Bio Bulletin 3(1): 56-66(2017)
(Published by Research Trend, Website: www.biobulletin.com)

ISSN NO. (Print): 2454-7913
ISSN NO. (Online): 2454-7921

Biomechanics Analysis of Jaw Musculature of the common Kestrel (*Falco tinnunculus*) and the Budgerigar (*Melopsittacus undulatus*)

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(Published by Research Trend, Website: www.biobulletin.com)
*(*Received 27 December 2016; Accepted 02 February 2017*)*

ABSTRACT: The research present work deals with the anatomical description of the jaw muscle of two different birds; the common kestrel, *Falco tinnunculus* and the budgerigar, *Melopsittacus undulatus* and the analysis of the mechanical performance of jaw system during the feeding process. In the kestrel, the jaw muscles has complex muscle-fibers with multiple directions and are provided with a high complex aponeurotic and tendinous system, those properties of the muscle enable the adductor muscle of the kestrel potentially to produce a strong force bit. The bite force of the kestrel produces only from the mandible. While the jaw muscles of the budgerigar enable the movement of the upper jaw, as well as, the mandible.

Key words: Jaw, muscle, kestrel, Budgerigar, biomechanics

INTRODUCTION

In the absence of teeth, birds depend mainly on the bill and the tongue in manipulating the food. During the feeding process, the beak may serve as a tool. The beak of bird is a highly diverse organ showing considerable variability in its size, shape and much of which can be closely related to the feeding mechanism. The jaw apparatus is a part of the avian feeding system (McLelland, 1979). Bock (1964) illustrated that it consists of the following four functional and kinematical unites; the brain case, the upper jaw, the bony palate, the jugal bars, the quadrate, and the mandible. All these units form a highly complex integrated mechanical apparatus. The mechanism, evolution, diversity and functions of the avian cranial kinesis have great interest e.g. (Beecher, 1962; Bock, 1964; Bock and Morioka, 1971; Van Gennip and Berkhoudt, 1992; Hoese and Westneat, 1996; Bout and Zweers, 2001; Pascotto and Donatelli, 2003; Gussekloo and Bout, 2005; Van der Meij and Bout, 2004& 2008)

These previous studies were done on some birds such as pigeons, ducks, sparrow, finches. However, the prey- predator birds were given little attention in literature, e.g. (Hull, 1991; Shawki, 1998; Ladyguin, 2000; Sustaita, 2008)

The Psittaciformes is one of the most clearly defined avian orders, and their affinity with other groups are far from obvious (Burton, 1974a,b) and is recognized as an unusual avian order. In particular, the head morphology of parrots exhibits a number of novel features (Beecher, 1962; Dubale and Rawal, 1965; Burton, 1974a &b; Zusi, 1993; Homberger, 2003; Tokita, 2003, 2004).

However, the present study is given anatomical details of the jaw muscles of two bird species; the common kestrel, *Falco tinnunculus* and the budgerigar, *Melopsittacus undulatus* which play an important role as force generator during the feeding process.

MATERIAL AND METHOD

The specimens of the two bird species brought alive to the laboratory, and then were killed by ether or chloroform inhalation. The specimens of both birds were dissected under a wild M3-stereomicroscop and used an iodine solution for staining the anatomical material to improve the color contrast between muscles and connective tissues. The figures were prepared by outlining the anatomical preparations with the help of the camera Lucida.

RESULT

Anatomical Description.

A. The common kestrel, *Falco tinnunculus*

The jaw muscles of the common kestrel, *Falco tinnunculus* can be classified into four functional groups; Adductors of the mandibular, Adductors of the mandibula and depressors of maxilla, Depressor of the mandibular, and Elevator of the maxilla.

1. Adductors of the mandibula

The adductors of the mandibula comprise of two muscles; muscle adductor mandibulae externus and pseudotemporalis superficialis.

M. adductor mandibulae externus. The muscle adductor mandibulae externus is a complex muscle which comprises of three parts; muscle adductor mandibulae externus pars rostralis, muscle adductor mandibulae externus pars ventralis and muscle adductor mandibulae externus pars profunda.

M. adductor mandibulae externus pars rostralis (Amer). Fig. (A-1). The muscle adductor mandibulae externus pars rostralis is a fan-shaped fleshy muscle which is occupied the temporal region of the brain case. That muscle seems broad dorsally and narrow ventrally, where the muscle fibers run antero-ventrally to form an apex. That apex is attached on the medial surface of a thick aponeurosis (Zygamotic aponeurosis, Ap.Z) and emerges under the dorso-lateral fibers of the muscle adductor mandibulae externus pars ventralis. While, some muscle fibers extend dorso-ventrally from the base of postorbital process, then are attached on the medial surface of the thick aponeurosis (Zygamotic aponeurosis, Ap.Z) then runs ventrally to be attached on the anterior coronoid process of the mandible as a thick tendon.

M. adductor mandibulae externus pars ventralis (Amev). (Figs. (A-1), (A-2). The muscle adductor mandibulae externus pars ventralis is a triangular-shaped muscle with pinnate-muscle fibers which lies on the lateral surface of intermediate portion of the mandible. The dorsal muscle fibers form an apex which attaches on the thick aponeurosis (Zygamotic aponeurosis) and interfere with the muscle fibers of the muscle adductor mandibulae externus pars rostralis. Ventrally, the muscle fibers fan out to be inserted on the lateral surface of the intermediate portion of the mandible and covering the anterior foramen of the mandible.

M. adductor mandibulae externus pars profunda (Amep). Fig. (A-1). The muscle adductor mandibulae externus pars profunda is pinnate-fibered muscle, which lies on the lateral surface of the quadrate, posterior to the muscle adductor mandibulae externus pars ventralis and lateral to the muscle adductor mandibulae posterior. The muscle adductor mandibulae externus pars profunda originates from the distal portion of the otic process of the quadrate. Some muscle fibers attach on the posterior edge of the thick aponeurosis (Zygamotic aponeurosis), then the muscle runs parallel to the muscle adductor mandibulae externus pars ventralis to be inserted on the posterior coronoid process of the mandible by an aponeurosis.

M. pseudotemporalis superficialis (Ps). Fig. (A-3). The muscle pseudotemporalis superficialis is a spatula-shaped with parallel-muscle fibers. The muscle *pseudotemporalis* superficialis originates from the postero-dorsal surface of the interorbital septum and runs ventrally cross over the antero-lateral surface of the muscle adductor mandibulae posterior. The ventral half of the muscle pseudotemporalis superficialis incubates a medial tendon which extends ventrally to be inserted on the medial surface of the posterior portion of the mandible.

2. Adductors of the mandibula and depressors of maxilla.

The adductor of the mandible and depressor of the maxilla group comprise of four muscles; muscle adductor mandibulae posterior, muscle pseudotemporalis profundus, muscle pterygoideus ventralis and muscle pterygoideus dorsalis.

M. adductor mandibulae posterior (Amp). Figs. (A-1) & (A-3). The muscle adductor mandibulae posterior is a rectangular-shaped muscle with parallel-muscle fibers, which lies on the lateral surface of the quadrate. The muscle adductor mandibulae posterior originates from the orbital process of the quadrate, and then runs postero-ventrally to be inserted on the dorsal surface of the posterior portion of the mandible (articular). The ventro-lateral surface of the muscle adductor mandibulae posterior covers by thin aponeurosis. This aponeurosis and some fleshy muscle fibers attach on the dorsal surface of the posterior portion of the mandible acting as insertion site.

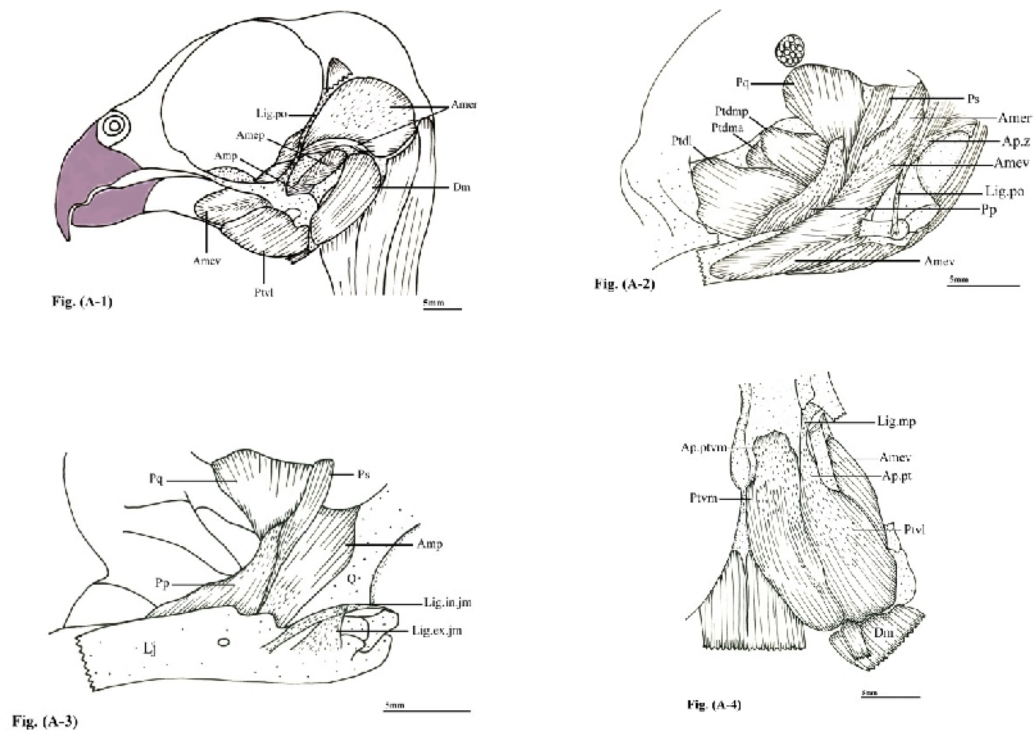

Fig. A. Lateral view of the jaw muscles of the common kestrel (*Falco tinnunculus*) ,include figures (A-1), (A-2), (A-3), and (A-4).

M. pseudotemporalis profundus (Pp). Figs. (A-2)& (A-3). The muscle pseudotemporalis profundus is parallel-fibered muscle. The muscle pseudotemporalis profundus originates from the orbital process of the quadrate via a thick, broad and expanded aponeurosis. Then the muscle runs antero-ventrally to be inserted on the medial surface of the intermediate portion of the mandible, covering the anterior and posterior foramens of the mandible, as well as, coincide with the muscle adductor mandibulae externus pars ventralis.

M. pterygoideus ventralis. The muscle pterygoideus ventralis is composed of two parts; muscle pterygoideus ventralis pars lateralis and muscle pterygoideus ventralis pars medialis.

M. pterygoideus ventralis pars lateralis (Ptvl). Fig. (A-4). The muscle pterygoideus ventralis pars lateralis is massive parallel-fibered muscle, which lies on the ventro-lateral surface of the palatine bone. The muscle originates from the lateral edge of the palatine bone by a thick aponeurosis (the pterygoid aponeurosis, Ap.pt) which is connected anteriorly with the mesethmopalatinum ligament and runs posteriorly covering the antero-ventral half of the muscle. Then the muscle extends postero-dorsally to be inserted on the lateral surface of the posterior portion of the mandible (articular). Some muscle fibers are inserted fleshy on the lateral surface of the external jugomandibular ligament, on the lateral surface of the lateral process of mandible and on the postero-lateral surface of the posterior portion of the mandible (articular). While, few medial muscle fibers form an internal aponeurosis that attaches on the ventral edge of the posterior portion of the mandible (articular).

M. pterygoideus ventralis pars medialis (Ptvm). Fig. (A-4). The muscle pterygoideus ventralis pars medialis is parallel- fibered muscle. The muscle pterygoideus ventralis medialis originates from the ventral surface of the palatine bone via an aponeurosis (the aponeurosis of the muscle pterygoideus ventralis pars medialis, Ap.ptvm) which extends posteriorly over the antero-ventral half of the muscle. The most medial and posterior muscle fibers attach on the ventral crest of the posterior half of the palatine bone and on the ventral surface of the anterior portion of the pterygoid bone. Meanwhile, the muscle pterygoideus ventralis pars medialis runs postero-ventrally to be inserted on the ventral surface of the posterior portion of the mandible (articular), sharing the insertion of the muscle pterygoideus ventralis lateralis and on the medial process of the mandible.

M. pterygoideus dorsalis. The muscle pterygoideus dorsalis is divided into two parts;

muscle pterygoideus dorsalis pars lateralis and muscle pterygoideus dorsalis pars medialis.

M. pterygoideus dorsalis pars lateralis (Ptdl). Fig. (A-2). The muscle pterygoideus dorsalis pars lateralis is parallel-fibered muscle. The muscle pterygoideus dorsalis pars lateralis originates from the dorsal surface of the palatine bone, and then extend posteriorly to be fused with the posterior part of the muscle pterygoideus ventralis pars lateralis. Moreover, the muscle pterygoideus dorsalis pars lateralis turns dorsally to be inserted on the ventral edge of the posterior portion of the mandible, few posterior muscle fibers attach on the ventral edge of the posterior portion of the mandible via thin aponeurosis.

M. pterygoideus dorsalis pars medialis (Ptdm). The muscle pterygoideus dorsalis pars medialis is subdivided into two parts; muscle pterygoideus dorsalis pars medialis anterior and muscle pterygoideus dorsalis pars medialis posterior.

M. pterygoideus dorsalis pars medialis anterior (Ptdma). Fig. (A-2). The muscle pterygoideus dorsalis pars medialis anterior is parallel-fibered muscle. The muscle pterygoideus dorsalis pars medialis anterior originates from the dorsal surface of the posterior edge of the palatine bone and the lateral surface of the anterior portion of the pterygoid bone. Then the muscle pterygoideus dorsalis pars medialis anterior runs posteriorly to be inserted via an aponeurosis (the aponeurosis of the pterygoid dorsalis medialis anterior, Ap.ptdma), on the base of the medial process of the mandible.

M. pterygoideus dorsalis pars medialis posterior (Ptdmp). Fig.(A-2). The muscle pterygoideus dorsalis pars medialis posterior is parallel-fibered muscle. The muscle pterygoideus dorsalis pars medialis posterior envelopes the posterior half of the pterygoid bone, then extend ventro-laterally to be inserted on the anterior edge of the medial process of the mandible.

Depressor of the mandibula.

M. depressor mandibulae (Dm). Fig. (A-1). The muscle depressor mandibulae is a rectangular-shaped with parallel-fibered muscle which occupies the postero-lateral surface of the brain case, posterior to the external auditory meatus and lateral to the attachment site of the cervical muscle. The muscle depressor mandibulae originates from the subtemporal fossa, and then extends ventrally to be inserted on the ventral surface of the posterior portion of the mandible (articular). The surfaces of the posterior half of the muscle depressor mandibulae are covered by an aponeurosis. That aponeurosis attaches on the ventral crest of the subtemporal fossa then runs ventrally to attach on the dorsal crest and the ventral surface of the posterior portion of the mandible.

Elevator of the maxilla. The elevator of the maxilla is represented by single muscle, the muscle protractor quadrati.

M. protractor quadrati (Pq). Figs. (A-2) & (A-3). The muscle protractor quadrati is fan-shaped with parallel-fibered muscle, which is located ventral to the foramen of the optic nerve. The muscle protractor quadrati originates from the postero-lateral surface of the parasphenoid rostrum bone and then extends ventrally to be inserted on the medial surface of the orbital process of the quadrate, dorsal to the quadrato-pterygoid articulation, as well as, few muscle fibers insert on the dorsal surface of the posterior edge of the pterygoid bone.

B. The budgerigar, Melopsittacus undulatus.

The jaw muscles of the budgerigar, *Melopsittacus undulatus* can be classified into six functional groups; Adductors of the mandibula, Adductors of the mandibula and depressors of maxilla, Adductor of the mandibula and elevator of maxilla, Depressors of the mandibula, Depressors of maxilla, and Elevators of the maxilla.

1. Adductors of the mandibula

The adductors of the mandibula comprise of three muscles; muscle adductor mandibulae externus, muscle ethmomandibularis and muscle pseudotemporalis superficialis pars lateralis.

M. adductor mandibulae externus: The adductor of the mandible is represented by two parts of the muscle adductor mandibulae externus; muscle adductor mandibulae externus pars rostralis and muscle adductor mandibulae externus pars ventralis.

M. adductor mandibulae externus pars rostralis (Amer). Figs.(B-1)& (B-2). The muscle adductor mandibulae externus rostralis is a rectangular-shaped muscle. The muscle adductor mandibulae externus pars rostralis originates from the lateral surface of the temporal fossa, passing medial to the suborbital arch to attach on its postero-medial surface, as well as, attach on the posterior wall of the interorbital septum, then extends antero-ventrally to be inserted on the dorso-medial surface of the intermediate portion of the mandible. The dorso-lateral surface of the muscle adductor mandibulae externus pars rostralis is covered by an aponeurosis (the aponeurosis of the muscle adductor mandibulae externus pars rostralis, Ap.Amer) that runs anteriorly to attach on the postero-dorsal edge of the suborbital arch.

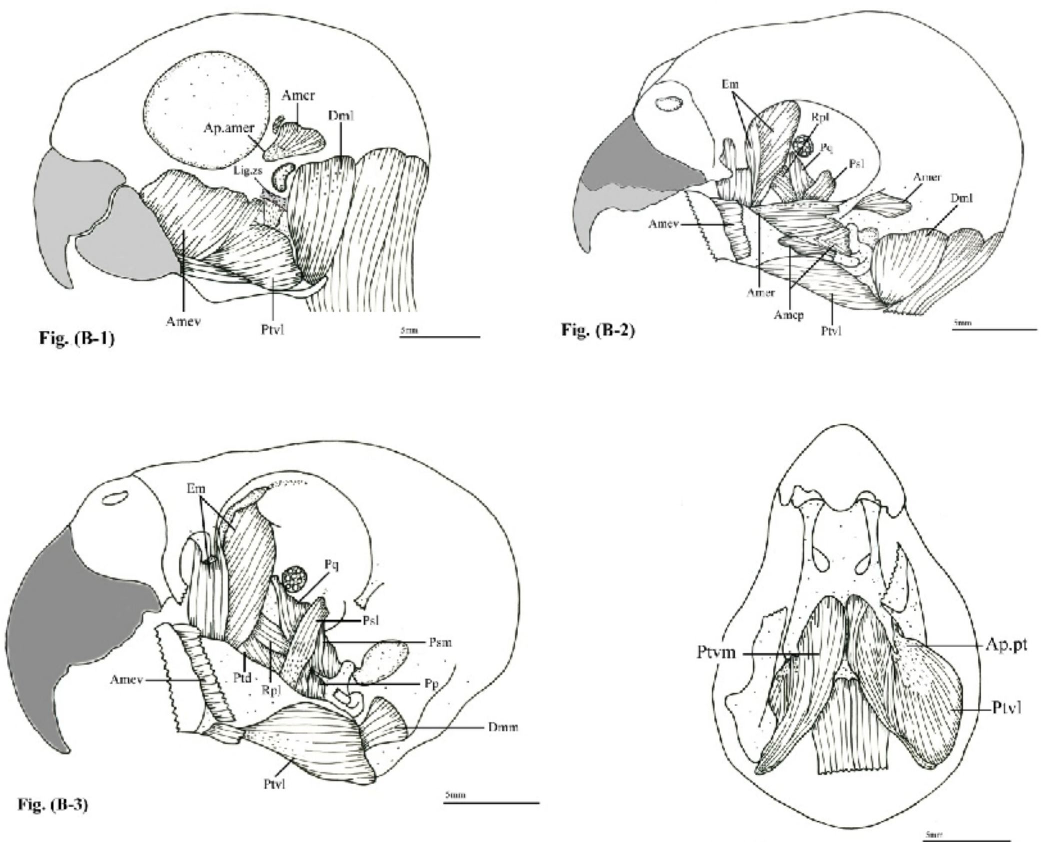

Fig. (B-1) Fig. (B-2) Fig. (B-3) Fig. (B-4)

Fig. B. lateral view of the budgerigar (*Melopsittacus undulatus*) include figures; (B-1), (B-2), (B-3), and (B-4).

M. adductor mandibulae externus pars ventralis (Amev). Fig.(B-1). The muscle adductor mandibulae externus pars ventralis is a rectangular-shaped with parallel fibered muscle, which occupies the antero-lateral half of the intermediate portion of the mandible. The muscle adductor mandibulae externus pars ventralis originates from the lateral and postero-medial surfaces of the suborbital arch, passing lateral to the jugal bar and then runs antero-ventrally to be inserted on the lateral surface of the anterior half of the intermediate portion of the mandible

M. ethmomandibularis (Em). Fig. (B-2). The muscle ethmomandibularis is the most massive jaw muscle with multiple directed muscle fibers which is located on the most antero-lateral surface of the interorbital septum. The anterior muscle fibers of the muscle ethmomandibularis run vertically while the posterior muscle fibers run antero-obliquely. The anterior muscle fibers of the muscle ethmomandibularis originates from the ventral surface of the ectoethmoid bone , while the posterior fibers originates from the ventral surface of the frontal bone, and antero-dorsal surface of the interorbital septum, then runs ventrally to be inserted on the antero-medial surface of the intermediate portion of the mandible. Moreover, the lateral surface of the posterior muscle fibers of the muscle ethmomandibularis is raped by thin aponeurotic sheet.

M. pseudotemporalis superficialis pars lateralis (Psl). Fig. (B-3). The muscle pseudotemporalis superficialis pars lateralis is a sheet-like with parallel fibered muscle. That muscle originates from the posterior wall of the interorbital septum, dorsal to the muscle pseudotemporalis superficialis pars medialis, then runs ventrally perpendicular on the lateral surface of the muscle protractor quadrati to be inserted on the postero-medial surface of the intermediate portion of the mandible by an aponeurosis.

2. Adductors of the mandibula and depressors of maxilla.

The adductors of the mandibula and depressors of maxilla group comprise of three muscles; muscle pseudotemporalis profundus, muscle pterygoideus dorsalis and muscle pterygoideus ventralis pars lateralis.

M. pseudotemporalis profundus (Pp). Fig. (B-3). The muscle pseudotemporalis profundus is a small rectangular-shaped with parallel fibered muscle. The muscle pseudotemporalis profundus originates from the ventral edge of the orbital process of the quadrate and then runs ventrally to be inserted on the dorso-medial surface of the posterior portion of the mandible.

M. pterygoideus dorsalis (Ptd). Fig. (B-3). The muscle pterygoideus dorsalis is a complex parallel-fibered muscle that their muscle fibers run in multiple directions. That muscle occupies the dorso-lateral surface of the palatine bone. The muscle pterygoideus dorsalis originates from the dorso-lateral surface of the palatine bone and anterior portion of the pterygoid bone. Then the muscle runs postero-ventrally to be inserted on the dorsal and ventro-medial surface of the posterior portion of the mandible (articular), as well as, some muscle fibers insert on the posterior portion of the mandible via an aponeurosis.

M. pterygoideus ventralis pars lateralis (Ptvl). Fig. (B-4). The muscle pterygoideus ventralis pars lateralis is a massive triangular and parallel-fibered muscle, which envelopes the posterior portion of the mandible (articular). The muscle pterygoid ventralis pars lateralis originates from the postero-lateral edge of the palatine bone by a thick aponeurosis (The pterygoid aponeurosis, Ap.pt), that aponeurosis spreads posteriorly over the anterior portion of the muscle. Meanwhile, some sheet-like muscle fibers of the muscle pterygoideus ventralis pars lateralis extend dorsally leave the body of the muscle to attach on the lateral surface of the posterior edge of the suborbital arch. Then the muscle pterygoideus ventralis pars lateralis runs postero-dorsally to be inserted on the ventral surface of the posterior portion of the mandible.

3. Adductor of the mandibula and elevator of maxilla.

The adductor of the mandible and the elevator of the maxilla are represented by the posterior branch of the adductor mandibulae externus muscle which is known as the adductor mandibulae externus pars profunda.

M. adductor mandibulae externus pars profunda (Amep). Fig.(B-2). The muscle adductor mandibulae externus pars profunda is a rectangular-shaped muscle which occupies the whole lateral surface of the quadrate. The fibers of the muscle adductor mandibulae externus pars profunda are distinguished into two types; a dorsal pinnate and a ventral parallel-shaped muscle fibers which interferes with the postero-ventral fibers of the muscle adductor mandibulae externus pars rostralis. The fibers of the muscle adductor mandibulae externus pars profunda originates fleshy from the lateral surface of the body of the quadrate, as well as, tendinous from the medial surface of the posterior portion of the jugal bar anterior to the quadrato-jugal articulation. Then the muscle adductor mandibulae externus pars profunda runs antero-ventrally to be inserted on the dorso-lateral surface of the intermediate portion of the mandible.

4. Depressors of the mandibula.

The mandible is depressed by two muscles; muscle depressor mandibulae lateralis and muscle depressor mandibulae medialis.

M. depressor mandibulae lateralis (Dml). Fig. (B-1). The muscle depressor mandibulae lateralis is a rectangular-shaped with parallel fibered muscle, which occupies the postero-lateral surface of the brain case, posterior to the external auditory meatus and lateral to the attachment site of the cervical muscle. The muscle depressor mandibulae lateralis originates from the subtemporal fossa, as well as, some medial muscle fibers attach on the lateral surface of the zygomatic-suborbital ligament (Lig.zs). Moreover, the dorso-lateral surface of the muscle depressor mandibulae lateralis is covered by thin aponeurosis. Then the depressor mandibulae lateralis muscle runs ventrally to be inserted on the dorsal crest of the posterior portion of the mandible (articular).

M. depressor mandibulae medialis (Dmm). Fig. (B-3). The muscle depressor mandibulae medialis is a rectangular-shaped with parallel-fibered muscle. The muscle depressor mandibulae medialis originates from the ventral crest of the subtemporal fossa then runs ventrally to be inserted on the postero-dorsal surface of the posterior portion of the mandible.

5. Depressors of maxilla.

The maxilla is depressed by two muscles; muscle pterygoideus ventralis pars medialis and muscle retractor palatini.

M. pterygoideus ventralis pars medialis (Ptvm). Fig. (B-4). The muscle pterygoideus ventralis pars medialis is a massive, elongated and, club-shaped muscle with parallel-fibers running in multiple directions. The pterygoideus ventralis pars medialis originates from the basisphenoid bone and from the suprameatic process via an aponeurosis, and then runs antero-ventrally to be inserted on the posterior edge of the palatine bone.

M. retractor palatini (Rpl). Fig. (B-3). The muscle retractor palatini is a sheet-like with parallel-fibered muscle which is located on the dorso-lateral surface of the palatine bone. The muscle retractor palatini originates from the ventro-lateral surface of the basisphenoid bone and the lateral surface of the metotic bone. The muscle retractor palatini runs anteriorly to be inserted on the dorso-lateral surface of the palatine bone and antero-lateral surface of the pterygoid bone.

6. Elevators of the maxilla

The maxilla is elevated by two muscles; muscle protractor quadrati and muscle pseudotemporalis superficialis pars medialis.

M. protractor quadrati (Pq). Fig.(B-3). The muscle protractor quadrati is a rectangular and parallel-fibered muscle which is located just ventral to the foramen of optic nerve. The muscle protractor quadrati originates from the lateral surface of the parasphenoid bone and the posterior wall of the interorbital septum, and then runs postero-ventrally to be inserted on the medial surface of the body of the quadrate, as well as, on the base of the orbital process of the quadrate and the dorso-lateral surface of the posterior end of the pterygoid bone, anterior to the quadrato-pterygoid articulation.

M. pseudotemporalis superficialis pars medialis (Psm). Fig. (B-3). The muscle pseudotemporalis superficialis pars medialis is a sheet-like with parallel-fibered muscle. The muscle pseudotemporalis superficialis pars medialis originates from the posterior wall of the interorbital septum and then runs postero-ventrally perpendicular on the postero-lateral surface of the muscle prot ractor quadrati to be inserted on the dorsal edge of the orbital process of the quadrate.

Biomechanical analysis of the jaw apparatus.

The external jaw movements of each bird species are recognized in laboratory during manipulate of the food items but the internal movements are impossible to recognize because it is hidden system. However, on the base of the present morphological investigation a graphic of vectors illustrating the analysis of the recognized movements was done. The movements which were recognized using this technique are; the adduction and depression of the mandible (lower jaw), as well as, the elevation and depression of the maxilla (upper jaw) which includes the protraction and retraction of the quadrate-palatine-pterygoid complex.

In the common kestrel, *Falco tinnunculus*, the muscle adductor mandibulae externus; pars rostralis (Amer), pars ventralis (Amev) and pars profunda (Amep), and its synergistic adductor mandibulae posterior (Amp), pseudotemporalis (superficialis (Ps), profundus (Pp)) and pterygoideus (dorsalis (Ptd) and ventralis (Ptv)) perform the adduction of the mandible. Thus, Famer, Famev and Famep represent the line of action of the muscle adductor mandibulae externus; pars rostralis, pars ventralis and pars profunda (Fig. 1); Famp represents the line of the action of the muscle adductor mandibulae posterior (Fig. 5); Fps and Fpp represent the line of the action of the muscle pseudotemporalis superficialis and profundus (Fig. 3), and Fptdl, Fptdm and Fptvl represent the line of the action of the muscle pterygoideus; dorsalis (para lateralis and pars medialis) and ventralis pars lateralis (Fig. 2) respectively. However, the resultant force causing the adduction of the mandible is represented by the vector Radd.

Meanwhile, in the budgerigar, *Melopsittacus undulatus* the muscle adductor mandibulae externus; pars rostralis (Amer), pars ventralis (Amev) and pars profunda (Amep), pseudotemporalis superficialis pars medialis (Psm), pseudotemporalis profundus (Pp), and pterygoideus (dorsalis (Ptd) and ventralis (Ptv) adduct the mandible. Moreover, the ethmomandibularis muscle (Em) cooperates in adduction of the mandible. However, the force arm of the muscle adductor mandibulae externus is represented by the vector Famer, Famev, and Famep (Fig. 6) and the force arm of the muscle ethmomandibularis, pseudotemporalis and pterygoideus are represented by the vector Fem, (Fpsm & Fpp) and Fpt respectively, (Fig. 7). The resultant force is illustrated by the vector Radd. The depression of the mandible of each bird species must do by the contraction of the muscle depressor mandibulae (Dm). Its force arm is represented by the vector Fdm, (Fig. 4). Moreover, the budgerigar has two depressor muscles; the depressor mandibulae lateralis (Dml) and the depressor mandibulae medialis (Dmm). Thus, the mandible is depressed by two force arm which are represented by the vector Fdml & Fdmm, (Fig. 8.). However, the muscle depressor mandibulae affects the Articulatio quadrato-mandibularis resulting in turning the mandible with counterclockwise on the quadrate (Q). During the elevation of the posterior portion of the mandible (articular), its anterior end depresses, causing the depression of the mandible (Rd).

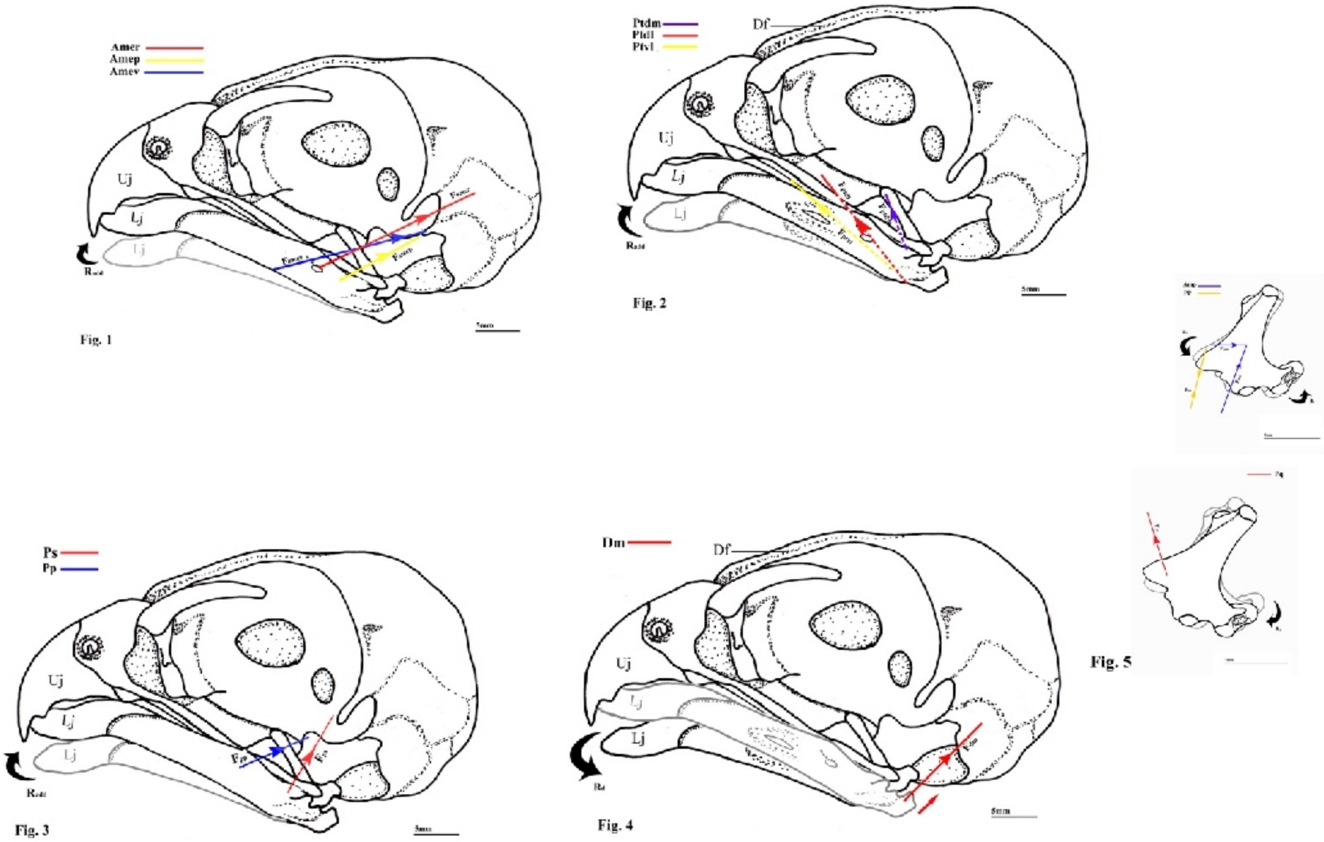

Fig. C. Lateral view of the jaw apparatus of *Falco tinnunculus* showing the mechanics analysis of jaw apparatus, include figures. 1, 2, 3, 4, and 5.

The rotation of the maxilla (upper jaw) occurs in one axis, related to the naso-frontal hinge which acts as a kinetic hinge. The mobility of the quadrate, palatine and pterygoid bone contribute to upper jaw elevation.

The elevation of the upper jaw of the kestrel is impossible because it has an immovable naso-frontal hinge. The mobility of the quadrate, palatine and pterygoid bones occur in the kestrel but the resultant force may be absorbed by the flexion-zone between the connection of the jugal bar and palatine bone with the upper jaw and/or the connective tissue around the tympanic cavity. Consequently, the movements of the upper jaw of the kestrel are restricted in the protraction and retraction of the quadrate. The protraction of the quadrate of the kestrel performs by the contraction of the muscle protractor quadrati (Pq), its force arm is represented by the vector Fpq, (Fig.5). The resultant force is illustrated by the vector Rp. That muscle is antagonistic to the pseudotemporalis profundus (Pp), pterygoideus (Ptd & Ptv) and adductor mandibulae posterior (Amp). The contraction of the muscle pseudotemporalis profundus (Fpp) and adductor mandibulae posterior (Famp), (Fig. 5) affect the orbital process of the quadrate resulting in turning the quadrate with counterclockwise on the articular facet of the mandible. During the retraction of the quadrate, the quadrate draws to its original closed position. While, the contraction of the pterygoideus (Ptd & Ptv) pulls the palatine-pterygoid complex backward, transferring force to the mobile quadrate which swings backward on the articular facet of the mandible. The resultant force as illustrated by the vector Rr.

Meanwhile, the budgerigar posses a high movable upper jaw. The mobility of the upper jaw is allowed by the presence of the movable naso-frontal hinge, as well as, the mobile quadrate and palatine-pterygoid complex.

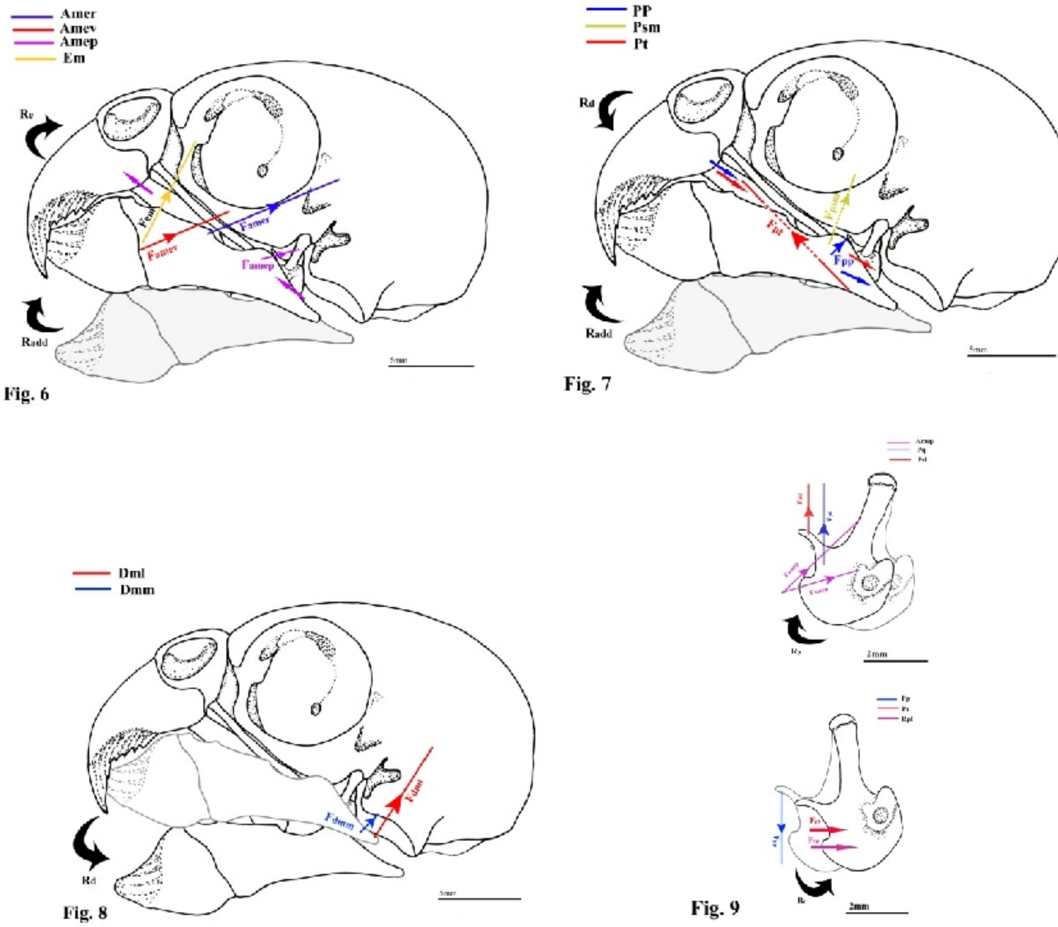

Fig D. Lateral view of the jaw apparatus of *Melopsittacus undulatus* showing the mechanics analysis of jaw apparatus, include figures. 6, 7, 8, and 9.

Considering the articular facet of the mandible with antero-medially curvature, the movement of the quadrate occurs in antero-medially to postero-laterally direction and vise versa, this movement is allowed by the contraction of the muscle adductor mandibulae externus pars profunda (Amep), protractor quadrati (Pq) and pseudotemporalis superficialis pars lateralis (Psl). Thus, Famep, Fpq and Fpsl (Fig. 9) represent the line of the action of the muscle adductor mandibulae externus pars profunda, protractor quadrati and pseudotemporalis superficialis pars lateralis, respectively,. The resultant force of these muscles (Rp) pull the orbital process of the quadrate and the whole body of the quadrate forward resulting in gliding the quadrate with clockwise on the articular facet of the mandible. Thereby pushes the palatine-pterygoid complex. Consequently, elevate the upper jaw (Re).

The depression of the upper jaw of the budgerigar must do by retraction of the quadrate, palatine and pterygoid bones. This retraction (Rr) performs by the contraction of the muscle pseudotemporalis profundus (Pp), retractor palatini (Rpl) and pterygoideus ventralis; pars medialis (Ptvm) and lateralis (Ptvl). The force arm of the muscle pterygoideus is illustrated by the vector Fpt (Fig. 9). While Frpl and Fpp (Fig. 9) represent the lines of action the muscle retractor palatini and pseudotemporalis profundus respectively. However, the resultant force causing the depression of the upper jaw is represented by the vector Rd.

DISCUSSION

The power supply for the jaw apparatus is allowed by several muscles, some of which have a complex arrangement of separate parts. Strength and direction of the force provided by each muscle depend upon its attachments, mass, internal structure including arrangement of fibers, exact position of the bony elements of the jaw apparatus, type of contraction of the muscle, interaction with other muscles.

The jaw muscles of each bird species are generator of forces exerting on the jaws. The mandible swing over the condyle of the quadrate, that swing movement is expressed by the adduction and depression of the mandible. The adduction of the mandible (Bite force) is performed by the contraction of the muscle adductor mandibulae externus parts. In the kestrel, this muscle has complex muscle-fibers with multiple directions, as well as, this muscle is provided with a high complex aponeurotic and tendinous system. Those properties of the muscle enable the adductor muscle of the kestrel potentially to produce a strong bit. The efficiency of the bite force increasing by the contraction of the pseudotemporalis muscle. Bock (1964) noted that the pseudotemporalis group is important to kinetic movement and Zweers (1974) who was described them as "guiding" muscles. But Hull (1991) suggested that the pseudotemporalis muscle is the most important muscle group in Falco berigora, and it is associated with closing the mandible quickly but not contributing much power to the bite force. The pseudotemporalis profundus muscle of the kestrel produces a high mechanical force which may be related to the short moment arm of the muscle. While, the contraction of the muscle pseudotemporalis superficialis produces a low mechanical force which provides a quickly closing the mandible might be due to the long moment arm of the muscle.

In the budgerigar, the pseudotemporalis superficialis muscle is divided into medial and lateral part them are sharing the site of origin but differ in insertion sites. Hence, only the pseudotemporalis superficialis pars lateralis helps in the adduction of the mandible, while the medial part cooperates in the protraction of the quadrate thereby elevates the upper jaw. The bite force of the budgerigar depends on the movement of the upper and lower jaw while the bite force of the kestrel produces only from the mandible. That explains that the number of muscles is assisted with each other to produce a large bite force in the kestrel. Hull (1991) suggested that large adductor muscles particularly the muscle adductor mandibulae externus group is more important in contributing to the bite force than a large pseudotemporalis and pterygoideus muscle.

Some jaw muscles have double function; the adduction of the mandible with the depression of the upper jaw and the depression of the mandible with the elevation of the upper jaw, e.g. the pterygoid muscle complex of each bird species share in the adduction of the mandible by pulls the posterior portion of the mandible, leads to elevate the anterior portion of the mandible thereby closing the lower jaw. Simultaneously, this muscle pulls the palatine bone backward, thus depress the upper jaw. Physically, the palatine bone can glide over the parasphenoid bone that mechanical performance depends on the shape of the palatine bone and its position on the parashenoid bone. The palatine bone of the budgerigar has vertical orientation that may gives flexibility for the gliding movement of the palatine bone. Furthermore, the palatine bone glides antero-posteriorly over the semicircle-shaped parasphenoid bone. While, the kestrel has horizontal palatine bone this lies lateral to the parasphenoid bone. In fact, that horizontal shape doesn't affect the glide movement, but is affected by controlling through the mesethmopalatinum ligament.

Moreover, the branching and subdividing of the pterygoid muscle of the budgerigar increase its efficiency. In addition, the budgerigar possesses the retractor palatini muscle which acts as the branch of the pterygoid muscle. Consequently, the total force of this muscle occurs on the mandible and the upper jaw simultaneously.

The budgerigar possesses a unique adductor muscle, the ethmomandibularis muscle; this muscle is not recognized in the kestrel. Tokita (2004) was detected that the muscle ethmomandibularis initially grows as the rostral budding of the muscle pterygoid at the Cockatiel (Nymphicus hollandicus) at stage 28, while after stage 32 the muscle significantly elongates rostro-dorsally toward the interorbital septum following a course lateral to the palatine bone. The muscle ethmomandibularis correspond the master muscle of mammals.

In conclusion, the jaw apparatus of each bird species plays an important role in the feeding process which acts as the integrated mechanical apparatus of the feeding system. So, the analysis of the mechanical performance of feeding system is depended on how much allowed knowledge of the multiple features of its components through the morphological investigation and by using the available updated techniques.

ACKNOWLEDGEMENTS

The authors highly appreciate to the Department of Zoology, Faculty of Science, Assuit University for supporting the study.

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