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A segmental analysis of the beetle antenna

Alessandro MINELLI

Department of Biology, University of Padova, Via Ugo Bassi 58 B, I-35131 Padova, Italy
E-mail: *alessandro.minelli@unipd.it*

SUMMARY - *A segmental analysis of the beetle antenna* - Number of antennal articles in adult and larval Coleoptera is surveyed. Eleven articles must be credited to the ground-plan of the adult beetle antenna, and three, or possibly four, to the larval one. A new model is presented, aiming at explaining, in terms of segmentation process, the origin of the typical 11-article antenna of the adult beetle and the frequency distribution of antennae with less than that number. Basically, an 11-article antenna is interpreted as comprising the scape, the pedicel, an intermediate 8-article region and the apical article. It is suggested that the intermediate eight (flagellar) articles derive from the splitting of two primary articles, each of which gives rise to four secondary elements. Incomplete segmentation of either or both of these quartet-forming flagellar articles gives rise to adult antennae with less than 11 elements. The rare antennae with 12 articles are interpreted as deriving from the typical 11-article appendage, with additional segmentation of the originally undivided apical element.

RIASSUNTO - *Un'analisi segmentale dell'antenna dei Coleotteri* - Viene presentato un quadro dei valori del numero di antennomeri riscontrati nelle larve e negli adulti dei Coleotteri. È da ritenere che il numero primitivo di antennomeri nei Coleotteri adulti sia 11, nelle larve 3 oppure 4. Viene suggerito un modello di produzione dei segmenti antennali dell'adulto, che darebbe ragione sia del numero base (11 unità), sia della diversa frequenza delle antenne con numeri inferiori. Schematicamente, l'antenna comprende lo scapo, il pedicello, una regione intermedia di 8 flagellomeri e un segmento apicale. Viene proposto che gli otto segmenti flagellari intermedi derivino dalla suddivisione di due segmenti di primo ordine, ciascuno dei quali si suddividerebbe in quattro unità di secondo ordine. Dalla segmentazione incompleta di uno dei segmenti intermedi primari, o di entrambi, risulterebbero le antenne con meno di 11 elementi. Le rare antenne con 12 articoli vengono interpretate come derivanti da una tipica appendice con 11 articoli, in cui l'articolo apicale, di regola indiviso, si presenterebbe qui segmentato in due unità secondarie.

Key words: Coleoptera, antenna, double segmentation, flagellum, evo-devo (evolutionary developmental biology)
Parole chiave: Coleotteri, antenna, doppia segmentazione, flagello, evo-devo (biologia evoluzionistica dello sviluppo)

1. INTRODUCTION

It does not require specialist knowledge to appreciate the diversity in shape and also in size, both absolute and relative to the insect's body, of the antennae of the Coleoptera. What is less obvious is how far this diversity is grounded in, or correlated to, a diversity in the *number* of antennal articles. The question seems a sensible one, especially in cases such as the long-horn beetles (Cerambycidae), where the antennae are occasionally short, as in our *Spondylis buprestoides* (Linnaeus, 1758), but usually much longer, often longer than the body. In most long-horn beetles, however, the number of antennal articles is fixed at 11, as it is in the majority of beetles. This numerical stability parallels the near-invariance of the number of cervical vertebrae in mammals. These are nearly always seven, so that the difference between the long neck of the giraffe and the short neck of the hippo is correlated with size and shape differences in the supporting vertebrae rather than with differences in their number. In both cases – the neck of mammals and the antenna of beetles – natural selection was seldom offered a numerical variation to work on (Minelli 2004). There is clearly scope to think that these well-entrenched numbers (seven cervical vertebrae, 11 antennal articles) are the outcome of particularly robust developmental processes. This has been indirectly demonstrated in the case of the mammals, where a diversity of defects seems to derive from developmental disturbance during the short temporal window in which the cervical vertebrae are specified (Galis 1999). Unfortunately, we do not have equivalent evidence for the beetles; indeed, we know very little about the morphogenesis of the adult antenna and the relationship of the latter to the larval one. On the other hand, as in the common saying, that there is no rule without exceptions, there are many exceptions to the broad generalization that the beetle antenna is comprised of 11 articles, as there are a few exceptions to the rule that mammals have seven cervical vertebrae. The distribution of the different antennal numbers across the order may prove interesting, not so much as a possible phylogenetic marker of smaller or larger clades, but mainly as a source of insight as to the possible origin of the most frequent number of articles, i.e. 11, and as to a possible morphogenetic interpretation of the number of antennal articles across the insects, or the arthropods at large.

2. THE NUMBER OF ANTENNAL ARTICLES IN ADULT COLEOPTERA

The antennae of most adult beetles have 11 articles, but there are many exceptions (Tab. 1). An antenna with 11 articles must be ascribed to the ground-plan of the Coleoptera, as it is present in all four suborders, including the basal Archostemata. In this group numbers other than 11 are exceptional, as are in the Adephaga and in several superfamilies within the Polyphaga. The Myxophaga is the only suborder where numbers smaller than 11 are relatively common: Hydroscaphidae have either 5 or 8 articles, Lepyceridae

Tab. 1 - Families of Coleoptera in which numbers of antennal articles other than 11 have been recorded. Data mainly after Lawrence (1982), Arnett & Thomas (2001), Arnett *et al.* (2002); also Español (1992), Lawrence & Reichard (1969), Ratcliffe *et al.* (2002). X symbols record the presence, within each family, of one or more species with the specified number of antennal articles (2 to 11, or >11).

Tab. 1 - Famiglie di Coleotteri nelle quali sono stati registrati numeri di articoli antennali diversi da 11. Fonti principali dei dati: Lawrence (1982), Arnett & Thomas (2001), Arnett et al. *(2002); inoltre Español (1992), Lawrence & Reichard (1969), Ratcliffe* et al. *(2002). Le X indicano la presenza, all'interno della famiglia, di una o più specie con il numero di antennomeri indicato (da 2 a 11, o maggiore di 11).*

	2	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**>11**
Anthicidae										X	X[1]
Cerambycidae										X	X[2]
Rhipiceridae										X	X[3]
Apionidae									X	X	
Colydiidae									X	X	
Cryptophagidae									X	X	
Histeridae									X	X	
Jacobsoniidae									X	X	
Propalticidae									X	X	
Rhipiphoridae									X	X	
Salpingidae									X	X	
Sphindidae									X	X	
Staphylinidae									X	X	
Torridincolidae								X		X	
Anthribidae								X	X	X	
Drilidae								X[4]	X[5]	X	
Heteroceridae								X	X	X	
Latridiidae (incl. Merophysiidae)								X	X	X	
Phengodidae								X	X	X	
Zopheridae								X	X	X	
Anobiidae							X	X	X	X	
Bostrichidae							X	X	X	X	
Ciidae							X	X	X	X	
Corylophidae							X	X	X	X	
Gyrinidae							X	X	X	X	

[1] Also 12.
[2] Also 12 in *Agapanthia* Serville, 1835, *Calamobius* Guérin-Méneville, 1849 and male *Prionus* O.F. Müller, 1864; a few dozen in some exotic genera.
[3] Up to 40.
[4] Some females only.
[5] Some females only.

(Tab. 1, continued)
(Tab. 1, continua)

	2	3	4	5	6	7	8	9	10	11	>11
Hydraenidae							X	X	X	X	
Ptiliidae							X	X	X	X	
Coccinellidae						X	X	X	X	X	
Elminthidae						X	X	X	X	X	
Trogositidae						X	X	X	X	X	
Meloidae					X	X	X	X	X	X	
Cerylonidae					X	X	X	X	X	X	
Dermestidae				X	X	X	X	X	X	X	
Dryopidae		X					X	X	X	X	
Carabidae		X[6]	X								
Chrysomelidae		X	X	X	X	X	X	X	X	X	X[7]
Ptinidae	X	X			X				X	X	
Pselaphidae	X	X	X	X	X	X	X	X	X	X	
Diphyllostomatidae									X		
Passalidae									X		
Phycosecidae									X		
Rhizophagidae									X		
Trogidae									X		
Sphaerosomatidae									X		
Ceratocanthidae								X	X		
Clambidae							X	X	X		
Discolomidae							X	X	X		
Scarabaeidae							X	X	X	X	X
Hydrophilidae					X	X	X	X	X		
Lucanidae						X	X		X		
Micropeplidae								X			
Georissidae						X		X			
Hydroscaphidae				X			X	X			
Lepiceridae						X					
Families including species with 2-10 antennnal articles	2	5	2	4	7	12	22	31	46		

[6] 3-10 articles, often indistinct, in the Paussinae.
[7] 12 articles in some Clytrinae.

4, Torridincolidae either 9 or 11, while only the Sphaeriusidae (= Microsporidae) are fixed at 11. Myxophagans, however, are a very small group of tiny beetles, where a reduction in the number of antennal articles can be expected as a part of a miniaturization syndrome (cf. Beutel & Haas 1998). Within the Adephaga, antennae with less than 11 articles are present in two specialized groups only, i.e. the Gyrinidae, where a very short antenna is clearly required by the unique locomotory mechanics on the water surface (in this case, only eight articles are left), and in the paussine Carabidae, where different degrees of fuzziness and reduction are seen in the antenna distal to the two proximal, conservative, articles.

Among the polyphagan families, antennae with less than 11 articles are often found in miniaturized forms such as the Ptiliidae, where 9 and 10 articles (but also 11) are found. Same trend in the Clambidae, with 8, 9 or 10 articles; same in the Georyssidae, with either 7 or 9 articles, and in the Pselaphidae where, however, the whole series from 2 (but see below) to 11 articles has been recorded.

On the other hand, a size effect cannot be advocated in other cases, e.g. in the Scarabaeoidea, where 10 is the most common number (11 antennal articles being present in the Geotrupidae only) and lower numbers, down to 7, have been recorded in several lineages, the Lucanidae included.

Of special interest are those families where a discontinuous series of numbers of antennal articles is found. In addition to the Torridincolidae and the Hydroscaphidae, already mentioned, there are the Dryopidae, the Endomychidae, and possibly the Ptinidae. As an interpretation of these numerical differences in terms of adaptation is utmost unlikely, it may be sensible to see whether these preferred numbers can be explained in developmental terms, that is, as numbers more easily obtained than others.

Numbers smaller than 11 crop up here and there across the whole order, sometimes just in one or very few members of a family or subfamily, sometimes more numerous and diversified. In the latter case, however, the "exceptions" are generally clustered within small clades. An isolated exception within its family is provided, e.g. by *Trypeticus* Marseul, 1864, the only genus of the Histeridae with 10 rather than 11 articles. Isolated exceptions within the Chrysomelidae (which also generally have 11-article antennae) are the alticine genera *Psylliodes* Latreille, 1827, with 10, and *Nonarthra* Baly, 1862, with 9. In the same family Chrysomelidae, however, there is a group where the plesiomorphic 11-article condition is much more seriously disrupted. This group, sometimes granted the status of separate family, is the Hispinae, where a large number of genera with 11-article antennae is accompanied by *Leucispa* Chapuis, 1875 with 10 articles, *Platypria* Guérin-Méněville, 1840 and *Cassidispa* Gestro, 1899 with 9, *Microrhopala* Chevrolat, 1837, *Uroplata* Dejean, 1835 and *Octotoma* Dejean, 1835 with 8, *Physocoryna* Guérin-Méněville, 1844 with 7 and *Acanthispa* Chapuis, 1875 with either 7, 6, 5, 4 or even just 3 articles.

Within a single genus, a unique range of numbers is found in *Anthrenus* Geoffroy, 1762 (Dermestidae), where the different species have either 4 (subg. *Ranthenus* Mroczkowski, 1962), 5 or 6 (subg. *Holocerus* Mulsant & Rey, 1868), 7 (subg. *Solskinus* Mroczkowski, 1951), 8 (subg. *Florilinus* Mulsant & Rey, 1868), 9 (subg. *Anthrenops* Reitter, 1880), 10 (subg. *Anthrenodes* Choband, 1898), or 11 (subg. *Nathrenus* Casey, 1900 and subg. *Anthrenus* Geoffroy, 1762) articles (Peacock 1992).

A similar diversity, as already mentioned, is found in another beetle group only, i.e. in the Pselaphidae (currently treated as a subfamily of the Staphylinidae). In this taxon, the genera in which antennae with less than 11 articles have been recorded are fairly numerous. I will give here only one example for each number smaller than 11. Thus, *Pyxidicerus* Jeannel, 1952 with 10, *Cerennea* Raffray, 1913 with 9, *Acrodimerus* Jeannel, 1954 with 8, *Heptaleptus* Jeannel, 1952 with 7, *Claviger* Preyssler, 1790 with 6, *Couloniella* Besuchet, 1983 with 5, *Diartiger* Sharp, 1883 with 4, *Adranes* Leconte, 1850 with 3, and *Mastiger* Motschuslky, 1851 with 2. This smallest number is puzzling, indeed, as it would correspond to an antenna with less than the conventional basic complexity of an insect antenna (scape, pedicel, flagellum); see below for further comments.

Pselaphids also offer examples of sexual dimorphism in the number of antennal articles, for example *Dimorphozetus* Jeannel, 1952 (♂: 9 articles; ♀: 11 articles), *Diplomelinus* Jeannel, 1957 (♂: 8 articles; ♀: 9 articles), and *Poeciloceras* Comellini, 1985 (♂: 7 articles; ♀: 8 articles). In these three cases the females have a larger number of antennal articles than the corresponding males; the same is found in the merophysiid *Holoparamoecus ragusae* Reitter, 1875 (♂: 9 articles; ♀: 10 articles), but this trend is reversed in some members of the Drilidae. Here, males have always 11 articles, whereas females have either 9, 10, or 11. Sexual dimorphism is also found in *Prionus* Geoffroy, 1762 (Cerambycidae), where females have 11 articles, but males have 12.

This last example leads me to mention those few beetles where more than 11 articles have been recorded. In addition to male *Prionus*, 12 articles are found in the antennae of some other Cerambycidae, e.g. in *Agapanthia* Serville, 1835, in some clytrine Chrysomelidae, and in the South African genus *Afremus*, currently classified with the Anthicidae, but probably not belonging here (G. Nardi, *in litt*.). Larger numbers, up to a few dozen, are only found in the Rhipiceridae and in some Cerambycidae. This aspect of diversity in beetle antennal articles will be analysed more closely in another paper.

3. A SEGMENTATION MODEL FOR THE BEETLE ANTENNA

In the holometabolous insects, it is not that easy to study the process of segmentation of the antenna, which occurs in one burst, during the pupal stage, starting from an imaginal disc. In a sense, conditions are comparable here to those of the embryonic stage, where the larval antennae of the holometabolans and the (definitive) antennae of the other antennate arthropods are laid out. This contrasts with the events observed in the post-embryonic development of the antennae of many arthropods (in practice, all antennate arthropods to the exception of the holometabolans), where the increase in length of the appendage is mostly accompanied by an increase in the number of its articles, with the first post-embryonic moults at least. It is worth remarking, however, that there are also arthropods, like the epimorphic centipedes (all geophilomorphs and the majority of scolopendromorphs; Minelli *et al.* 2000), where the definitive number of segmental articles is obtained during embryonic development, and no further article is added during subsequent stages.

In my opinion, knowledge of the antennal segmentation process as observable during the post-embryonic development of many arthropods is our best guide towards understanding the segmentation of the adult antenna in the beetles, and holometabolous insects in general. Patterns and processes observed along the increase in antennal segment number during post-embryonic life of arthropods like malacostracan crustaceans or hemimetabolous insects should help us developing interpretative models and planning those observations and experiments we need eventually to perform on the developing stages of beetles and other arthropods. Unfortunately, the numerous studies hitherto performed on several genes involved in the development and patterning of the antenna in *Drosophila* (e.g. Dong *et al*. 2001, 2002; Chu *et al*. 2002; Cummins *et al*. 2003; Emerald *et al*. 2003), in the lesser flour beetle *Tribolium* (Beermann *et al*. 2004), in the cricket *Gryllus* (Miyawaki *et al*. 2002) or in the pill millipede *Glomeris* (Prpic & Tautz 2003) do not open far-reaching vistas towards an understanding of antennal segmentation. Even in those cases (e.g. Beermann *et al.* 2004) in which a mutation in one of these genes gives rise to phenotypes with defective antennal numbers, the available data help understanding the genetic control of the proximo-distal patterning of the appendage, but are largely mute in respect to the mechanism of segmentation per se.

The main reason why I suggest extrapolating back in ontogenetic time from post-embryonic overt segmentation to the less observable embryonic or pupal segmentation of the antenna, is that it is unlikely that completely different mechanisms are involved in embryonic, pupal, and overt post-embryonic segmentation of the same kind of appendage. What we can reasonably expect are, indeed, differences in timing, giving rise to differences in the total number of articles in the appendage, or in the degree of variation (individual, sex-related, or among the species of a smaller or larger clade) of this very number.

Tradition requires that a distinction is made between "true articles" and "flagellar articles", but this distinction, principally based on the presence vs. absence of musculature to the service of both the proximal and the distal joint between which an article is comprised, is sometimes less clear than textbooks would imply (see Boxshall 2004 for insightful comments on this point). Moreover, as I am focussing on the segmentation process rather than on descriptive or functional morphology, I will follow a different path of analysis, whose different units do not fit always and strictly into the conventional distinction between "true articles" and "flagellar articles".

Let's then start with the hypothesis that an arthropod antenna is a sequence of primary segments more or less uniformly subdivided into secondary segments. I formulated this hypothesis in a paper (Minelli 2000a) where a comparable model of two-stage segmentation was mainly applied to the segments of the body, rather than to those of the antenna, or of other appendages. But I could show that similar rules do probably apply to segmented structures generally, in different groups of segmented animals. This is indeed one of the arguments upon which another principle is grounded, the principle of axis paramorphism according to which the appendages (those of the arthropods, for example) originated from duplicate expression of the same set of genes which are originally involved in controlling the elongation and the patterning of the main body axis in the same animal (Minelli 2000b). The two concepts (axis paramorphism and double segmentation) have been simultaneously applied to an understanding of segmentation of the trunk and the appendages of the Chilopoda, including the antennae (Minelli *et al.* 2000).

As for the antennae, double segmentation is very clearly seen, for instance, in crickets and in many crustaceans. The periodical arrangement of sensory structures along the antennule of the copepods has been the subject of a careful study by Boxshall & Huys (1998), but the best detailed analysis, with abundant information on the stage-by-stage increase along the post-embryonic life, is currently available for the II antenna of the isopod *Asellus aquaticus* (Linnaeus, 1758) (Racovitza 1925; Ronco & Maruzzo unpublished data). In this crustacean, two main antennal regions are distinguished: a proximal peduncle of five articles, all of which are formed during the embryonic life, and a distal flagellum which comprises some 10-12 articles in the new-born animals but eventually grows to a few dozen articles. It is right in the flagellum that a distinction between primary and secondary units clearly emerges. New primary units are formed by the meristematic activity of the first flagellar article and progressively develop, through a series of three further asymmetric divisions, into quartets of secondary articles. Owing to a peculiar arrangement of morphological markers (different sets of sensory setae at the distal end of the first, second, third and fourth element of each tetrad), a primary segment is clearly recognizable all along its development, from the beginning, when it comprises one article only, until the fully-fledged 4-article stage. Each primary segment undergoes maturation independent of the other primary segments. As a consequence, in a developing antenna the flagellum usually comprises the different products of segmentation of a primary article (singletons, doublets, triads and quartets, in this proximo-distal sequence). Finally, a specialized five-article complex occupies the tip of the appendage.

In the case of *Asellus*, double segmentation is a fact. In the case of other arthropods, this is a model that can help us understanding how segmentation is obtained. For example, it seems to be quite meaningful to interpret in terms of double segmentation the 14-article antenna of the geophilomorph centipedes. In this case, no cue is offered by the post-embryonic development, as the whole set of articles is already present in the first juvenile stage. However, the common occurrence of morphological markers on articles II, V, IX and XIII, and a comparison to the sequence of stages of antennal development in other centipedes such as the lithobiomorphs, provide strong support for this interpretation (Minelli *et al.* 2000).

Evidence of double segmentation is also clear in some insects, for example in the crickets, where the flagellar articles are arranged in small chains each of which probably corresponds to one primary article.

The question now is if and how the double-segmentation model applies also to the holometabolous insects and, in particular, to the beetles.

The two basic facts to be accounted for are (1) the overwhelming primacy of antennae with 11 articles and (2) the distribution, both numerical and taxonomic (as a proxy for phylogenetic), of numbers of antennal articles other than 11 (Tab. 1).

What I am about to sketch in the following lines is "version 0" of an hypothesis of double-segmentation mechanism as tentatively applied to the antenna of beetles. It is to be expected that many details, especially those of quantitative nature, may eventually prove to be wrong, but this will not necessarily imply that the basic idea of double segmentation does not apply to these insects. I hope that observation and experiment will soon test the validity of the argument. Therefore, I will present it in the following articulated form.

1. If the antennal articles are (mainly) secondary segments, this will probably not apply to the scape and the pedicel neither, to some extent at least, to article XI. This is suggested by a comparison to the crustacean model *Asellus* (in this respect, I retain the traditional distinction between "true articles" – the peduncle of *Asellus* II antenna, scape+pedicel of the beetle antenna and flagellum). A "strong", basically undivided apical article is also suggested by a comparison to other arthropod antennae, e.g. the antenna of the geophilomorph centipedes (Minelli *et al.* 2000).
2. Within this framework of "fixed" articles I-II and XI, a typical beetle antenna will thus have eight secondary articles, this number progressively decreasing in the species with a total article number lesser than 11.
3. It would be tempting to interpret these eight intermediate articles as two quartets, i.e. as the product of secondary subdivisions of two primary articles into four units each. This is indeed what is observed in *Asellus*, and what has been hypothesized in the geophilomorph centipedes. To be sure, numbers of secondary units per primary unit other (higher) than four are found in the antennae of other arthropods, for example in the previously mentioned flagellar chains of the crickets, but this could be a derived feature accompanying the often extreme elongation of the antennae in the ensiferan clade. If, indeed, articles III-X of an 11-article beetle antenna are two quartets of secondary units, this means that article VI is the last unit of the first quartet, and article VII the first unit of the second.
4. A 5-article antenna would thus probably have (a) scape, (b) pedicel, (c) the undivided precursor of the (here virtual) first quartet (= articles III-VI of the typical antenna), (d) the undivided precursor of the (here virtual) second quartet (= articles VII-X of the typical antenna), and (e) the apex (article XI of the typical antenna). (Less probable in my opinion, but theoretically possible, is the following alternative: (a) scape, (b) pedicel, (c) two secondary articles of the same (virtual) quartet, the other quarted being suppressed, and (e) the apex. Corresponding interpretations involving the suppression of one of the two primary intermediate articles could be offered for a 6- and a 7-article antenna.
5. The interpretation of the segmental composition of antennae with number of articles other than 5 or 11 is more tentative. As we will see soon, it is quite possible that for those with a number of articles larger than 5 but smaller than 11, an identical number of segments, e.g. 9, may be obtained in different ways in different species.
6. Arthropod appendages are "closed" structures, that is, their distal tip does not correspond to the appendage's growth zone but, to the contrary, it is the first feature to be fixed, as demonstrated, for example, by the early expression of the *Distal-less* gene, a characteristic marker of the apical part of the limb, in the embryonic locations where an appendage is about to emerge, and by the quick reorganization of apical structures in autotomized or damaged appendages in early stages of the regeneration process. As a consequence, there are good reasons to believe that the differentiation of the apical article precedes the distinction between the two intermediate primary segments. Therefore, a 4-article antenna is probably comprised of (a) scape, (b) pedicel, (c) the undivided precursor of articles III-X of the typical antenna, and (d) the apex (article XI of the typical antenna). More tentatively, a 3-article antenna is probably comprised of (a) scape, (b) pedicel, and (c) the undivided precursor of articles III-XI of the typical antenna (that is, the whole of the flagellum, apex included). I do not dare to suggest the segmental composition of those very rare antennae that have been described as of 2 articles only. It is possible, indeed, that in this case the flagellum is completely lacking, but it could be otherwise so small as to have been overlooked. Interestingly, Luna de Carvalho (1951; cf. also Nagel 1979) demonstrated that even in those paussine carabids that had been described as provided with a 2-article antenna, this appendage is in fact 3-articulated. On the other hand, a partial fusion of scape and pedicel has been found in the newly described adephagan family Aspidytidae (Ribera *et al.* 2002; Balke *et al.* 2003).
7. If articles III-VI and VII-X, respectively, are the two quartets of secondary units deriving from the segmentation of two primary articles, we have very little reason to expect that the two quartets are formed simultaneously, or that the offspring of one primary segment is formed in just two steps, the

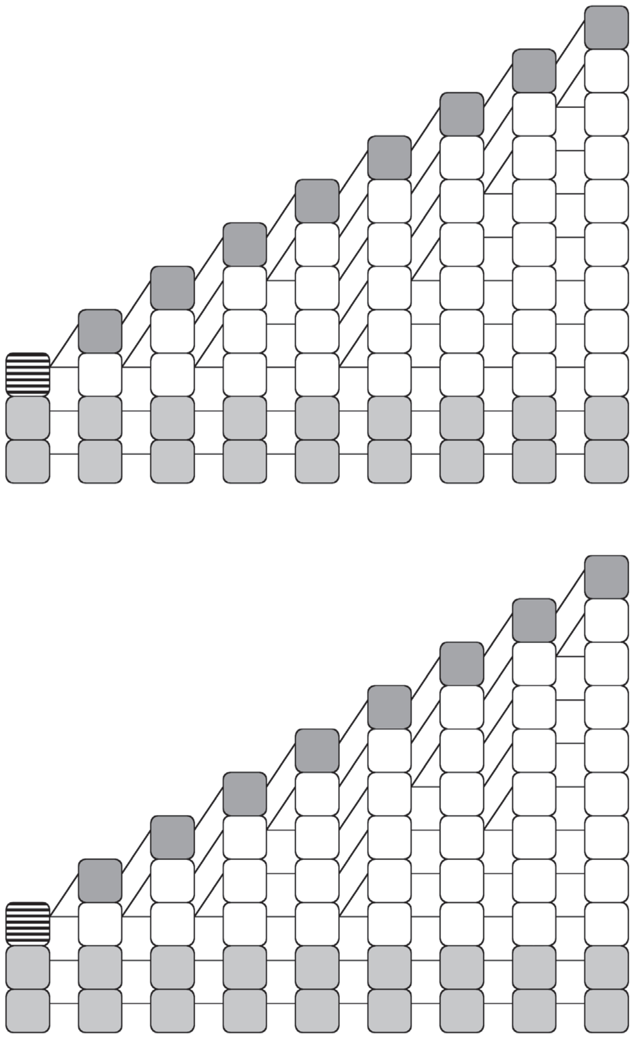

Fig. 1 - Two of the possible sequences by which the number of articles of a beetle antenna may increase, according to the model described in the text. In each diagram, the two lower squares filled with light grey are the two proximal "true articles" (I = scape and II = pedicel), whereas the distal square filled with darker grey represents the usually undivided apical article (article XI in an 11-article antenna). The terminal article of the 3-article antenna (black-filled square) is hypothesized to give rise to the apical article as well as to a more proximal element (article III of the 4-article antenna), which in turn will give rise to article III and IV of the 5-article antenna. Each of these two elements will give rise to four secondary articles. According to the model presented in this paper, the fixed part of the developmental schedule ends here. The temporal sequence by which the two quartet-founders will segment is supposed to be open to variation. Two of the possible alternatives are presented here. According to the splitting process in the upper figure, the developmental identity of the subapical flagellar articles is as follows: 5-article antenna: 1, 2; 6-article antenna: 11, 12, 2; 7-article antenna: 11, 12, 21, 22; 8-article antenna: 111, 112, 12, 21, 22; 9-article antenna: 111, 112, 121, 122, 21, 22; 10-article antenna: 111, 112, 121, 122, 211, 212, 22. According to the splitting process in the lower figure, the corresponding identities are: 5-article antenna: 1, 2; 6-article antenna: 11, 12, 2; 7-article antenna: 11, 12, 21, 22; 8-article antenna: 111, 112, 12, 21, 22; 9-article antenna: 111, 112, 12, 211, 212, 22; 10-article antenna: 111, 112, 121, 122, 211, 212, 22.

Fig. 1 - Due tra le possibili sequenze attraverso le quali il numero di articoli antennali di un coleottero può aumentare, secondo il modello descritto nel testo. In ciascun diagramma, i due quadrati inferiori in grigio chiaro sono i due "veri articoli" prossimali (I = scapo e II = pedicello), mentre il quadrato distale in grigio scuro rappresenta l'articolo apicale (articolo XI di un'antenna con 11 articoli). Si ipotizza che l'articolo terminale di un'antenna con 3 articoli (quadrato nero) dia origine sia all'articolo apicale, sia ad un elemento prossimale rispetto a questo, cioè all'articolo III di un'antenna a 4 articoli. Questo, a sua volta, darà origine agli articoli III e IV di un'antenna a 5 articoli. Ciascuno di questi due elementi produrrà un quartetto di articoli secondari. Secondo il modello presentato in questa nota, la parte fissa di questa sequenza di sviluppo termina qui. La sequenza temporale secondo la quale i due articoli fondatori di quartetti si divideranno è passibile di variazioni. Due fra le alternative possibili sono presentate in questa figura. Secondo il processo di suddivisione mostrato in alto, l'indentità degli articoli flagellari subapicali, in termini di sviluppo, è la seguente: antenna di 5 articoli: 1, 2; antenna di 6 articoli: 11, 12, 2; antenna di 7 articoli: 11, 12, 21, 22; antenna di 8 articoli: 111, 112, 12, 21, 22; antenna di 9 articoli: 111, 112, 121, 122, 21, 22; antenna di 10 articoli: 111, 112, 121, 122, 211, 212, 22. Secondo il processo di suddivisione presentato nella figura inferiore, le corrispondenti identità sono: antenna di 5 articoli: 1, 2; 6-antenna di 6 articoli: 11, 12, 2; antenna di 7 articoli: 11, 12, 21, 22; antenna di 8 articoli: 111, 112, 12, 21, 22; antenna di 9 articoli: 111, 112, 12, 211, 212, 22; antenna di 10 articoli: 111, 112, 121, 122, 211, 212, 22.

two products of its first division dividing, in turn, simultaneously. Indeed, any temporal schedule of segmentation can be expected, as suggested by the diversity of schedules similarly reported by Aguesse (1965) for the splitting of the flagellar articles in the growing antenna of a few species of dragonfly nymphs: the resulting number of articles is here always the same (namely, seven), despite the differences in segmentation schedules. It may be interesting, therefore, to calculate in how many ways the initial number of two (the two intermediate primary segments) may theoretically increase to three, four etc., up to eight. For the sake of simplicity (this is indeed a "version 0" model!), in my calculations I have supposed that (1) there is only one article dividing at each step of segmentation, so that it requires six steps to move from the initial two to the final eight articles, and (2) all articles present at the end of the previous segmentation step have the same probability of undergoing the next split, unless they have completed their maximum number of divisions, in which case they will be out of game (Fig. 1). Under the further assumption (3a) that each of the two products of the first division of each primary article (e.g. article 1) will sooner or later divide in turn [(111, 112)(121,122)], there are 2, 6, 16, 40, 80 and 80 ways to respectively produce 3, 4, 5, 6, 7 and 8 secondary articles out of the two founding ones. The corresponding numbers would rise to 2, 6, 24, 104, 480, 11904 if (3b) a comb-like division of the founder article [e.g. from article 1, (((1111, 1112) 112) 12)] is also admitted, what however seems to me highly unlikely.

8. It is quite probable that the rare antennae with 12 articles evolved by differentiation and eventual splitting of the usual apical article into two units. A transition between antennae with incompletely subdivided eleventh article and antennae with twelve articles is found in some clytrines (Chrysomelidae). In this case, too, the segmental composition of the antenna seems to be perfectly compatible with the basic model advanced in this paper. At present, however, I do not have information sufficient to suggest the possible segmental composition of the antennae with a still higher (and quite higher) number of antennal articles, as found among the Rhipiceridae and the Cerambycidae.

4. THE LARVAL ANTENNA

According to the author of the currently best available account of beetle larvae (Lawrence 1991), the "basic number" of articles in the larval antenna of the Coleoptera should be three, interpreted as scape, pedicel and flagellum respectively. However, antennae with four articles are found in the primitive Archostemata (Cupedidae) and in most of the Adephaga, and this circumstance would suggest that four, rather than three, should be regarded as basal in the Coleoptera. Two arguments were presented by Lawrence (1991) to support the hypothesis that three articles is, nevertheless, the plesiomorphic condition in the antenna of larval beetles. First, the developmental schedule of the cupedid *Distocupes varians* (Lea, 1902), with 3 antennal articles in the first larval stages, but 4, 5 or 6 in the mature larva, due to divisions of the *scape* (something without its equivalent in any *adult* beetle). Second, the position, along the 4-article antenna of the typical adephagan larva, of the hyaline vesicle (the sensorium), which is found here on article III, while in the 3-article antenna of the other beetles it is found near the distal tip of article II (the pedicel). Thus, the 4-article antenna of the Archostemata and the Adephaga is regarded as a novelty

Tab. 2 - Number of antennal articles in the larvae of selected beetle families. Data after Lawrence (1991).
Tab. 2 - Numero di articoli antennali nelle larve di alcune famiglie di Coleotteri. Fonte dei dati: Lawrence (1991).

	1	2	3	4	5	6	7	8	9
ARCHOSTEMATA									
Cupedidae				X	X	X			
MYXOPHAGA									
Torridincolidae		X	X						
Sphaeriidae= Microsporidae			X						
Hydroscaphidae		X							
ADEPHAGA									
Carabidae			X[1]	X					
Amphizoidae				X					
Dytiscidae				X	X	X	X	X	X
POLYPHAGA									
Scydmaenidae		X	X	X[2]					

[1] Anthiinae.
[2] *Mastigus* Latreille, 1806.

(Tab. 2, continued)
(Tab. 2, continua)

	1	2	3	4	5	6	7	8	9
Staphylinidae			X[3]	X[4]					
Pselaphidae		X	X						
Hydrophilidae			X	X					
Scirtidae = Helodidae								up to ca. 100	
Dascillidae			X						
Lucanidae			X	X					
Passalidae		X							
Scarabaeidae s. l.			X	X					
Buprestidae	X	X	X						
Rhipiceridae	X								
Callirhipidae	X								
Throscidae		X	X						
Eucnemidae		X							
Lycidae		X							
Bostrichidae		X	X						
Anobiidae	X	X							
Ptinidae	X								
Lymexylidae			X						
Cucujidae		X[5]	X						
Phalacridae			X						
Corylophidae		X	X						
Discolomidae		X							
Coccinellidae	X	X							
Ciidae		X	X						
Melandryidae		X	X						
Mordellidae	X	X	X						
Rhipiphoridae[6]	X	X	X						
Tenebrionidae	X[7]	X[8]	X						
Meloidae	X								
Cerambycidae	X	X							
Bruchidae		X	X						
Chrysomelidae	X[9]	X[10]	X[11]						
Nemonychidae	X								
Anthribidae	X								
Oxycorynidae	X								
Belidae		X							
Ithyceridae	X								
Aglycyderidae	X	X							
Attelabidae	X								
Brenthidae	X								
Apionidae	X								
Curculionidae	X								

[3] Proteininae, Omaliinae, Piestinae, Osoriinae, Oxytelinae, Oxyporinae, Euaesthetinae, Phloeocharinae, Tachyporinae, Aleocharinae.
[4] Steninae, Paederinae, Xantholininae, Staphylininae.
[5] Silvanini.
[6] Two or three articles in the triungulin, one article in later larval stages.
[7] Some Leiochrini.
[8] Lagriinae.
[9] Alticinae p.p., Cassidinae p.p., Galerucinae p.p.
[10] Alticinae p.p., Cassidinae p.p., Chlamisinae, Clytrinae, Galerucinae p.p.
[11] Chrysomelinae, Criocerinae, Cryptocephalinae, Donaciinae, Eumolpinae, Hispinae, Orsodacninae, Synetinae, Zeugophorinae.

produced by subdivision of the scape. Larval antennae with 4 articles, however, are also found in other families: Leiodidae (*Prionochaeta* Horn, 1880), Scydmaenidae (*Mastigus* Latreille, 1806), Staphylinidae (Staphylininae, Paederinae, Steninae) and Scarabaeidae (Aphodiinae, Scarabaeinae, Ochodaeinae, Glaphyrinae, and all Pleurosticta). More than 4 antennal articles are found in representatives of the Cupedidae, Carabidae, Dytiscidae, Aphodiinae and Helodidae. In the Helodidae, in particular, the (obviously apomorphic) flagellum may have up to about one hundred articles.

On the other hand, antennae reduced to two articles, or to one, are known from many families (Tab. 2). According to Lawrence (1991), this reduction is sometimes the consequence of the loss of a segment, either basal or apical, or of the "fusion" of two segments. The antenna of *Phalacrus* Paykull, 1800 and *Phalacropsis* Swinhoe, 1895 (Phalacridae) has three articles, but the presence of the sensorium at the distal tip of the first segment suggests to Lawrence that the scape has disappeared, while the flagellum is subdivided into two units. I wonder whether this faith in the invariant position of the sensorium as necessarily occurring at the tip of the pedicel is actually warranted. At any rate, it is clear that the limited amount of variation in segment number found in the larval antennae follows rules other than those found in the corresponding variation in the adult antenna.

In many families where less than 11articles are found in the adult, reduced numbers are also found in the larvae, although not necessarily in the same genera. This is true for the Torridincolidae, Hydroscaphidae, Pselaphidae, Bostrichidae, Anobiidae, Ptinidae, Corylophidae, Discolomidae, Coccinellidae, Ciidae, Meloidae, and Chrysomelidae. However, opposite trends are found in the Rhipiceridae and Cerambycidae, where the adults may have more (but never less) than 11 antennal articles, while the larvae have reduced antennae, and the reverse is true of the Lucanidae, with 3 or 4 antennal articles in the larvae, but 7, 8 or 10 in the adult.

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