attached item to be plucked off resists and applies a force which tends to protract the upper jaw. This passive protraction lessens the clamping force and thence increases the risk that the item gets out of the bill. It is however important to mention here that fixed items can be taken off in two ways. In the first one the item is pulled along the axis of the bill whereas in the second, as described by Fjeldså (1996), the bird tears off the fragment from the plant by moving the head downwards towards the breast. So the item is no more pulled along the axis of the bill. This causes an unfavourable condition which requires a much more important resistance of the upper jaw to the passive protraction force (Fig. 8). In both cases the success of the browsing depends on the clamping force which itself settles the friction forces between the bill and the item, friction forces which oppose the resistance force from the item.

In Neognaths there exist two main kinds of osteomuscular mechanisms for clamping in the bill an attached item in order to pluck it off (for details see Dzerzhinsky 1972; Korzun *et al.* 2003, 2004a, b).

The most widespread is the one that uses the joint muscular control of the jaws where the clamping depends entirely on the resultant of the forces produced by the dorsal adductors alone. This resultant has two simultaneous effects: one raises the mandible while the other, transmitted by *m. pterygoideus* (which plays only this role), retracts the upper jaw. At equilibrium, the jaws exert on the item equal but opposed forces. In that case the resultant of the forces of the dorsal adductors has a well-defined orientation (established through a static mechanical graphical analysis; for details see Dzerzhinsky 1972 and Korzun *et al.* 2003, 2004a, b). By voluntarily changing the orientation of this resultant (by differential action on the muscles), the bird can leave the equilibrium and give the advantage either to the upper or to the lower jaw. The birds characterized by this joint muscular control and which have to browse fixed items must, in order to avoid the passive protraction

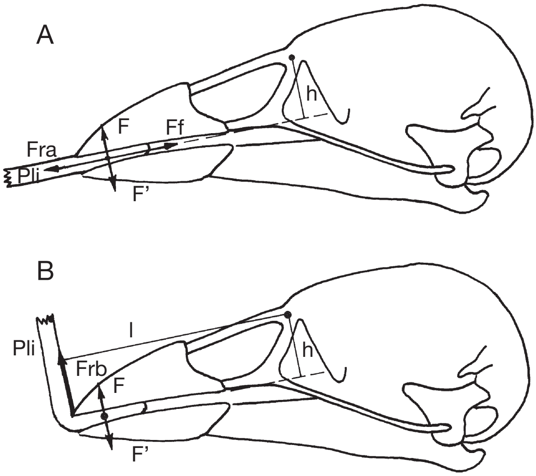

FIG. 8. — Forces in action when a fixed plant item is taken off; **A**, a plant item is pulled along the axis of the bill; **B**, a plant item is torn off by moving the head downward towards the breast. Abbreviations: **F** (= **F'** at equilibrium), clamping forces respectively exerted by the mandible and the upper jaw; **Fr**, resistance force of the item, labelled **Fra** when this item is pulled along the axis of the bill and **Frb** when this item is torn off by moving the head downward towards the breast (**Fra** = **Frb**); **Ff**, friction force which depends on the clamping forces: **Ff** = 2 k **F** (k = coefficient of friction); the lever arms of **Fra** and **Frb** are respectively indicated **l** and **h**, with **l** > **h**; so **Fra** has a less favourable lever arm than **Frb**: the action of these forces depending on their respective momentum, we have **Fra** × **h** < **Frb** x **l**; for the item to be maintained in the bill it is necessary to have **Ff** greater than or at least equal to **Fr**; all this means that when the item is pulled along the axis of the bill the upper jaw can more efficiently resist the passive protraction (due to **Fr**) than when the item is taken off by a downwards movement of the head; **Pli**, plant item.

of the upper jaw, give the advantage to this latter at the very moment when the item is bitten off.

The second clamping mechanism is the one based on the separate muscular control of the forces of the jaws. It is characteristic of the vegetarian birds highly adapted to pluck off fixed items. The classical example is that of the Galliformes and Anseriformes (Gambaryan 1978; Dzerzhinsky 1980, 1995). In this mechanism the dorsal adductors mainly raise the mandible whereas *m. pterygoideus* is the independent and sole retractor of the upper jaw.

The instauration of this separate muscular control has been favoured by the disappearance of the external jugo-mandibular ligament in the mandibular joint and by the very slanting orientation (i.e. much more horizontal than vertical, tending towards the plane of action of *m. pterygoideus*) of the occipito-mandibular ligament directly joining that muscle with the braincase. Indeed in the case of clamping by joint muscular control (where the external jugo-mandibular ligament is necessarily present) *m. pterygoideus* produces two equal but opposed forces. The first one is applied to the mandible, the second to the upper jaw. This second force is transmitted via the palatine and pterygoid to the quadrate which retracts. This stretches the external jugo-mandibular ligament which then passes the force to the mandible where it meets and annihilates the force directly applied to the mandible by *m. pterygoideus*. This is why *m. pterygoideus* cannot retract the upper jaw independently in the case of the joint muscular control. With the disappearance of the external jugo-mandibular ligament in the case of the separate muscular control, the forces produced by the *m. pterygoideus* do not meet and thence do not annihilate each other. Furthermore, in this case and when the occipito-mandibular ligament is almost horizontal (i.e. in the plane of action of *m. pterygoideus*) the force exerted on the mandible by *m. pterygoideus* is transmitted to the base of the skull. Therefore in the separate muscular control *m. pterygoideus* applies its forces on one side to the upper jaw and on the other side to the base of the skull.

In the case of the joint muscular control, at the very moment when the item is taken off, the resistance of the upper jaw to the passive protraction is produced by a change in the balance of forces in favour of the upper jaw. This is due to a change in the orientation against the equilibrium state of the resultant of the forces originating from the dorsal adductors. This resultant is thence very slanting and below the point z (Fig. 9). But to this new slanting resultant participate only some muscles the vector of force of which acts below the resultant characterizing the equilibrium state. This means that the clamping of the item will be lessened. However we underlined above that the success of the browsing does not depend only on the ability to counteract the passive protraction of the upper jaw but also on a clamping or grasping force which prevents the item from sliding along the jaws. There is then a kind of contradiction which is solved by a separate muscular control, characteristic of the Thinocoridae. As indicated above, these birds lack the external jugo-mandibular ligament and, independently of the dorsal adductors, their *m. pterygoideus* retracts the upper jaw, with the caudal support of the base of the skull as the occipito-mandibular ligament is almost along the same axis as *m. pterygoideus*.

Are sneedsnipes equipped for an efficient browsing?

In Thinocoridae the upper jaw is relatively short (thus the lever arm of the force that clamps the item is relatively short) and high at base (thus the lever arm of the force exerted by *m. pterygoideus* is relatively long). This is why the force exerted by *m. pterygoideus* on the upper jaw acts in a quite favourable state of lever arm. The length of the mandible is twice that of the upper jaw (which is the lever arm of the force that clamps the item) whereas the adductors insert on the mandible close to the centre of rotation of the mandibular joint and have thence a short lever arm. This means that on the whole the adductors work in unfavourable conditions of lever arm. This is why in Thinocoridae the tendency to strengthen the efficiency of the dorsal adductors is quite evident. Their main aponeuroses attach to the mandible at its highest point. Thanks to this specific height the axis of action of the force produced by these muscles is set away from the centre of rotation of the mandibular joint. This increases the length of its lever arm. The bumps (where attach the aponeuroses of insertion of the external adductors) located at the highest point of the mandible testify of the intense forces that apply to this area. The fundamental specificities of the separate muscular control give the adductors additional possibilities to increase their efficiency, thanks to the more vertical orientation with respect to the mandible of the resultant of the forces from the adductors.

For the external adductor, the more vertical orientation increasing the efficiency of the muscle is particularly pronounced in *Thinocorus*. In this genus, the medial portion, the largest one, of this adductor originates from well forward on the axial skull thanks to the presence of the specific orbito-zygomatic process from where it spreads almost vertically to the mandible. Furthermore it possesses a very complex aponeurotic skeleton and because of that is made of a great number of relatively short muscular fibres. It results of course mechanically from this a diminution of the amplitude of the contraction but also an increase of the produced force. Field observations (e.g., MacLean 1969) of foraging Thinocoridae show that they do not need to open widely their bill during food acquisition. Then, diminished amplitude of contraction does not penalize them and is not for them a contradiction in their trophic adaptation as they benefit from the increase of the clamping force. The tendency toward a sharp increase of the number of muscular fibres in this well-oriented medial portion clearly appears in the number of aponeuroses which increases as one gets closer to the mandibular joint. This increase is possible because the required amplitude of contraction diminishes also as one gets closer to the mandibular joint. Thanks to its V-shaped section the orbito-zygomatic process is specifically adapted to resist very intense bending forces coming from the extremely powerful medial portion.

In *Attagis* the medial portion of the external adductor is of a generalized type common to many birds. But here the potentialities allowed by the separate muscular control are used by *m. pseudotemporalis superficialis* which is a little less slanting and has an internal system of aponeuroses more complex than in *Thinocorus*.

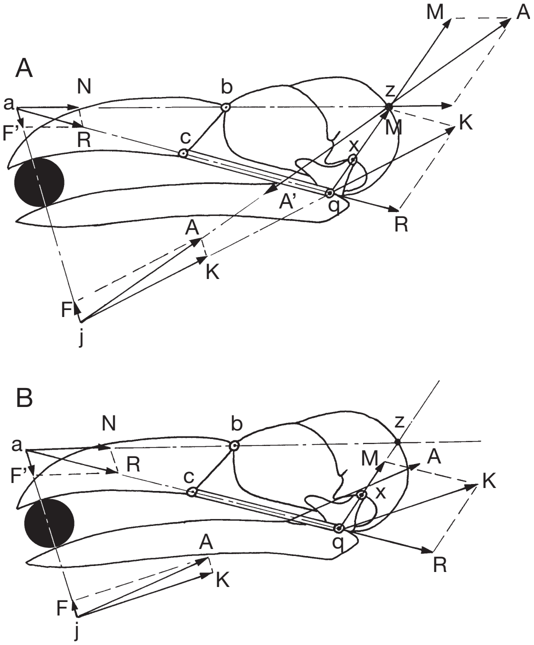

FIG. 9. — **A**, static graphical analysis of the equilibrium of forces when a food item is clamped in the bill (for more details see Dzerzhinsky 1972; Korzun *et al*. 2003, 2004a, b); adductors exert force **A** from the mandible towards the cranium and force **A'**, superimposed, opposite and equal to **A** (for the clarity of the figure, **A** has not been represented on its point of application but directly placed at **j** along its axis of action); force **A** is decomposed into **F** (mandibular clamping force applied along the axis going through the clamping points of the item in the bill) and **K** (force of the quadrate applied on the quadrato-mandibular joint **q**); force **K** is itself decomposed into **M** (pressure force of the quadrate on the cranium along the axis **q**-**x**) and **R** (retraction force of the upper jaw along the axis of the jugal bar); in turn **R** is decomposed into **F'** (clamping force of the item by the upper jaw, opposed and equal to **F**) and **N** (pressure force of the upper jaw on the cranium at the level of the prokinetic hinge **b**); at the equilibrium, forces **M**, **N** and **A** (so **A'**) are applied to point **z** where they cancel each other; **a**, meeting point of the three axes of 1) clamping, 2) action on the cranium via the prokinetic joint, and 3) retraction of the upper jaw along the jugal bar; **j**, meeting point of the axes of 1) clamping, 2) action of the adductors, and 3) action on the cranium through the mandibular joint; **x**, joint of the quadrate on the neurocranium; **c** = meeting point of the jugal bar and the maxilla.
B, the same analysis as above but with a more slanting force **A** from the adductors at the very moment when the attached item is taken off; then this force **A** passes below the point **z** of the equilibrium state and **F'** from the upper jaw becomes greater than **F** from the mandible, so the advantage is given to the upper jaw and this difference between **F** and **F'** allows to resist the passive protraction of the upper jaw.

In Thinocoridae the total quantity of muscular fibres of the adductors has also been increased thanks to the great expansion of the superficial portion, especially in *Thinocorus*, which attaches to the mandible very frontal below the eye, almost at the level of the lateral wing of the mesethmoid. Attachment of **amq** to the zygomatic process besides of quadrate is very unusual and noteworthy;

it represents an additional evidence of the rostral expansion of the external adductor.

In Thinocoridae an additional vertical force comes from *m. pterygoideus* because as described above the origin of the dorsal part of this muscle on the surface of the palatine and pterygoid is located much higher than its point of insertion on the mandible. Thus *m. pterygoideus* is not only the sole retractor of the upper jaw but it also contributes to the adduction of the mandible.

It is fitting to note here that although rhynchokinetic the bill of the Thinocoridae (which in its appearance recalls that of the Galliformes, see Dzerzhinsky 1980) with its robust structure (e.g., thickness of the bones of the rostral part of the upper jaw and mandible, extension of the internasal wall) fulfils well the requirements of resisting intense forces.

The hyoid apparatus of Thinocoridae is relatively typical of most Neognaths which take relatively small food items (Korzun 1978). *M. branchiomandibularis* is made of two portions (rostral and caudal); this indicates the presence of a tongue raising mechanism (Korzun *et al.* 2008). The main characteristic of this mechanism is the ability of the tongue to rise towards the palate and to support and hold there small items at the moment the bird opens its bill to take another item. In this mechanism an important role is played by the caudal portion of *m. branchiomandibularis* which acts like the string of the bow formed by the hyoid horn. When stretched this portion applies a pressure on the occipital surface of the head. This force generates from this surface a reaction force applied to each hyoid horn. This reaction force separates itself into two forces. The first one is directed downwards and, with the upward force from *m. mylohyoideus*, constitutes a torque which turns the hyoid apparatus so that its rostral part (the tongue) is raised towards the palate. Both *m. ceratoglossus anterior* and *m. ceratoglossus posterior* allow the dorsal surface of the tongue to match the surface of the palate. Furthermore it must be noted that this mechanism allows also the tongue to be raised above the dorsal edge of the mandible and thence to be maintained against the palate even when the bill opens.

Theoretically seedsnipes could thus tear off small plant fragments without necessitating stopping browsing in order to swallow an item before taking another one. By using their salivary secretions they could glue and clump items and thus constitute an alimentary bolus easier to swallow. This hypothesis is supported by the fact that, as mentioned above, there specifically exist several groups of voluminous and well-individualized salivary glands. Its thickness and flexibility, together with enlarged *m. ceratoglossus anterior* and *m. hypoglossus*, show that the tongue possesses great capabilities to manipulate in the bill flat items which usually are rather difficult to handle. Glued items are moved inside the buccal cavity to the oesophagus in the course of retractions of the tongue and pharynx thanks to the crenellations located along the caudal edge of the tongue and also caudal to the glottal slot. The crenellations located on the palate and on the serrated fold at the entrance of the oesophagus prevent the alimentary bolus from moving back toward bill tip during the protraction of the tongue and of the buccal floor. This mechanism of transport of the item inside the bill is similar to that described as "side-and-glue" by Zweers (1982) for the domestic pigeon.

WHICH OTHER GROUP OF BIRDS HAS THE MOST SEEDSNIPE-LIKE BILL?

The main characters of the bill and hyoid apparatus of Thinocoridae correspond rather well with those of generalized Charadriiformes like *Pluvialis squatarola* (Linnaeus, 1758). However, it must also be noted that against the general arrangement and nomenclature of the aponeuroses of the external adductor established by Dzerzhinsky & Potapova (1974) and applicable to Charadriiformes, Thinocoridae possess neither the fourth aponeurosis of origin **aq** in the caudal part of the deep portion nor the aponeurosis of origin **alt** of the rostral part of this deep portion. *Thinocorus* is also very peculiar in having aponeurosis of origin **apo** which is absent in generalized Charadriiformes. However because of their strictly vegetarian diet Thinocoridae are quite peculiar among Charadriiformes which indeed have a wide food spectrum but which do not include any other group with a bill apparatus directly comparable to that of Thinocoridae.

On the other hand, sandgrouse (Pteroclididae) represent a most adequate group for a comparison with the seedsnipes of the morpho-functional and feeding adaptation of their bill apparatus. Both groups have bills which look much alike in general appearance and in the location of the kinetic areas. Both use the separate muscular control of their jaws (external jugo-mandibular ligament absent, almost horizontal orientation of the occipito-mandibular ligament). This allows sandgrouse to feed on plant matter and, above all, while being able to peck at very small seeds they can take off fixed items (Korzun *et al.* 2008). In sandgrouse the adaptation to the removal of fixed items corresponds to a more vertical orientation of the medial portion of the external adductor, with a particularly enlarged zygomatic process in *Pterocles alchata* (Linnaeus, 1766) and *Syrrhaptes paradoxus* (Pallas, 1773). In the seedsnipes there is likewise a vertical orientation of the medial portion of the external adductor thanks to the fact that the zygomatic process fuses with the ossified base of the aponeurosis **apo** (the postorbital ligament does not participate in this fusion) forming a long orbito-zygomatic process. It is however interesting to note that between the zygomatic and postorbital processes there remains in *Syrrhaptes* Illiger, 1811 a tendinous link, a relict of the postorbital ligament which is totally absent in other Pteroclididae. There is thus a strong functional similarity in the bill apparatus of these two groups but the origin of the methods of operation is not really the same. In all sandgrouse *m. pseudotemporalis superficialis* which gives an almost vertical component of the force from the external adductors is quite large as in *Attagis*. It can be mentioned that Pteroclididae as well as Thinocoridae lack the aponeurosis of origin **aq** of the caudal part of the deep portion of the external adductor which is present in many Charadriiformes. Two characters show that the adaptation to the separate muscular control is more strongly developed in sandgrouse than in seedsnipes. The first one is the presence of a muscular portion in *m. pterygoideus* which links the palate to the base of the skull (so called *m. retractor palatini*). The second one is that the posterior adductor is enlarged as in certain Galliformes (Dzerzhinsky 1995), a particularity which allows to clamp the mandibular joint and thence to resist the passive protraction of the upper jaw at the moment of the removal of an attached item (cf. Korzun *et al.* 2008). It can be added that adult sandgrouse have the basipterygoidal joint that adult seedsnipes lack, although their young have it. We did not find any significant difference between the two groups in their buccal cavity and hyoid apparatus, nor in the relative size of their salivary glands: apparently they use the same operating procedure to transport food items inside the buccal cavity, a "slide-and-glue" mechanism *sensu* Zweers (1982).

WHICH MORPHO-FUNCTIONAL PATHWAY DID SEEDSNIPES FOLLOW DURING THE ADAPTATION OF THEIR BILL APPARATUS?

In the diagram of the successive changes, during their evolution, of the adaptation of the bill apparatus of pigeons and sandgrouse to a diet based on the removal and ingestion of large plant items (Korzun *et al.* 2008), the first step of the adaptation is the disappearance of the internal jugo-mandibular ligament. This adaptation developed from an initial generalized state with: 1) a joint muscular control of the jaws; 2) a tongue raising mechanism; 3) schizorhiny; and 4) a capability to remove attached items thanks to a very slant orientation of the resultant of the forces from the dorsal adductors (resistance to the passive protraction of the upper jaw). The obliquity of this force from the dorsal adductors has been mainly realized in "pre-sandgrouse" by *m. pseudotemporalis profundus* but, in "pre-seedsnipes", by the superficial portion of the external adductor which was placed in a favourable state of lever arms thanks to the shape of the mandible.

There are indications that "pre-seedsnipes" possessed an external jugo-mandibular ligament and thence used the joint muscular control of the jaws. These indications are the existence of a quite enlarged superficial portion of the external adductor and the presence of a caudal condyle of the quadrate in the mandibular joint. As shown by Dzerzhinsky (1972: fig. 28) the main role of this condyle is, with the external jugo-mandibular ligament, to lock the mandibular joint and allow the mandible and the quadrate to work together as if they were a monolith. This condition can be considered as an adaptation to the removal of attached items (Trounov *et al.* 1996). When the external jugo-mandibular ligament is missing, the articular surface of the quadrate is simplified and usually there is no caudal condyle (case of Galliformes and Anseriformes, Dzerzhinsky

1972: fig. 6). Extant Thinocoridae lack the external jugo-mandibular ligament but keep a caudal condyle of the quadrate. However this condyle has lost its direct application on the mandible so that the locking of the mandibular joint is no more possible.

In a second step, and different from pigeons (but not from *Otidiphaps* Gould, 1870 and *Didunculus* Peale, 1848), sandgrouse lost the external jugo-mandibular ligament and thus acquired the separate muscular control of the jaws. From the same initial generalized state, seedsnipes directly went to this second stage bypassing the first one. The change from the joint to the separate muscular control came with a change in the orientation of the resultant of the forces from the adductors which became more vertical. Keeping the relative size of their *m. pseudotemporalis profundus* sandgrouse got a vertical resultant by expanding their *m. pseudotemporalis superficialis* and, in *Pterocles alchata* and *Syrrhaptes*, also by a more vertical orientation of the medial portion of the external adductor thanks to the enlargement of the zygomatic process. In seedsnipes the slanting superficial portion of the external adductor has been conserved. The vertical resultant has been obtained in *Thinocorus* thanks to the orbito-zygomatic process which insures the vertical orientation of the specifically enlarged medial portion of the external adductor. In *Attagis* the vertical resultant has been obtained through the expansion of *m. pseudotemporalis superficialis*. In both thinocorid genera the dorsal part of *m. pterygoideus* has acquired the role of an effective additional adductor of the mandible.

Both sandgrouse and seedsnipes have specialized in the occupation of very open, steppe, even desert (particularly sandgrouse) habitats. Because they also specialized on small food items (in particular seeds and plant fragments), contrary to *Didunculus* and *Otidiphaps*, they retained the tongue raising mechanism. Sandgrouse developed further their adaptive radiation in habitats where their diet must be based on small, often minute, seeds and where the vegetation is usually very low and succulent plants (from which water can be extracted) occur only on particular substrates. So, joint to the often severe thermal conditions of their habitats, that makes necessary for them to drink regularly. This is why they developed particular specific behaviours and feathers. On the other hand, seedsnipes mainly occupy habitats where: 1) thermal conditions (at least the highest temperatures) are less constraining; 2) seed productions are more seasonal (maybe with general wetter conditions less favourable to their conservation); and 3) the vegetation consists mainly in spongy or succulent plants so that these birds could live without drinking, although this needs confirmation.

The diversification of seedsnipes gave two species pairs of different size: *Attagis* species are indeed three to six times larger than *Thinocorus* species (see data in Fjeldså 1996). Detailed analyses of the diet of the four seedsnipe species remain to be done. Though scanty, available data suggest that this difference in size has not affected the diet which remains based on the consumption of fragments removed from succulent plants. The morphological differences in the bill apparatus between *Attagis* and *Thinocorus* that we described above can paradoxically be explained by the similarity of their diet. It can be supposed that the vegetal matter taken by all seedsnipes has the same physical properties (particularly strength) for resisting to the removal. This means that the removal of a fragment of this vegetal matter requires the application of a force with a given absolute value. This absolute value is not here significant; what is important is the fact that small as well as large birds must produce a force with the same absolute value. The dramatic difference in accessibility of this force is of primary interest here. A large bird will more easily produce this absolute force than a smaller bird. Because both large and small seedsnipe species use their bill with the same mechanical system and in order to produce the same absolute force as large species, small species must have set up a proper device. So in small seedsnipes (*Thinocorus*), it is the zygomatic process which has created a more favourable lever arm for the medial portion of the external adductor and moreover thanks to the system of internal aponeuroses it was possible to wrap up in this portion a great number of muscular fibres.

CONCLUSIONS

The present morphological and functional study of the skeleto-muscular structures proper to the jaw and hyoid apparatus of Thinocoridae is the first one of this kind for this group of birds whose biology and particularly diet remain imperfectly known. So the conclusions that we can draw probably raise more questions than they solve and call for more exhaustive field eco-ethological studies and more advanced quantitative functional analyses. It is also important to point out here that we did not neglect the few morphological particularities that we described but did not discuss. We are still unable to give a sound functional explanation for them (they may be merely neutral) but we checked that they do not contradict the morpho-functional hypotheses we develop in this paper.

A first conclusion is that Thinocoridae are actually quite well adapted to browsing, i.e. to remove attached plant materials. Their feeding apparatus is well suited as an instrument for performing procedures necessary to the utilization of these food resources. They solved the problem of removing fixed items by evolving the separate control of the movements of their jaws. This was done through the modification of the osteo-muscular structures of their bill which originally used the joint muscular control of the jaws, a mechanism characteristic of birds that take free (i.e unattached) food items.

A second conclusion is that, in order to evolve this separate control and because they belong to two quite different size-classes, all seedsnipe species did not modify the same osteo-muscular structures. The large *Attagis* species expanded their *m. pseudotemporalis superficialis* of which they also increased the intricacy of the internal aponeurotic system. On the other hand, the small *Thinocorus* species evolved an orbito-zygomatic process (mainly by expansion of the zygomatic process and its fusion with the ossified aponeurosis **apo**), enlarged the medial portion of the external adductor of the mandible and increased the complexity of the aponeurotic structure of this medial portion.

A third conclusion is that Thinocoridae specialized on the continuous removal of small, mainly succulent, attached plant fragments thanks to a tongue raising system coupled to a system of large salivary glands and a device of crenate areas in the buccal cavity.

A fourth conclusion is that, as far as functional morphology is concerned, the birds which have a bill directly comparable to that of Thinocoridae are the sandgrouse (Pteroclididae). These two groups appear as having indeed followed a similar not to say common morpho-functional evolutionary pathway (which of course does not imply a close phylogenetic relationship) in the course of the adaptation of their bill and hyoid apparatus to a vegetarian diet essentially based on the removal of small attached plant items in rather relatively similar conditions of habitats. We have discovered a good deal of similarity in basic traits of the trophic niches with external properties and facilities of the feeding apparatus, and feeding behaviour, though internal design of apparatus is somewhat (or rather) different in both cases. This is most probably a case of ecomorphological and thence functional convergence.

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