AN APPROACH TO THE NOMENCLATURE OF ANURAN MUSCULATURE

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R E S U M E N. — Se propone un método particular para seleccionar, de los nombres ya existentes, el más apropiado para cada músculo, y un método general para escoger los nombres apropiados de las estructuras anatómicas. Estos nombres están basados en los Nomina Anatomica y en el Código de Nomenclatura Zoológica. Se utiliza la ley de prioridad para seleccionar el nombre del músculo, y se discuten los criterios de homología primaria, homología secundaria e identidad topográfica para reforzar la idea de estabilidad nomenclatural. Se sugiere una secuencia para establecer la correspondencia entre los nombres y la homología de las estructuras, comenzando con la identificación de la correspondencia topológica (homología primaria) y terminando con el reconocimiento de la identidad topográfica y las homologías secundarias.

Palabras clave: músculos, nomenclatura, Amphibia, Anura.

A B S T R A C T. — A new nomenclature of anuran muscles and a general method to choose the appropriate names of anatomical structures are proposed. These names are based on the Nomina Anatomica and on the Code of Zoological Nomenclature. The law of priority is used to select the muscle name to adopt, and the criteria of primary homology, secondary homology, and topographic identity are discussed to encourage the idea of nomenclatural stability of anatomical structures. A sequence to establish a correspondence between names and the homology of structures is suggested, beginning with the identification of topological correspondence (primary homology) and ending with the recognition of the topographic identity and secondary homologies. Key words: Muscles, nomenclature, Amphibia, Anura.

INTRODUCTION

When working with anatomical structures, it is difficult to name them owing to nomenclatural disparities. The myological nomenclature of anuran amphibians is an example of this problem. This paper does not pretend to present a history of muscle terminology, but we consider that it is important to know the different «styles» that have been used in naming them in the past.

Myolological terminology derives from a variety of criteria: points of origin and insertion of muscle (e.g., iliofibularis); topological relationships to bones (e.g., tibialis posticus); muscle position relative to the planes of symmetry (e.g., adductor magnus caput ventralis); the size of one muscle in relation to another having the same name (e.g., gracilis major and gracilis minor); muscle function (e.g., flexor tibialis magnus); muscle names with a special meaning (e.g., tensor fascia latae, it pulls on the broad fascia of the thigh).

Most anatomists of the past two centuries adopted the Latin nomenclature, but some adopted a nomenclature using their native language, e.g., French (Dugès, 1835; Cuvier, 1835, in Hoffmann, 1873-1878; de Man, 1874-1875), and German (e.g., Meckel, 1824, in Hoffmann, 1873-1878).

We discuss some circumstances in which the identification of a muscle is difficult. Some muscles have been identified using different names since the 19th Century and their nomenclature remains problematic. Unfortunately, a code (or Nomina) for amphibian structures has not been adopted. Given this situation we think that it would be important to review some historical aspects of the codes of anatomical terminology.

The first assemblage of rules about anatomical parts was adopted in 1895 by a group of German anatomists. These rules were known as the Basle Nomina Anatomica (Anonymous, 1966). However, these rules were not adopted internationally until 1955 at the VIth International Congress of Anatomists, in Paris, when the Paris Nomina Anatomica (PNA) was approved (Anonymous, 1966). In 1957, the International Association of Veterinary Anatomists established the International Committee on Veterinary Anatomical Nomenclature, primarily based on the Paris Nomina Anatomica. This nomenclature, basically concerning mammalian anatomy, was published in 1968 (Baumel, 1979). A subcommittee of this international committee published the Nomina Anatomica Avium (Baumel, 1979). At present, there are three Nomina Anatomica to guide anatomical nomenclature in vertebrates: Nomina Anatomica (IANC) (Anonymous, 1966), Nomina Anatomica Veterinaria (ICVAN) (Anonymous, 1973), and Nomina Anatomica Avium (NAA) (Baumel, 1979). These guides are for human anatomy, for mammalian anatomy, and bird anatomy, respectively.

MATERIALS AND METHODS

We discuss the nomenclature of muscles in anuran amphibians and use some examples of hind limbs, forelimbs, throat, and jaw to illustrate the methodology proposed. We choose muscles, because their nomenclature is less stable than that for the bones, and in particular these muscle groups (hind limbs, forelimbs, throat and jaw) are important as systematic characters in anurans.

Anatomical nomenclature should have the same properties advocated for the taxonomic system, universality, homogeneity and stability (Dubois, 1990). Because these properties currently do not characterize anuran myological nomenclature, we will apply the rules advocated by the Nomina Anatomica (Anonymous, 1966). In general, these rules are common to the Nomina Anatomica Veterinaria (Anonymous, 1973) and to the Nomina Anatomica Avium (Baumel, 1979). The principles guiding the I.A.N.C. (International Anatomical Nomenclature Committee) (Anonymous, 1966:4) are as follows: «1) to make no changes in familiar terms for purely pedantic or etymological reasons; 2) to keep terms as short and simple as possible; 3) to discard eponyms; 4) to use terms with informative or descriptive value; 5) to arrange differentiating adjectives as opposites (e.g., major and minor, superficialis and profundus); 6) to adopt single terms as a rule and to allow official alternatives only as exceptions; 7) to resist pressures to name numerous small and often unconfirmed structures: and 8) to use Latin names for all terms.»

In applying these principles, we have examined the oldest citations reported for the anuran musculature nomenclature. Besides using the principles related above for choosing the nomenclature, we accept the name as spelled in the Nomina Anatomica, if it corresponds to that registered there. We recommend choosing the oldest appropriate name noted in the literature (except if the oldest is in a language other than Latin) in parallel

with the law of priority established for the names of species in the Zoological Code of Nomenclature (ICZN, 1999) if this name complies with the rules above. We believe that this law is a good choice that has resolved many nomenclatural problems in taxonomy then, its application in muscle nomenclature, may be very important also. If the name of a muscle in anurans is the same of that in the humans beings, we take the same spelling, in accordance with the Nomina Anatomica. From the anatomical point of view, it is very important to determine if there are true anatomical associations, accurate identifications, and/or correct descriptions in the selected oldest designations. If the oldest name is hyphenated, we remove the hyphen (as has been proposed for species names in the Zoological Code of Nomenclature). If the oldest name applies to several muscles, we select the next oldest designation (thereby introducing an exception to the rule of antiquity). The name at the begining of each group of synonyms below corresponds to the name proposed. If necessary, we will explain the name adopted to avoid confusion.

Whenever possible, the original source of the muscle nomenclature was consulted. However, some references in the list of synonyms do not appear in the bibliography because we could not locate the original paper. These names were obtained from Hoffmann (1873-1878), which is our main reference for 19th Century synonyms.

RESULTS

Throat Muscles

M. submaxillaris (Gaupp, 1896): mylo-hyoideus (van Altena, 1829; Hsiao, 1933-1934); mylo-sternohyoideus (Ledeboer, 1829); sous-maxillaire (Dugès,1835); submaxillaris (Gaupp, 1896); intermaxillaris anterior (Hoffmann, 1873-1878); submaxillaris and subhyoideus (Beddard, 1908); intermandibularis posterior (Edgeworth, 1935; Emerson, 1976) intermandibularis (Trewavas, 1933; Tyler, 1972; Horton, 1982; Burton, 1983; Duellman and Trueb, 1986)

Remarks: We did not select *mylohyoideus* (van Altena, 1829) because the prefix mylo- refers to "molar" (e.g., molar teeth; Vanden Berge, 1992), and thus is inappropiate in anurans.

M. geniohyoideus medialis (Trewavas, 1933; Horton, 1982): geniohyoideus (van Altena, 1829; Ledeboer, 1829; Gaupp, 1896); genio-hyoidien (Dugès, 1835); maxillo-hyoideus (Hoffmann, 1873-1878); geniohyoideus lateralis medius (Davies and Burton, 1982); geniohyoideus medialis (Horton, 1982; Duellman and Trueb, 1986).

Remarks: The m. geniohyoideus comprises two muscles. Therefore, we selected the names m. geniohyoideus medialis (Trewavas, 1933) and m. geniohyoideus lateralis because they are anatomically descriptive (Principle 4 and brief).

Jaw Muscles

M. masseter (van Altena, 1829): masseter (van Altena, 1829; Ecker, 1888); zygomato-maxillaire (Dugès, 1835); jugali-maxillaris (Hoffmann, 1873-1878); masseter minor (Gaupp, 1896; Kesteven, 1944); adductor mandibulae posterior lateralis (Luther, 1914; Säve-Soderberg, 1945); levator mandibulae anterior lateralis (Edgeworth, 1935); levator mandibulae lateralis (Starrett, 1968; Duellman and Trueb, 1986).

Remarks: We choose *masseter* following principles 2 and 6.

M. adductor mandibulae posterior articularis (Luther, 1914): adductor mandibulae posterior articularis (Luther, 1914; Säve-Soderberg, 1945); temporalis internus (Bigalke, 1927, in Edgeworth, 1935); levator mandibulae anterior articularis (Edgeworth, 1935; Limeses, 1965); adductor mandibulae externus lateralis (Starrett, 1968); levator mandibulae posterior articularis (Duellman and Trueb, 1986; Lynch, 1993).

Remarks: Following the International Anatomical Nomenclature Committee Principle 4, we select adductor mandibulae posterior articularis (Luther, 1914) to replace the shorter name m. temporalis internus (Bigalke, 1927, in Edgeworth, 1935), because a m. temporalis externus does not exist.

Forelimb Muscles

M. anconaeus (Zenker, 1825, in Hoffmann, 1873-1878): triceps brachii (Kloetzke, 1816; Ledeboer, 1829; van Altena, 1829; Klein, 1850, in Hoffmann, 1873-1878; Pfeiffer, 1854, in Hoffmann, 1873-1878; Ecker, 1864); dreibäuchiger Strecker (Meckel, 1824, in Hoffmann, 1873-1878); triceps brachial (Cuvier, 1825, in Hoffmann, 1873-1878); anconaeus (Zenker, 1825, in Hoffmann, 1873-1878); scapulo-bihuméro-olecranien (Dugès, streckemuskelmarsse des Vorderarms (Stannius, 1856, in Hoffmann, 1873-1878); anconaeus (Fürbringer, 1874, in Hoffmann, 1873-1878); anconeus (Burton, 1983; Duellman and Trueb, 1986).

Remarks: In acordance with International Anatomical Nomenclature Committee Principle 2, we chose m. anconaeus for the muscle of the stylopodium because anconaeus signifies «elbow.» Moreover, the term anconaeus formerly was applied to the muscle that inserts on the olecranon in humans. The latter muscle, the triceps (Skinner, 1961), is homologous with the m. anconaeus of anurans.

Hindlimb Muscles

M. gastrocnemius (Kloetzke, 1816): gastrocnémien externe (Cuvier, 1815, in Hoffmann, 1873-1878); gastrocnemius (Kloetzke, 1816; Zenker, 1825, in Hoffmann, 1873-1878; Ledeboer, 1829; Collan, 1847, in Hoffmann, 1873-1878; Klein, 1850, in Hoffmann, 1873-1878; Stannius, 1856; Ecker, 1864; Burton, 1983); wadenbeinmuskel (Meckel, 1824, in Hoffmann, 1873-1878); gemelli minores (van Altena, 1829); bi-fémoro-plantaire (Dugès, 1835); bi-femoro plantaris (Hoffmann, 1873-1878); plantaris longus (Dunlap, 1960; Duellman and Trueb, 1986).

Remarks: Gastrocnemius (Kloetzke, 1816) replaces the longer and newer m. plantaris longus (Dunlap, 1960; Duellman & Trueb, 1986), based upon the principle 4 and in applying the law of priority of the IZCN.

M. popliteus (Kloetzke, 1816); popliteus (Kloetzke, 1816); tibialis anticus simplex (Zenker, 1825, in Hoffmann, 1873-1878); peroneus (Ledeboer, 1829); pré-fémoro-tibial (Dugès, 1835); tibialis anticus minor (Collan, 1847, in Hoffmann, 1873-1878); extensor cruris brevis (Ecker, 1864; Dunlap, 1960; Burton, 1983; Duellman and Trueb, 1986); femoro-cruralis lateralis (Hoffmann, 1873-1878).

Remarks: *Popliteus* (Kloetzke, 1816) replaces the longer and newer *extensor cruris brevis* (Ecker, 1864; Dunlap, 1960; Burton, 1983; Duellman and Trueb, 1986), based upon the principle 4 and in applying the law of priority of the IZCN.

DISCUSSION

Nomenclatural Stability

Anatomical nomenclature should be as stable as taxonomic nomenclature. However, we could not attain this stability without keeping in mind the systematic theory about homology. Although in the different Nomina Anatomica the need to stabilize the names of structures is not discussed, the principles stated above are not enough to construct a strong nomenclature free of ambiguities. To show

its paramount importance, we discuss the relationship between homology and anatomical nomenclature in examining several ideas.

In fact, the muscle nomenclature is based upon a criterion known as the principle of organic connections (Corsi, 1988) that was proposed by Etienne Geoffroy Saint-Hilaire in 1830. This principle established that "...the organs and systems in the vertebrates' structural plan were to be found in all classes and families of the great division of the animal kingdom, even if the enlargement or reduction of a part could significantly alter other parts connected to it" (Corsi, 1988: 233). From this, his theory of analogues is derived: "...to identify all variations of form and function undergone by the organs in the structural plans specific to each class" (Corsi, 1988: 233). This terminology actually corresponds to Owen's (1866: xii) concept of homology: "A 'homologue' is a part or organ in one organism so answering to that in another as to require the same name." We can see that the first criterion for identifying "analogous" structures was the positional appraisal, or as Jardine (1969: 328) has recognized, "...that a basic empirical criterion of homology is correspondence in relative position."

This criterion is based upon topological correspondences that De Pinna (1991) identified as positional homology or primary homology; this type of homology was based upon a character similarity. De Pinna's (1991: 373) definition states that "A primary homology is conjectural, based on similarity, and reflects the expectations that there is a correspondence of parts that can be detected by an observed match of similarities." This concept had already been expressed by Woodger (1937:137; cited by Jardine, 1969) when he stated that "...we must possess some criteria of homology which the earlier morphologist also possessed

before phylogenetic questions are considered at all. There is primary sense of 'homology'..."

At this point we still cannot consider a synapomorphy, but only a shared derived character. It is only in considering the secondary homology that one can talk about synapomorphy (De Pinna, 1991). Likewise, as of this moment we can treat synapomorphy as a synonym of homology (Patterson, 1982; Nelson, 1994).

Brower and Schawaroch (1996) developed De Pinna's theory, terming topographic identity and characterstate identity to De Pinna's primary homology. A topographic identity corresponds to the relative position of structures (primary homology sensu stricto), and character-state identity comes after characters are identified via topographical identity; it is at this point that «.....the various character states in the study are hypothesized to be identical, or not...Character states among taxa are classified either identical or not, when entered in a column of the data matrix» (Brower and Schawaroch, 1996: 267). For these authors, homology is the same that De Pinna's secondary homology, and stated that we cannot talk about primary homology because «...that use of the term «homology» is premature when applied to conjecturally identical character states» (Brower and Schawaroch, 1996).

As can be seen, primary homology and topographic identity are the main concepts applied to give stability to the names of the anatomical structures. We do not need to confirm the homology of two structures in order to confer a name. We need only to identify them as comparable categories (Hawkins *et al.*, 1997) i.e., names can be assigned before phylogenetic analysis (*a priori* assignment), when the identification of homologous character states in muscles occurs after a phylogenetic analysis (*a posteriori* assign-

ment). De Pinna (1991) stated that the disagreement between the primary and secondary homologies does not invalidate the significance of the primary homology; in fact, this is the same relation found between putative synapomorphy (primary homology) and unambiguous synapomorphy (secondary homology) (De Pinna, 1991). Thus, if anatomical names are based on primary homologies (or topographic identities), the anatomical nomenclature will not change if the primary homology supposition is not preserved in a phylogenetic analysis.

In giving names to structures, we consider the notions of character and character states proposed by Hawkins et al. (1997). However, we cannot consider structures as characters; rather we consider only the different traits that can be distinguished. At the same time, if we detect some character variability that is potentially codifiable, this will be cataloged as character states which will be entered in a data matrix, such as proposed by Brower and Schawaroch (1996), and Hawkins et al. (1997) have claimed. In this manner, we recognize the character-state identity as an evidence of potential homology in the phylogenetic analysis (Brower and Schawaroch, 1996).

NAMES AND TOPOGRAPHIC IDENTITY

We prefer Brower and Schawaroch's (1996) notion of topographic identity instead of primary homology in comparing the distinction between topographic identity, primary homology, and secondary homology concepts, because «topographic identity» is more precise for our line of reasoning.

Many muscle names used today are based implicitly on the criterion of topographic identity (or topological correspondence) because earlier authors used this type of reasoning for naming and synonymizing muscles.

It is clear that this criterion could be applied to the muscles in all groups of vertebrates. If the names of two muscles identified as homologues do not coincide, it is important to indicate that synonymy and homology are independent concepts, but it would be very difficult to get these correlations because the selection of structure names is an a priori assignment, but revelation of homologies is an a posteriori one. It is imperative to establish that if a researcher identifies non-homologous muscles with the same name, it will be enough to state this fact without changing the nomenclature: therefore, the names will remain stable (see above).

Among the names proposed here, we can see that many of those accepted since the end of 19th Century have been changed owing to the law of priority. It is important to note that the "authorities" for many of the names also have changed. In the past, the standard references have always included Gaupp (1896), Noble (1922), or Dunlap (1960), leaving aside important (but rarely cited) anatomists such as Dugès (1835), Hoffmann (1873-1878), Luther (1914) or Edgeworth (1935). Furthermore, we discovered some important, yet modest, publications from relatively unknown anatomists on anuran muscle nomenclature. Among them, Kloetzke (1816), Ledeboer (1829) and van Altena (1829). The main problem with these three papers is the absence of drawings. These are the first references about anuran muscle nomenclature and should be consulted to the extent that they comply with the principles expresed above.

An essential guide to the establishment of a Nomina Anatomica Batrachologica and a Nomina Anatomica Herpetologica could be the Nomina Avium (Baumel, 1979) or the Nomina Anatom-

ica Veterinaria (Anonymous, 1973), because they are based upon vertebrates anatomy rather than on human anatomy. We sustain, however, that the primary guide to naming muscles must be the *Nomina Anatomica* (Anonymous, 1973) because it was the first Anatomical Code written for the nomenclature of vertebrate structures.

ACKNOWLEDGMENTS

We thank Rafael Miranda for his constructive comments, Sara Acosta and Jeff Jorgenson for reviewing the English text.

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